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A GENERAL TEXTBOOK OF ENTOMOLOGY

PREFACE

SINCE it first appeared in 1925, this textbook was revised several times by the late Dr A. D. Imms, but the changes made were relatively small and a more extensive revision has now become necessary. The immense volume of published work—about 4,000 papers and books on insects now appear annually—has meant that new material has had to be selected very rigorously and though we have not attempted systematically to cover the literature after 1952, some later information has, in fact, been included. Apart from innumerable minor changes, a few points of greater importance have had to be considered.

The last twenty-five years have seen unexampled progress in insect physiology which has already been recorded in detail in well-known works. We have, nevertheless, thought it desirable that the present book should retain its comprehensive character, since it has been so widely used as a work of reference, and we have therefore rewritten most of the physiological sections in Part I.

The chapters dealing with systematic entomology were already considerably out of date by 1934 and in trying to bring them more into line with modern practice we have met several difficulties. The tendency of all authors to multiply the number of families and other divisions of major groups is not easy to present in a general textbook. Quite apart from doubts as to the value of systems which have not been widely adopted, the sheer number of families now recognized by most authorities makes great demands on space. A more serious difficulty is that new and improved classifications are frequently proposed for a limited part of the world fauna. These partial revisions often could not be fully used since a system which seems to work for Europe or North America is often inapplicable to the fauna of Australia or the Orient without undertaking a major piece of original research. No doubt our attempts at compromise will seem conservative to many specialists while other readers will find them too timid or too bold according to their view-point. Our appreciation of Dr Imms' work has, in fact, been greatly enhanced by seeing the difficulties which he had to overcome. We hope we have always aimed at the better but we are well aware that this ideal sometimes conflicts with the best.

There are a number of minor technical points in which we have tried to be more consistent than were the earlier editions. Originally, authorities for specific names were given for about half the species and not for the others. We decided to omit them altogether as they do not in practice seem to be very useful in work of this type. The question of nomenclature is always troublesome in a textbook as Dr Imms noted in the first edition. We have felt it necessary to bring the nomenclature more or less up to date because otherwise the information becomes gradually less and less available to other entomologists. We have put a good deal of synonymy into the index and in the same place we have cross-referenced a large number of the better known

common names. Dr Imms was not very consistent in his treatment of bibliographical references and the great difficulty we had in tracing some of his more cryptic abbreviations suggested to us that they would be almost useless to anyone working away from large libraries. We have therefore collected all the references together at the end of each chapter and quoted them in standard form. A few additions and corrections will be found on p. 832. It is well known that this bibliographical work is particularly prone to error but we have devoted a great deal of time to an attempt to check all the references.

In prefaces to earlier editions Dr Imms made the following acknowledgements: to Messrs George Allen & Unwin for allowing blocks to be made from several illustrations in the English edition of Korschelt & Heider's *Textbook of Embryology*; Messrs A. & C. Black for two illustrations from Curtis' *Farm Insects*; Prof. E. Bugnion for the loan of blocks and of several published figures; Cambridge University Press for blocks from Tillyard's *Biology of Dragonflies* and from Latter's *Natural History of some Common Animals*; Clarendon Press for illustrations from Miall and Hammond's work on *Chironomus*; Mr J. E. Collin for the loan of a number of drawings made for Verrall's *British Flies*; Prof. J. H. Comstock for figures from his *The Wings of Insects* and from his *Introduction to Entomology* and for supplying the electrotypes; *Faune de France* (the director), for lending 2 figures; Prof. J. W. Folsom (also his publishers P. Blakiston & Sons & Co.) for the loan of figures from his *Entomology*; Messrs Longmans Green & Co. for 3 figures from Shafer's *Essentials of Histology*; Messrs Macmillan & Co. for figures from the *Cambridge Natural History* and from Sladen's *Humble Bee*; Mm. Masson et Cie for 3 figures from Henneguy's *Les Insectes* and 1 figure from Brumpt's *Précis de Parasitologie*; McGraw-Hill Book Co. of New York for an illustration from Snodgrass' *The Anatomy and Physiology of the Honey Bee*; Mr John Murray for a block from Darwin's *Descent of Man*; Princeton University Press for 2 figures from Nelson's *Embryology of the Honey Bee*; Sir Arthur Shipley and Dr Hugh Scott for figures from the *Fauna of British India* and to Mr W. Foster of the India Office for providing the electrotypes which are indicated by *F.B.I.* in the legends; L. Upcot Gill Ltd for permission to reproduce what is now fig. 547 from Cheshire's *Bees and Beekeeping*; U.S. Dept. Agriculture (Chief of division of publications) and U.S. National Museum for the loan of a number of figures; Prof. W. M. Wheeler and his publishers, Columbia University Press, for figures from *Ants*.

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For the present revision 51 new figures have been provided and we are grateful to the following for permission to reproduce some of them: to Cornell University Press and Mr J. H. Comstock for our figs. 30A and C, and 285A from *The Wings of Insects*; Cornell University Press and Dr R. E. Snodgrass for our fig. 220 from *A Textbook of Anthropod Aratomy*; to Messrs Methuen and Prof. V. B. Wigglesworth for fig. 3 taken from *Principles of Insect Physiology*; to the McGraw-Hill Book Co. and Dr R. E. Snodgrass for our fig. 5,

55, 82, 83, 86, 103, 332A–D and 393A, taken from *Principles of Insect Morphology* and from *The Anatomy and Physiology of the Honey Bee*; to Dr R. E. Snodgrass and the Smithsonian Institute for fig. 185 from *Male Genitalia of the Hymenoptera*, for fig. 497 from *The Skeletal Anatomy of the Fleas* and for fig. 327 from *The Feeding Apparatus of Biting and Sucking Insects affecting Man and Animals*. Some other acknowledgements, at the request of the authors and copyright owners concerned, are made beneath the legends of the figures in question and we would also like to thank the following, whose published illustrations formed the basis of some of our figures: Dr F. O. Albrecht, Dr A. E. Cameron, Dr L. E. Chadwick, Prof. P. Cazal, Prof. W. T. M. Forbes, Dr H. R. Hagan, Dr N. E. Hickin, Dr A. D. Imms, Mr T. Jones, Mr J. C. Kershaw, Mr F. A. Laing, Miss H. T. Lee, Dr A. Moscona, Mr J. W. H. Rehn, Dr E. S. Ross, Prof. F. Silvestri, Prof. M. Thomsen, Dr R. L. Usinger, Mons. P. Viette, Prof. H. Weber.

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Part I

ANATOMY AND PHYSIOLOGY

INTRODUCTORY REMARKS

Definition of the Insecta (Hexapoda)

THE members of this class are tracheate Arthropods in which the body is divided into head, thorax and abdomen. A single pair of antennae (homologous with the antennules of the Crustacea) is present and the head also bears a pair of mandibles and two pairs of maxillae, the second pair fused medially: the thorax carries three pairs of legs and usually one or two pairs of wings. The abdomen is devoid of ambulatory appendages, and the genital opening is situated near the anal extremity of the body. Postembryonic development is rarely direct and a metamorphosis is usually undergone.

Relationships with Other Arthropods

The Arthropoda (Snodgrass, 1952) constitute the largest phylum of the animal kingdom and, although they include animals differing widely in structure, they agree in certain fundamental characters. The body is segmented and invested with a chitinous exoskeleton. A variable number of the segments carry paired jointed appendages exhibiting functional modifications in different regions of the body. The heart is dorsal and is provided with paired ostia, a pericardium is present and the body-cavity is a haemocoele. The central nervous system consists of a supra-oesophageal centre or brain connected with a ganglionated ventral nerve-cord. The muscles are composed almost entirely of striated fibres and there is a general absence of ciliated epithelium. No animals other than Arthropods exhibit the above combination of characters. Apart from the Insecta, the various classes of the phylum are as follows.

The **Onychophora** (*Peripatus* and its allies) are in some respects annectent between the Annelida and Arthropoda, but the reason for their inclusion in the latter phylum is not evident from superficial examination. They are perhaps to be derived from Polychaete ancestors which had forsaken a marine habitat and become terrestrial. Parapodia are consequently no longer present as swimming organs, but have become modified for locomotion on land without having acquired the jointed Arthropod character. The integument is soft, though it contains chitin, and the excretory organs take the form of metamerically repeated coelomoducts. Arthropodan features are exhibited in the possession of tracheae, salivary glands, and the terminal claws to the appendages. The presence of jaws of an appendicular nature, the paired ostia to the heart, the pericardium, the haemocoelic body-cavity and the reduced coelom are further important characters allying them with that phylum.

The **Trilobita** (Trilobites) are an extinct class of Palaeozoic marine forms with the body moulded longitudinally into three lobes. They possess a single pair of antennae followed by a variable number of pairs of biramous limbs little differentiated among themselves. Four pairs of these appendages belong to the head and the remainder to the trunk region.

The **Crustacea** (Lobsters, Shrimps, Crabs, Barnacles, etc.) are characterized

by the possession of two pairs of antennae and at least five pairs of legs. In the higher forms the body-segments are definite in number and arranged into two regions—the cephalothorax and abdomen. Respiration almost always takes place by means of gills, and the excretory organs are, at least in part, modified coelomoducts usually represented by green glands or shell glands. The genital apertures are situated anteriorly, i.e. on the 9th postoral segment in some cases, up to the 14th in others.

The **Arachnida** (Scorpions, King Crabs, Spiders, Mites, Ticks, etc.) are distinguished by the body usually being divided into cephalothorax and abdomen; the legs consist of four pairs and there are no antennae. The primitive forms respire by means of branchiae which, in the higher forms, are insunk to form lung-books, or atrophied and replaced by tracheae. Spiracles when present are generally abdominal and consist at most of four pairs. The gonads open near the base of the abdomen and the excretory organs are usually Malpighian tubes. The presence of chelicerae, in place of sensory antennae, and the general characters of the remaining appendages mark off the Arachnida very definitely from all other Arthropoda.

The next four classes (often known collectively as the Myriapoda) are characterized by the presence of a single pair of antennae and the absence of any differentiation of the trunk into thorax and abdomen. Each segment usually bears appendages.

The **Diplopoda** (Millipedes) have the greater number of the body-segments so grouped that each apparent somite carries two pairs of legs and two pairs of spiracles. The gonads open behind the 2nd pair of legs.

The **Pauropoda** are characterized by the legs being arranged in single pairs although the terga are mostly fused in couples. The antennae are biramous and there are only twelve postcephalic segments, nine of which bear legs. The gonads open on the 3rd segment.

The **Symphyla** have long antennae and most of the body segments bear a single pair of legs. The gonads open on the 4th postcephalic segment and there is a single pair of spiracles which are situated on the head.

The **Chilopoda** (Centipedes) are usually provided with a single pair of appendages and a pair of spiracles to each of the postcephalic segments. The first pair of legs is modified to form poison claws and the gonads open on the penultimate segment of the abdomen.

The **Tardigrada** (Bear Animalcules) are very minute animals with four pairs of unjointed legs but devoid of antennae, mouth-appendages or respiratory organs. The gonads open into the intestine.

The **Pentastomida** are worm-like and devoid of appendages except two pairs of hooks near the mouth. Their arthropodan affinities are mainly suggested by the larvae which possess two pairs of clawed, leg-like processes.

The relationships of the Insecta with the other Arthropod groups have been the subject of much discussion and widely differing views have been proposed (see, for example, Calman (1936), Ewing (1942), Handlirsch (1937–39), Imms (1936), Manton (1949), Snodgrass (1938; 1951), Tiegs (1940; 1945; 1947), Tillyard (1930; 1935) and Weber (1939–43)). The insects share with the Crustacea and Myriapoda the possession of mandibles and antennae and agree with the Myriapods in having only a single pair of antennae, corresponding to the antennules of the Crustacea. The study of generalized insect embryos reveals the fact that insects pass through a developmental stage in which the head bears five pairs of appendages and the body is composed of fourteen segments, each bearing a pair of limbs, and a terminal non-segmental telson. The appendages of the first three body segments (legs) and of the 14th segment (cerci) continue to develop while most or all of the others remain vestigial. These embryological data confirm the anatomical view that the ancestors of insects were Myriapodan.

The most primitive insects are to be found in the Thysanura and Diplura and when these are compared with the Myriapod classes it is seen that the Symphyla exhibit most of the essential structural features required of an ancestral form. The presence of a Y-shaped epicranial suture and two pairs

of maxillae: of styli and eversible sacs on the abdominal segments: of cerci and Malpighian tubules are all characters shared by the Symphyla and *Campodea*. The main objection raised in the past to theories of a Symphylan-like ancestry for the insects was the fact that in the Insecta the gonopore opens near the posterior end of the abdomen, whereas in the Symphyla it occupies an anterior position. Tiegs (1945), however, has produced strong evidence that the progoneate condition of the Symphyla is a secondary specialization and the insectan stem presumably arose before this had taken place.

The references cited above provide a sufficient discussion of the out-moded theories that the Insecta were derived from the Trilobita (Handlirsch) or Crustacea (Hansen, etc.) or from a Collembolan-like form (Tillyard); Fig. 1 expresses the views outlined here and is modified slightly from a diagram of Imms (1936).

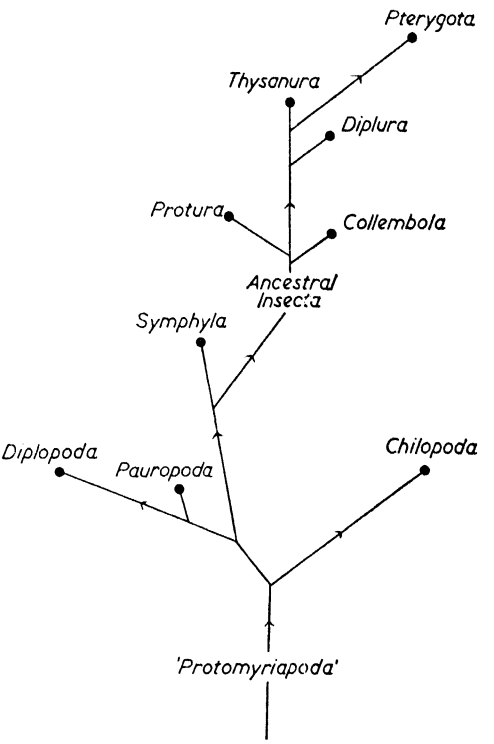


FIG. 1.—Probable phylogenetic relationships of the Myriapoda and Insecta (*after* Imms, 1936)

General Organization of an Insect

An examination of the structure and development of the most primitive representatives of the class renders it possible to construct the archetype or ancestral form of winged insect. This hypothetical organism was termed by Paul Mayer the *Protentomon* (Fig. 2) and it is convenient to retain that name although the results of more recent investigation have considerably modified our views with regard to its essential characters. The latter exhibit various secondary modifications in the different orders of insects, but the fundamental or primary features of the *Protentomon* are as follows.

The head is formed by the fusion of six embryonic segments of which the 2nd, and 4th to 6th carry appendages in the adult. These appendages are the antennae, mandibles, maxillae and labium (2nd maxillae). The head also carries a pair of compound eyes and three ocelli.

The thorax consists of three segments each of which bears a pair of legs, and the 2nd and 3rd segments carry a pair of dorsolateral membranous outgrowths or wings. The two pairs of wings are similar, and each is supported by a system of longitudinal cuticular ribs or veins which are formed around pre-existing tracheae. There are no true cross-veins but only an irregular network (archedictyon) formed by thickenings of the wing-membrane.

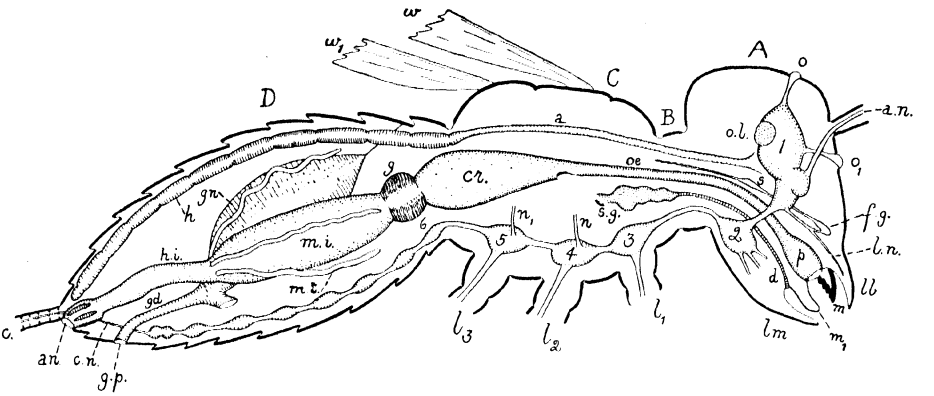


FIG. 2.—The general organization of a primitive winged insect

A, head; *B*, cervix; *C*, thorax; *D*, abdomen; *a*, aorta; *an*, anus; *a.n*, antennary nerve; *c*, cercus; *c.n*, nerve to cercus; *cr*, crop; *d*, salivary duct; *f.g.*, frontal ganglion; *g*, gizzard; *g.d*, gonoduct; *gn*, gonad; *g.p*, gonopore; *h*, heart; *h.i*, hind intestine; l_1–l_3, legs; *lb*, labrum; *lm*, labium; *l.n*, labral nerve; *m*, mandible; m_1, maxilla; *m.i*, stomach; *m.t*, Malphigian tube; *n*, n_1, alary nerves; o_1, median ocellus; *o*, lateral ocellus; *oe*, oesophagus; *o.l*, cut end of optic lobe; *p*, pharynx; *s*, oesophageal ganglion; *s.g*, salivary gland; *w*, w_1, wings; 1, brain; 2, suboesophageal ganglion; 3–5, thoracic ganglia; 6, 1st abdominal ganglion.

The abdomen consists of eleven segments together with a terminal region or telson: the 11th segment carries a pair of segmented cerci.

The digestive system is divisible into the fore intestine or stomodaeum, a simple sac-like mid gut or mesenteron and the hind intestine or proctodaeum. A pair of salivary glands lie along the sides of the fore intestine, and their ducts pass forwards to unite and form the main salivary duct which opens on the hypopharynx. Six Malpighian tubes are present and arise from the hind intestine near its junction with the mesenteron.

The central nervous system consists of two principal cephalic centres united with a ventral ganglionated nerve-cord. The supra-oesophageal centre or brain is formed by the fusion of the three preoral cephalic ganglia. It is joined by means of a pair of para-oesophageal connectives with the sub-oesophageal centre. The latter is formed by the fusion of the three postoral cephalic ganglia. The ventral nerve-cord consists of three thoracic and nine abdominal ganglia united by means of paired connectives. There is consequently one ganglion to each of the first twelve postcephalic segments.

The dorsal vessel consists of an abdominal portion or heart and a thoracic portion or aorta. The heart is metamerically divided into chambers and each of the latter is provided with paired lateral ostia. Beneath the heart is a transverse septum or pericardial diaphragm. The aorta is a narrow tubular extension arising from the first chamber of the heart and extending forwards through the thorax into the head, where it terminates just behind the brain.

The respiratory system consists of segmentally repeated groups of tracheae which communicate with the exterior by means of ten pairs of spiracles. These are situated on each of the two hinder thoracic and the first eight abdominal segments respectively.

The genital organs of the two sexes exhibit a very similar morphology. In the male each testis consists of a small number of lobes whose cavities communicate with the vas deferens. The vasa deferentia unite posteriorly and become continuous with a common ejaculatory duct which opens on the aedeagus. Vesiculae seminales are present as simple dilatations of the vasa deferentia and paired accessory glands open into the proximal portion of the latter. In the female each ovary consists of panoistic ovarioles similar in

number to the lobes of the testis. The oviducts combine posteriorly to form a common oviduct which is continued posteriorly as the vagina. A median spermatheca opens on the dorsal wall of the latter, and paired collaterial or accessory glands are also present.

Metamorphosis is of the gradual or hemimetabolous type.

Number and Size of Insects

Insects comprise about 70 per cent. of the known species of all kinds of animals. Approximately 700,000 species of insects have been described (Metcalfe, 1940), but it is doubtful whether this number represents even one-fifth of those existing today. The Coleoptera, with over 220,000 species, form the largest order and among them at least 35,000 species are included in the single family Curculionidae, while the Chrysomelidae are not much inferior in point of numbers.

Among living insects, the greatest size is found in individuals of the following species. In the Coleoptera, *Megasoma elephas* attains a length up to 120 mm. and *Macrodontia cervicornis* (including the mandibles) ranges up to 150 mm. Among Phasmida, *Pharnacia serratipes* may exceed 260 mm. long and the Hemipteron *Belostoma grande* attains a length of 115 mm. For the Lepidoptera their size may, perhaps, be best gauged by the wing-expanse. The latter reaches its maximum in *Erebus agrippina*, whose outspread wings measure up to 280 mm. from tip to tip and in large examples of *Attacus atlas* they measure 240 mm. With regard to the smallest insects certain Coleoptera (fam. Ptiliidae) do not exceed a length of 0·25 mm. while egg-parasites belonging to the family Mymaridae are, in some cases, even more minute. As Folsom has observed, some insects are smaller than the largest Protozoa and others are larger than the smallest Vertebrata.

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THE BODY-WALL OR INTEGUMENT

A REVIEW of the composition, structure and physiology of the integument of insects and other Arthropods is given by A. G. Richards (1951).

(*a*) Structure, Composition and Functions

The integument consists of the following layers: (i) the cuticle, (ii) the hypodermis and (iii) the basement membrane (Fig. 3).

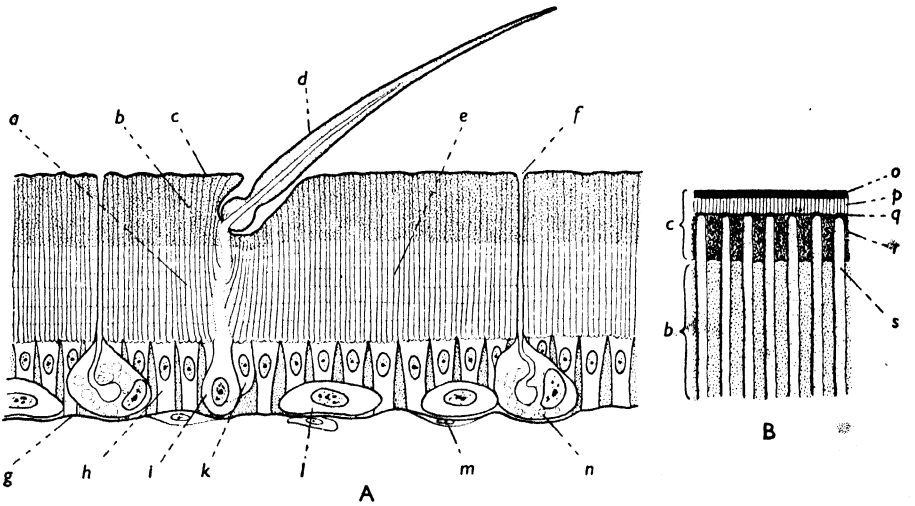


FIG. 3.—A. Section of typical insect cuticle. B. Details of epicuticle, schematic (*after* Wigglesworth)

a, laminated endocuticle; *b*, exocuticle; *c*, epicuticle; *d*, bristle; *e*, pore-canals; *f*, duct of dermal gland; *g*, basement membrane; *h*, epidermal cell; *i*, trichogen cell; *k*, tormogen cell; *l*, oenocyte; *m*, haemocyte adherent to basement membrane; *n*, dermal gland; *o*, cement layer of epicuticle; *p*, wax layer; *q*, polyphenol layer; *r*, cuticulin layer; *s*, pore-canal. *From* Wigglesworth, *Principles of Insect Physiology*, 4th Edn., p. 20, Fig. 16.

(1) The **cuticle** is a complex, non-cellular layer secreted largely by the hypodermis and though commonly considered as non-living material, is actually the seat of complex biochemical changes, some at least under enzymatic control. It forms the outermost investment of the body and its appendages but is invaginated locally to form endoskeletal structures (p. 59) and also provides the lining of the tracheal system, some glands and parts of the alimentary canal and reproductive tract. When newly formed it is flexible and elastic and in many larvae it remains so over much of the body. In most insects, however, the greater part of the cuticle undergoes a process of sclerotization whereby it becomes hardened and darkened to form more or less tough, rigid sclerites separated from each other by membranous zones

of unchanged soft cuticle. Such an arrangement combines rigidity with flexibility and in addition to its protective function the cuticle determines the form of the insect, its relative impermeability to water reduces desiccation and it provides a firm basis for the attachment of muscles. Two main layers may be discerned in the cuticle, an outer epicuticle and an inner procuticle, both generally compound structures. The epicuticle (Fig. 3) is 4 μ or less in thickness and in *Rhodnius* and *Tenebrio* (Wigglesworth, 1947; 1948) comprises four superimposed layers. Starting with the outermost, these are the cement layer, probably lipoprotein in character, a layer of partially orientated wax molecules which confers impermeability to water (Beament, 1945; Wigglesworth, 1945), a polyphenol layer and a cuticulin layer. The last mentioned is made up of a lipoprotein which is possibly elaborated by the oenocytes and subsequently transported through the hypodermal cells. In some cases the pore-canals (see below) pass into the inner part of the epicuticle. Other somewhat different types of epicuticle are described by Dennell (1946), Way (1950) and Kramer and Wigglesworth (1950).

The procuticle—which may be absent from the tracheoles—is secreted by the hypodermal cells from unknown precursors. It exhibits a multilaminar structure with layers 0·2–10 μ thick running parallel to its surface and, except in some thin cuticles, is pierced by pore-canals. The latter run through all or only the outer layers of procuticle perpendicular to its surface and are initially occupied by cytoplasmic filaments from the hypodermis though they may later become filled with cuticular material. They are very narrow (less than 1 μ in diameter) and helically coiled with a density of several thousand per square millimetre and may become arborescent near their outer ends. Their functions are uncertain but the procuticle may be secreted around them and they may also transport materials to the epicuticle or outer procuticular layers. In the case of soft, transparent membranes, the procuticle undergoes no apparent change after formation but in other cases the outer part becomes changed into a hard, dark, sclerotized exocuticle, while the inner part (endocuticle) remains unchanged. The process of sclerotization has been studied in detail in the development of the Dipteran puparium (Fraenkel & Rudall, 1940; 1947; Dennell, 1946; 1947). Here an oxidase, possibly produced by the oenocytoids of the blood, passes from the hypodermis through the procuticle to the epicuticle and is followed by tyrosine or one of its oxidation products. At the epicuticle the latter is converted into an *o*-quinone which tans first the epicuticle and then, by diffusion inwards, the outer layers of procuticle. The tanning process, which imparts to the exocuticle its tough, inelastic properties, consists in the formation of quinone cross-linkages between adjacent molecules of cuticular protein. The dark colour of the exocuticle is largely due to the tanned protein, but melanins (see below) may also be formed.

The two major components of insect cuticle are chitin, which accounts for about 25–60 per cent. of the dry weight of different cuticles, and protein, the two being associated in a manner still uncertain. The older view that there is a chitinous matrix impregnated with protein seems to be giving way to the opinion that the two are chemically combined to form a glycoprotein. Chitin, on hydrolysis, yields acetic acid and glucosamine and is a nitrogenous polysaccharide, being regarded as a high molecular-weight polymer of anhydro-N-acetyl glucosamine residues joined by β-glycosidic linkages (Fig. 4). The chains so formed consist of several hundred residues and are unbranched. They are associated in a highly ordered fashion, parallel chains being grouped into fibrous micelles which are visible under the electron microscope and may be randomly arranged or, as in apodemes for example, are aggregated in a

Chitin is insoluble in water, alkalis, dilute acids and organic solvents but dissolves with decomposition in concentrated mineral acids and sodium hypochlorite. It has a specific gravity of about 1·4, a refractive index of about 1·55 and is best detected by the van Wisselingh test—treatment with concentrated potassium hydroxide at 160° C. for 20 minutes converts it to chitosan which gives a rose-violet colour with 0·2 per cent. iodine in 1 per cent. sulphuric acid (Campbell, 1929). The protein

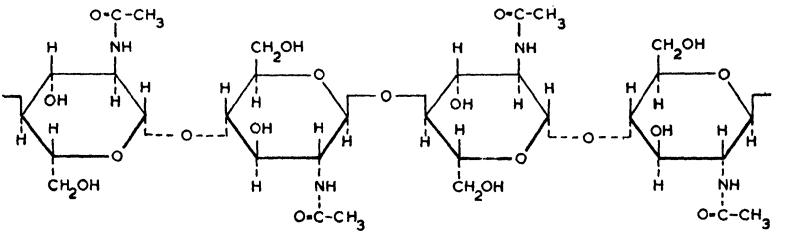


FIG. 4.—Structural formula of chitin

component of cuticle consists of a water-soluble fraction known as arthropodin and another fraction which may be extracted with dilute alkali or acid. The latter has not been adequately studied but arthropodin (Trim, 41; Fraenkel & Rudall, 1940; 1947) is chemically very distinct though not unlike the silk-protein sericin. It is unusual in that its molecules normally exist in the extended (β) configuration and in this form its molecular spacings agree closely with those of chitin—a circumstance which could greatly facilitate the formation of a mixed polymer.

Other components of the cuticle account for only a very small part of its weight though they are of great functional importance. Polyphenols are always present and play an important role in tanning the arthropodin in the formation of the exocuticle (Pryor, 1940; 1940a) since they are the precursors of the quinones which link the arthropodin molecules to form sclerotin. The cuticular lipoids responsible for water-proofing the epicuticle are waxes, i.e. paraffin hydrocarbons or esters of fatty acids with alcohols other than glycerol. Chemically, the waxes found in exuviae of *Bombyx mori* comprise a mixture of odd-numbered C_{27}–C_{37} paraffins with esters of even-numbered C_{26}–C_{30} fatty acids. The epicuticular lipoids studied by Beament (1945) have melting points varying from 36° C. (*Pteronidea* larvae) to over 100° C. (*Pieris* pupae). Below these temperatures they form a layer several molecules thick, the inner molecules being more highly oriented and apparently bound to the underlying protein. Although, on *a priori* grounds, one would expect the cuticle to contain at least four enzyme systems dealing with the synthesis or degradation of chitin, arthropodin and waxes and with the phenol/quinone hardening system, only tyrosinase—concerned with the last process—has been studied. It occurs in the blood and epicuticle and acts on monohydric phenols to convert them into quinones but it is possible that at least two enzymes are really concerned in the transformation (Nelson & Dawson, 1944). Inorganic cuticular constituents are rare but calcareous nodules may develop on the outside of Stratiomyid and Psychodid larvae while *Rhagoletis cerasi* larvae show intra-cuticular calcification (Wiesmann, 1938). Pigments occurring in the cuticle are discussed below.

(2) The **hypodermis** forms a continuous single layer of cells, the boundaries between which are often difficult to detect. Scattered amongst normal hypodermal cells are specialized gland cells and those concerned in the formation of cuticular sensilla (see p. 85). Muscle attachments penetrate the hypodermis, the myofibrillae usually being continued in the form of tonofibrillae through the hypodermis and into the procuticle, while the oenocytes (p. 165) which originate from hypodermal cells sometimes remain closely associated with this layer. Not only does the hypodermis secrete the greater part of the cuticle but it also produces the moulting fluid (Passonneau & Williams, 1953), which dissolves the old endocuticle before the immature insect moults (p. 228), it absorbs the digestion products of the old cuticle,

repairs wounds and differentiates in such a way as to determine the surface patterns of the insect.

(3) The **basement membrane** is, in many insects, a continuous sheet which, where muscles are attached, becomes continuous with the sarcolemma of the muscles. Chordotonal organs (*q.v.*) and tracheoles run to or through it and though its origin is uncertain it may be formed from blood cells.

(*b*) Cuticular Appendages

These structures include all outgrowths of the cuticle that are connected with it by means of a membranous joint. They may be classified into setae and spurs.

Setae or **Macrotrichia** (Fig. 5) are commonly known as hairs and each arises from a cup-like pit or *alveolus*. At its base the seta is attached by means of a ring of articular membrane. Setae are hollow structures developed as extensions of the exocuticle and each is produced by a single, usually enlarged, hypodermal cell or *trichogen*. The articular membrane is usually produced by a second hypodermal cell or *tormogen*. In recent years *chaetotaxy*, or the study of the arrangement of the more important setae, has assumed a good deal of significance from the taxonomic point of view, particularly in the Cyclorrhapha and larval Lepidoptera. The following are the principal types of setae commonly met with (Ferris, 1934): (1) *Clothing hairs.*—These invest the general surface of the body or its appendages and frequently exhibit various degrees of specialization. When furnished with thread-like branches as in the Apoidea they are termed *plumose hairs*. Setae which are particularly stout and rigid are known as *bristles*, which are well exhibited for example in the Tachinidae. (2) *Scales.*—These structures are highly modified clothing hairs and are characteristic of all Lepidoptera and many Collembola: they are also present in some members of several other orders. Transitional forms between ordinary clothing hairs and scales are frequent. (3) *Glandular setae.*—Grouped under this heading are those setae which function as the outlet for the secretion of hypodermal glands (vide p. 168). If they are especially stout and rigid they are then termed *glandular bristles* as in the urticating hairs of certain lepidopterous larvae. (4) *Sensory Setae.*—Very frequently the setae of certain parts of the body, or more particularly the appendages, are modified in special ways and become sensory in function. Sensory setae (vide p. 85) are in all cases connected with the nervous system.

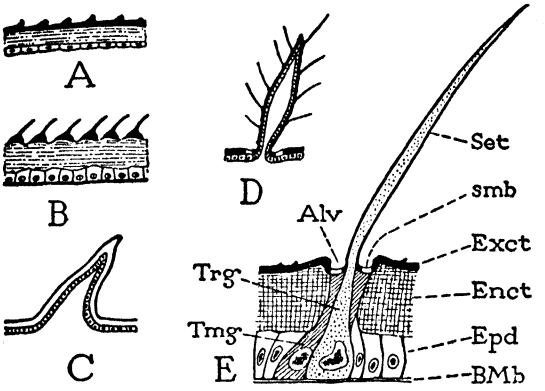


FIG. 5.—External processes of the body-wall, diagrammatic. A, B, noncellular cuticular processes. C, D, multicellular processes. E, a typical unicellular process or seta

Alv, setal socket or alveolus; *Set*, seta; *smb*, setal membrane; *Tmg*, tormogen or socket-forming cell; *Trg*, trichogen or seta-forming cell. Snodgrass, *Principles of Insect Morphology*, McGraw-Hill, 1935, fig. 28.

Spurs occur on the legs of many insects and differ from setae in being of multicellular origin (Comstock).

(*c*) Cuticular Processes

The external surface of the cuticle, in addition to being sculptured in various ways, bears a great variety of outgrowths which are integral parts of its substance. They are rigidly connected with the cuticle, having no membranous articulation and, in the absence of the latter feature, they are readily separable from cuticular appendages. The principal types of cuticular processes are as follows.

Microtrichia (fixed hairs or aculei).—These are minute hair-like structures found, for example, on the wings of the Mecoptera and certain Diptera. They resemble very small covering hairs, but the absence of the basal articulation is their distinguishing feature (Figs. 5 and 28).

Spines.—This expression has been used by various writers with considerable latitude and, in the present work, it is confined to outgrowths of the cuticle which are more or less thorn-like in form. According to Comstock spines differ from spine-like setae in being produced by undifferentiated hypodermal cells and are usually, if not always, of multicellular origin.

In addition to the above there is also a great variety of other cuticular processes which either take the form of more or less conical *nodules* and *tubercles* of different shapes, or of larger projections known as *horns* which are a characteristic feature in the males of certain Coleoptera.

(*d*) Coloration

The colours of adult and immature insects may be grouped into three classes: (1) pigmentary or chemical colours, (2) structural or physical colours, and (3) combination or chemico-physical colours.

1. Pigmentary Colours.—These owe their presence to substances of definite chemical composition which have the property of absorbing some light waves and of reflecting others. Such substances are for the most part by-products of metabolism and in some cases may be of an excretory nature. They may be classified into cuticular, hypodermal and subhypodermal colours according to their location. Frequently a colour pattern consists of a ground colour whose source lies in the hypodermis or underlying tissues, and is overlaid by blotches of a cuticular pigment.

Cuticular colours are mostly contained in the exocuticle: they consist of browns, blacks and yellows, which are permanent.

Hypodermal colours are lodged in the form of granules or drops of fat in the cells of the hypodermis. They may be red, orange, yellow or green and are very evanescent after death.

Subhypodermal colours are contained in the fat-body and blood.

Biochemical aspects of insect pigmentation have been reviewed by, among others, Lederer (1940), Timon-David (1947), Wigglesworth (1949) and Goodwin (1952). The substances concerned may be classified as follows:

(*a*) *Melanins.* These are amorphous, highly stable, dark brown or black cuticular pigments which are generally non-granular and are insoluble in the usual solvents though they are rapidly decolorized by oxidizing agents. Their chemical nature has not been satisfactorily elucidated and it is, in fact, difficult to distinguish between cuticular darkening due to sclerotization and that caused by the presence of true melanins. The mode of formation of melanins is uncertain (Lerner & Fitzpatrick, 1950) but they probably arise through polymerization of indole compounds which are derived initially from the amino-acid tyrosine by ring-closure and oxidation under the influence of the enzyme tyrosinase. Thus, *Aedes* larvae reared on a diet deficient

in tyrosine or the related phenylalanine together with the resulting pupae are unpigmented (Golberg & De Meillon, 1948). Where melanic pigmentation is discontinuous (e.g. dark spots, etc.) this is apparently the result of a localized distribution of the substrate tyrosine, the tyrosinase occurring also in areas which remain unpigmented.

(*b*) *Carotenoids.* These are polyene pigments usually containing 40 carbon atoms in the molecule; they are readily soluble in fat-solvents and are characteristically synthesized by plants (Lederer, 1938; Goodwin, 1952a). When ingested by animals they accumulate in the blood and tissues unchanged or after minor oxidative alterations and in some cases they form the prosthetic group of a chromoprotein. Carotene, derived from the tissues of the potato plant, occurs in the blood of the Colorado Potato-beetle, *Leptinotarsa decemlineata* and is responsible for the red and yellow coloration of the Pentatomid *Perillus bioculatus* which preys on larvae of the beetle (Palmer & Knight, 1924). Again, in *Coccinella*, the red colour is due to the presence of the plant carotenoids lycopene and α- and β-carotene (Lederer, 1938). Astaxanthin (3 : 3-dihydroxy-4 : 4-diketo-β-carotene) and β-carotene both occur as chromoproteins in the integument of locusts and the green chromoprotein pigment of many insects (known as insectoverdin) is a complex, the yellow-orange component of which may have as its prosthetic group β-carotene (*Dixippus*), lutein (*Sphinx*, *Tettigonia*) or astaxanthin.

(*c*) *Pterins.* These are a group of heterocyclic compounds constitutionally related to the purines and though particularly characteristic of the wings of Pieridae are also found in many other insects (Becker, 1937). They are deposited in the hypodermal cells or cavities of the scales and setae and the natural pigments appear to be mixtures of several pterins. Leucopterin (white), xanthopterin (yellow), chrysopterin (orange) and erythropterin (red) may be mentioned as examples.

(*d*) *Insectorubin* (*ommochromes*). Goodwin and Srisukh (1950) bring together under this name the reddish-orange redox pigments which are extractable from a number of insects with acidified ethanol. Formerly considered as a group of 'ommochromes', insectorubin has been extracted from the eyes of *Drosophila*, *Ephestia*, etc., and free or in combination with a protein it plays some part in the coloration of locusts. It is probably a pyrrol derivative.

(*e*) *Anthoxanthins* (*flavones*) and *Anthocyanins.* These substances, to which the colours of many flowers are due, are only occasionally found in insects, the former occurring in the wings of some Pierid and Satyrid butterflies.

(*f*) *Miscellaneous pigments.* Many other substances play a minor role as insect pigments, occurring either in small amounts or only in a few species. Among such are haemoglobin, derivatives of chlorophyll and anthraquinone, riboflavin (which accumulates as the greenish-yellow 'entomo-urochrome' of the Malpighian tubules) and purines. The bile pigment mesobiliverdin is perhaps more important since it is the prosthetic group of the blue component of the insectoverdins (complex green pigments) mentioned above in connexion with the carotenoids.

2. Structural Colours.—Structural colours differ from those due to pigments in that they are changed or destroyed by physical changes in the cuticle such as result from shrinkage, swelling, distortion or permeation with liquids of the same refractive index as the cuticle. They may also be duplicated by physical models, are not destroyed by bleaching and all the component wavelengths of the incident light are to be found in either the reflected, scattered or transmitted fractions. Of the many papers on this topic, see especially Mason (1926–29) and Anderson & Richards (1942). Four types of structural coloration may be distinguished: (i) *Structural white* is caused by the scattering, reflection and refraction of light by microscopic particles large in comparison with the wavelength of light and which, in themselves, are usually transparent. Probably most insect whites have a structural basis. (ii) *Tyndall blue*, though uncommon, occurs in some Odonata and is due to the scattering of the shorter wavelengths by particles with dimensions of about the same size as the wavelengths of light. (iii) *Interference colours* are produced by optical interference between reflections from a series of superimposed laminae or ribs. This is one of the commonest types of physical

coloration and the iridescent appearance is well seen, for example, in the wing-scales of *Morpho* butterflies, in the Diamond beetles *Entimus* and *Cyphus* and in the Chrysididae. (iv) *Diffraction colours*, resulting from the presence of closely spaced striae, 1–2 μ apart, occur in the beetle *Serica* but are not otherwise important.

3. Combination Colours.—These are produced by a structural modification in conjunction with a layer of pigment and are much commoner than purely structural colours. In the butterfly *Teracolus phlegyas* a red pigment in the scale wall (but not in the striae) combines with a structural violet to produce magenta: in *Ornithoptera poseidon* the emerald green is due to a structural blue combined with a yellow pigment in the walls and striae of the scales. In a number of cases (e.g. Lycaenids) there is no indication of the cause of colour. The golden iridescence of *Cassida* and its allies is produced by a film of moisture beneath the surface cuticle. These insects rapidly lose their colour when dried, but it returns after soaking in water provided the drying has not been too prolonged.

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SEGMENTATION AND THE DIVISIONS OF THE BODY

THE cuticle of an insect forms a more or less hardened exoskeleton and, although perfectly continuous over the whole body, it remains flexible along certain definite and usually transverse lines. In the latter positions the cuticle becomes infolded and is membranous in character. The body of an insect consequently presents a jointed structure which is termed *segmentation*, and is divided into a series of successive rings variously known as *segments*, *somites* or *metameres*. In many cases there is reason to believe (see p. 32) that the definitive segment incorporates part of what was primitively an intersegmental sclerite. The flexible infolded portion of the cuticle between adjacent definitive segments is the so-called *intersegmental membrane* whose function is to allow of the freedom of movement of the body.

It must be borne in mind that segmentation is not only manifested in the external differentiation of the body but it involves many of the internal organs also. In the Annelida and the Onychophora the internal structure of an individual segment is very similar to that of the segment preceding or following it. This is due to the fact that there is a repetition of the organs or parts through most of the segments of the body. In such highly evolved animals as insects the primitive segmentation, in so far as it affects the internal anatomy, has undergone profound modifications; the segmental repetition of parts is nevertheless to a large extent retained in the central nervous system, the heart, tracheal system and in the body musculature.

The cuticle also exhibits localized areas of hardening which are sometimes delimited by sutures. The latter name has been given to several somewhat different structures. It may denote (i) the external groove or sulcus corresponding to an internal ridge-like inflection of the cuticle which helps to provide mechanical rigidity, or (ii) a line of thinner, weaker cuticle along which rupture of the integument can occur at ecdysis, or (iii) a narrow, flexible, membranous zone of unsclerotized cuticle, or (iv) a linear impression without any obvious mechanical significance. In certain regions the sclerites do not come into apposition by sutures and are thus, as it were, islands of cuticle surrounded by membrane. Complete fusion of adjacent sclerites is common, particularly among the higher orders of insects, all traces of sutures being lost.

(*a*) The Divisions of a Body-Segment

In the majority of adult insects, and in many of their larvae, the body-wall of a typical segment is divisible into four definite sclerotized regions: a dorsal region or *tergum*, a ventral region or *sternum*, and a lateral region or *pleuron* on each side of the body. Each of these regions may be differentiated into separate sclerites. In this case the sclerites composing the tergum are

known as *tergites*, those of the sternum as *sternites*, and those constituting each pleuron as *pleurites*. Between adjacent segments there may be present small detached plates or *intersegmentalia* and such sclerites belong partly to the segment in front and partly to the segment behind them. According to their position they are termed *intertergites*, *interpleurites* and *intersternites*.

(*b*) The Appendages

In the embryo each body-segment may bear a pair of outgrowths or appendages which may, or may not, be retained in postembryonic life. Among adult insects, an appendage is normally attached to its segment between the pleuron of its side and the sternum. Typical appendages are segmented tubes invested with a dense cuticle. Between each pair of segments, the cuticle remains membranous and becomes infolded to form the articular membrane. On account of its jointed structure, the whole or part of an appendage is movable by means of its muscles. An insect appendage consists typically of a limb base and a shaft which represents the endopodite of Crustacea. There is no conclusive evidence of a biramous condition among the appendages in any insects.

(*c*) Processes of the Body-Wall

In addition to true segmental appendages numerous other outgrowths of the body-wall are found in various insects. Unlike true appendages, processes of the body-wall are by no means invariably represented by embryonic counterparts; they may or may not be segmentally arranged, they may be originally paired or unpaired, and more than a single pair is sometimes borne on a segment. They differ from cuticular processes in containing a definite extension of the body cavity and in some cases they are freely movable. It is sometimes difficult to distinguish between such processes and true appendages but the principal types of organs which have been included under this category are: (1) *Pseudopods*, which are characteristic of many dipterous larvae. (2) *Scoli*, or thorny processes, characteristic of Nymphalid and Saturniid larvae: the anal horn of Sphingid larvae is also of a very similar nature. (3) *Branchiae* or gills which are found in most larvae of aquatic insects (vide p. 146). (4) *Wings* (vide p. 38), which are always confined to the meso- and metathorax and attain their full development in adult insects.

(*d*) The Regions of the Body

The body-segments of an insect are grouped together to form three usually well defined regions—the *head*, the *thorax* and the *abdomen* (Fig. 1). In each of these regions certain of the primary functions of the organism are concentrated. The head carries the mouthparts, which are concerned with feeding, and the organs of special sense. The thorax bears the locomotor organs, i.e. legs and wings. The abdomen is concerned with reproduction and may carry appendages associated with the latter function; it is also the seat of many metabolic processes of the body.

In most orders an intersegmental region or *cervix* connects the head with the thorax and possibly also includes the posterior unsclerotized part of the labial segment and the anterior part of the prothorax.

THE HEAD AND CERVIX

THE insect head presents many morphological problems but it is convenient here to give a descriptive account of the head-capsule and cephalic appendages before discussing in section (*d*) the more important theories of the segmental composition of this region.

(*a*) The Head-Capsule

The exoskeleton of the head is composed of several sclerites more or less intimately welded together to form a hard, compact case or *head-capsule*, general works on which include those of Crampton (1932), Cook (1944), DuPorte (1946), Strenger (1952) and Snodgrass (1928; 1932; 1947; 1951). If an examination be made of the dorsal surface of the head of an orthopteroid, or other generalized insect, a Y-shaped *epicranial suture* will be seen. The stem of this Y forms a median line and the two arms diverge anteriorly. Unlike most of the other sutures of the head-capsule, which are inflected strengthening ridges, the epicranial suture represents an ecdysial cleavage line along which the head-capsule of the immature insect breaks open when it moults. Its morphological value is not as great as was once thought since its arms differ in position in different groups of insects but it is nevertheless a convenient reference point from which to start in describing the sclerites and regions of the head.

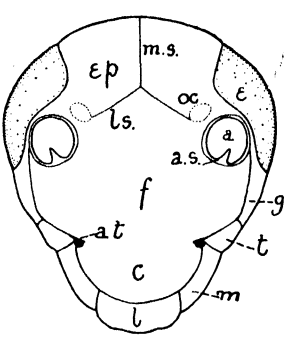


FIG. 6.—Frontal view of the head of *Blatta*

a, antennary socket; *a.s.*, antennary sclerite; *at*, point of invagination of anterior arm of tentorium; *c*, clypeus; *e*, compound eye; *ep*, epicranial plate; *f*, frons; *g*, gena; *l*, labrum; *ls*, lateral arm of epicranial suture; *m*, mandible; *m.s.*, median epicranial suture; *oc*, ocellus; *t*, mandibular sclerite.

The *frons* (or front) is the unpaired upper facial part of the head which often lies between the arms of the epicranial suture. More precisely, it may be defined as that region of the head-capsule on which arise the pharyngeal dilator muscles, but even this criterion is not wholly satisfactory. It usually bears the median ocellus and its distal limit is marked on either side by the invaginations which form the anterior arms of the tentorium (vide p. 59).

The *clypeus*, on which arise the cibarial dilator muscles, lies immediately anterior to the frons and, as a rule, the two sclerites are fused owing to the obliteration of the *clypeo-frontal suture*. In some insects the clypeus is partially or completely divided by a transverse suture into two sclerites—the *post-clypeus* and the *ante-clypeus* (Fig. 318). The former sclerite carries on either side a convex process serving for articulation with the ginglymus of the mandible.

The *labrum* is an unpaired sclerite usually movably articulated with the clypeus by means of the *clypeo-labral* suture. On its pharyngeal surface it bears lateral sclerotized pieces known as *tormae*.

The *epicranium* forms the whole of the upper region of the head from the frons to the neck. In generalized insects it is divided longitudinally into two *epicranial plates* by the median epicranial suture. That portion of the epicranium which lies immediately behind the frons, and between the compound eyes, is termed the *vertex*. It sometimes carries the paired ocelli, but is not differentiated as a separate sclerite. The *occiput* is the hinder part of the epicranium between the vertex and the neck: it is rarely present as a distinct sclerite.

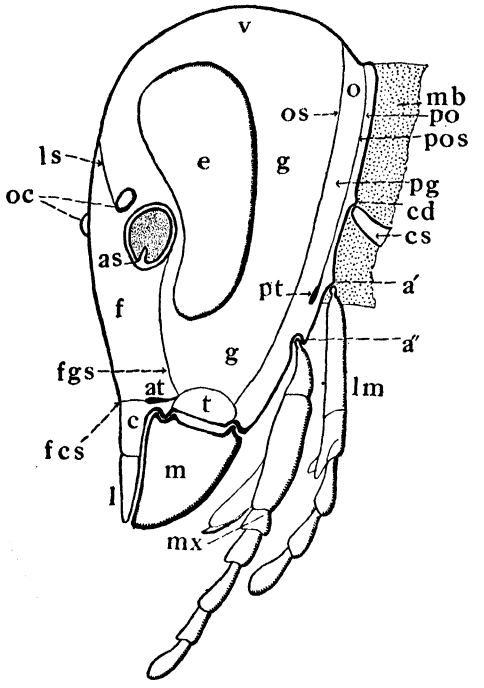


FIG. 7.—Lateral view of the head of an Orthopterous insect

a', articulation of labium; *a''*, articulation of maxilla; *as*, antennary sclerite; *at*, invagination of anterior arm of tentorium; *c*, clypeus; *cd*, occipital condyle; *cs*, cervical sclerite; *e*, compound eye; *f*, frons; *fcs*, clypeo-frontal suture; *fgs*, fronto-genal suture; *g*, gena; *l*, labrum; *lm*, labium; *ls*, lateral arm of epicranial suture; *m*, mandible; *mb*, neck membrane; *mx*, maxilla; *o*, occiput; *oc*, ocelli; *os*, occipital suture; *pg*, postgena; *po*, postocciput; *pos*, postoccipital suture; *pt*, invagination of posterior arm of tentorium; *t*, mandibular sclerite; *v*, vertex.

The *gena* (Fig. 7) forms the whole of the lateral area below and posterior to the eyes on each side: near its junction with the clypeus is the facet for articulation with the ginglymus of the mandible and proximally it bears a cavity which receives the mandibular condyle. Crossing the hind part of the cranium there is in some insects, especially Orthoptera, an *occipital suture*. When fully developed it extends on either side to end between the two points of articulation of the mandible. The areas posterior to this suture are the *occiput* dorsally and the *postgenae* laterally. The postgenae bear the condylar articulations for the maxillæ. In *Blatta* and *Periplaneta* only the lateral parts of the occipital suture are evident and are often termed *postgenal sutures*. The dorsal and lateral margins of the occipital foramen are commonly bordered by a narrow rim or *postocciput* with which the neck membrane is directly continuous. This rim is marked off from the rest of the cranium by a groove or *postoccipital suture* which ends at the posterior tentorial pit on either side. Along its course this suture is inflected to form an internal flange on which are inserted the dorsal prothoracic muscles moving the head.

The heads of insects are broadly divisible into two types (Fig. 8) depending upon the inclination of the long axis and the position of the mouthparts. In the *hypognathous type* the long axis of the head is vertical and the mouthparts ventral: the occipital foramen also lies in or near the vertical plane. In the *prognathous type* the long axis is horizontal, or slightly inclined ventrally, while the mouthparts are anterior in position or nearly so. The prognathous condition often involves an inclination of the occipital foramen or the latter may retain its vertical position owing to an elongation of the ventral region of the head. This may be achieved, as in the soldier caste of Isoptera, by a backward extension of the postmentum and genae. Or, as among Coleoptera,

ı median ventral sclerite or *gula* (not necessarily homologous in all the orders n which it occurs) extends from the occipital foramen to the base of the sub- ıentum. It occupies the area between the postoccipital sutures which, along

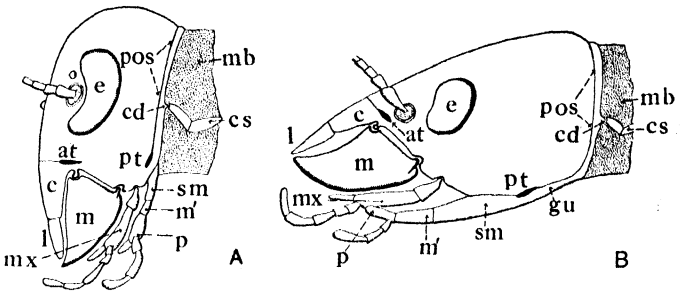


FIG. 8.—A. Hypognathous Head. B. Prognathous head

prementum; *m'*, mentum; *sm*, submentum; *gu*, gula. Other lettering as in Fig. 7. Adapted from Snodgrass.

with the posterior tentorial pits, have extended forwards on the head capsule. Where these sutures bound the gula laterally they are often termed *gular sutures*. In most cases the gula and submentum are fused into a single plate (Fig. 13) which may be termed the *gulamentum*. Yet a third type, the opisthognathous condition, occurs in the Homoptera, where the head is directed backwards so that the specialized mouthparts arise between the anterior legs.

In addition to the foregoing there are other sclerites of lesser importance which although not of general occurrence, are nevertheless present in certain insects or their larvae. These are—(1) The *antennal sclerites* (Fig. 6). Each is a ring of cuticle into which the basal segment of the antennae of its side is inserted. (2) The *ocular sclerites*. These are similarly annular in form and each surrounds the compound eye of its side. (3) *The mandibular sclerite*. A small sclerite close to the base of the mandible and separated by a transverse suture from the gena: it is found in many Orthoptera (Figs. 6 and 7).

(*b*) The Antennae

These are a pair of very mobile jointed appendages which are articulated with the head in front of or between the eyes. Imms (1939, 1940) has distinguished two main types of antennae. In the Collembola and Diplura all the antennal segments except the last contain intrinsic muscles, the antenna grows postembryonically by division of the terminal segment and Johnston's organ (p. 88) is absent. In the remaining insects only the basal segment contains muscles, Johnston's organ is present and increase in the number of segments occurs through division of the 3rd segment or sometimes also of some or all of the more distal segments. In the more generalized insects the antennae are filiform and many-segmented, the segments being equal or subequal in size. They vary, however, very greatly in form in the higher orders and certain of the segments are frequently differentiated from their fellows. In the more specialized insects the antenna is divisible into scape, pedicel and flagellum (Fig. 9).

The *scape* is the first or basal segment of the antenna and is often conspicuously longer than any of the succeeding segments.

The *pedicel* is the segment which immediately follows the scape. In geniculate antennae it forms the pivot between the scape and flagellum.

The *flagellum* forms the remainder of the antenna. It varies greatly in

form among different families in adaptation to the particular surroundings and habits of the species concerned. In some insects, e.g. Chalcidoidea, the flagellum is divisible into the ring-segments, the funicle and the club. The ring-segments are the basal segment or segments of the flagellum, are of much smaller calibre than the segments that follow, and are ring-like in form. The *club* is formed by the swollen or enlarged distal segments of the antenna.

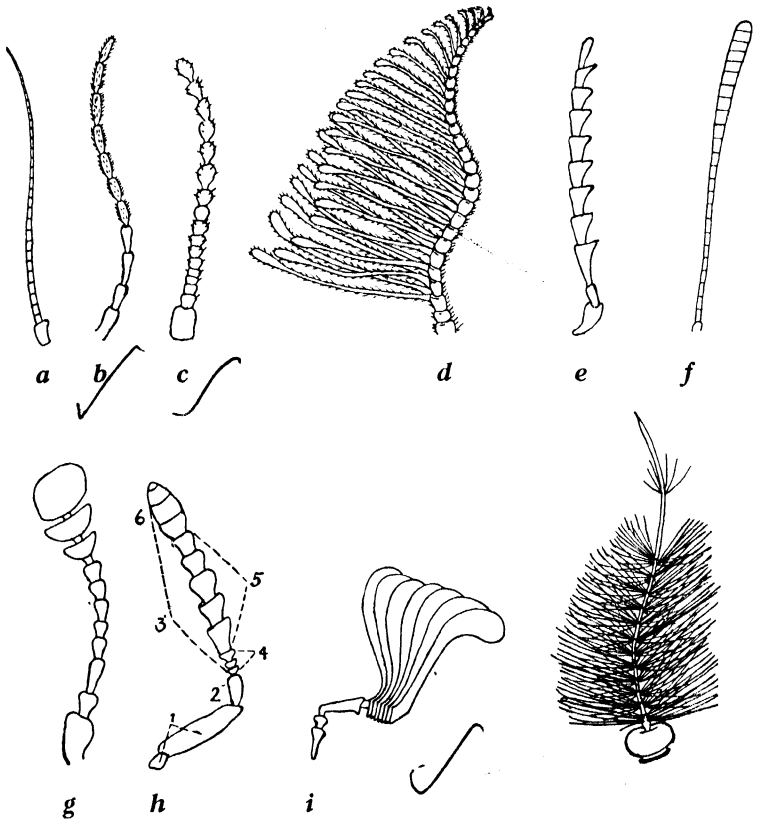


FIG. 9.—Types of antennae

a, setaceous (*Blatta*); *b*, filiform (*Carabus*); *c*, moniliform (*Calotermes*); *d*, pectinate (Tenthredinid, after Enslin); *e*, serrate (Elaterid); *f*, clavate (Lepidopteron); *g*, capitate (*Necrobia*); *h*, geniculate (Chalcid); *i*, lamellate (*Melolontha*, after Newport); *j*, plumose (male of *Culex*); 1, scape; 2, pedicel; 3, flagellum; 4, ring-segments; 5, funicle; 6, club.

The *funicle* comprises those segments which intervene between the ring-segments and the club, or between the latter and the pedicel in cases when the ring-segments are not differentiated.

The antennae afford important secondary sexual characters which are particularly well exhibited in the pectinated or bipectinated organs of certain male Lepidoptera, and in the densely plumose antennae of male Culicidae and Chironomidae. Functionally the antennae are organs of special sense (vide p. 95) but in a few exceptional cases they are modified for other uses. Thus in the larvae of *Chaoborus* and its allies they are adapted for seizing the prey, while those of the male of *Meloë* and several other insects are used for holding the females. In larvae of the Hymenoptera Apocrita and the higher Diptera the antennae are often reduced to minute tubercles or are atrophied. They are wanting in all Protura.

(*c*) The Mouthparts or Trophi

These organs consist typically of the *labrum* or upper lip, the *labium* or lower lip, an anterior or upper pair of jaws termed the *mandibles* and a posterior or lower pair of jaws termed the *maxillae*. Arising from the floor of the mouth is a median tongue-like structure or *hypopharynx*, and associated with the latter in the more primitive orders are small paired lobes or *superlinguae* The mouthparts vary in form to a greater degree than almost any other organs, the variation being correlated with the method of feeding and other uses to which they may be subjected. An examination of the structure of the mouthparts, therefore, will give a clue to the method of feeding and frequently to the nature of the food of an insect. The various modifications which these organs undergo are of fundamental importance for purposes of classification and are dealt with in the chapters devoted to the different orders of insects. Most of the latter fall into two groups, viz., those with mandibulate or biting mouthparts and those with suctorial or haustellate mouthparts. Both these functions are combined in most Collembola and in many Hymenoptera: in the Hemiptera, Thysanoptera and certain Diptera the mouthparts are adapted for piercing the tissues of plants or animals. In the Ephemeroptera, and certain Lepidoptera and Diptera, these organs are greatly reduced or non-functional.

(1) The *labrum* (Fig. 6) is a simple plate hinged to the clypeus and capable of a limited amount of up and down movement. It overlies the bases of the mandibles and forms part of the roof of the preoral food cavity. Morphologically it represents the most anterior region of the head and has secondarily acquired a basal hinged attachment. Its ventral (inner) surface is usually provided with gustatory organs and is produced into a small lobe-like epipharynx in the Hymenoptera and a long epipharyngeal stylet in the Siphonaptera.

(2) The *mandibles* (Fig. 10) or true jaws each represent the basal segment or coxopodite of the typical Arthropod limb (Snodgrass, 1950). They are adapted for cutting or crushing the food and frequently also for defence: more rarely they are modified into either sickle-like or stylet-like piercing organs. In the soldiers of the Isoptera they assume grotesque and inexplicable forms and in certain Coleoptera (*Lucanus*, *Chiasognathus*, etc.) they exhibit dimorphism, attaining relatively enormous proportions in the male. Typically, the mandible is

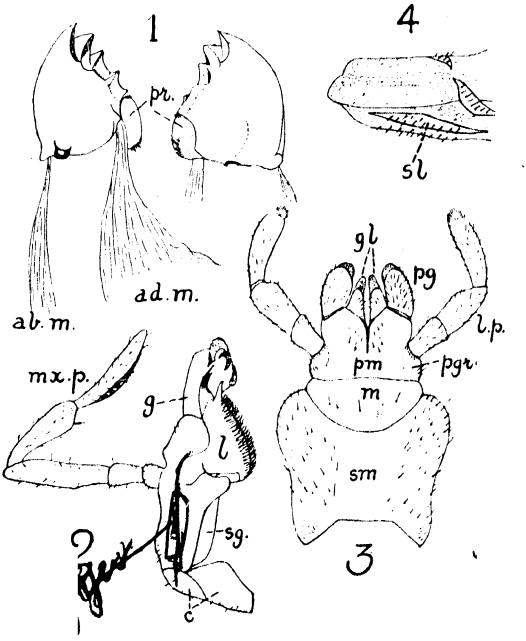


FIG. 10.—Mouthparts of *Blatta*

1, Mandibles—*ab.m*, abductor muscle; *ad.m*, adductor muscle; *pr*, prostheca; 2, Maxilla—*c*, cardo; *g*, galea; *l*, lacinia; *mx.p*, maxillary palp; *s*, stipes; *sg*, subgalea; 3, Labium—*gl*, glossa; *l.p*, labial palp; *m*, mentum; *pg*, paraglossa; *pgr*, palpiger; *pm*, prementum; *sm*, submentum; 4, Hypopharynx—*sl*, part of suspensory apparatus.

a solid compact piece articulating with the head by means of a *ginglymus* and *condyle*. The former is a groove or cavity which articulates with a convex process of the clypeus and the condyle is a rounded head adapted to fit into a socket placed at the lower end of the gena or postgena. Only the posterior articulation is present in the Machilidae and nympmhal Ephemeroptera while the entognathous Apterygotes (Collembola, Diplura and Protura) have peculiar methods of mandibular articulation. Each jaw is moved by means of powerful adductor and abductor muscles. In phytophagous insects the mandibles are bluntly toothed and often bear a molar or crushing surface near the base of the biting margin. In carnivorous forms the teeth are sharply pointed, being adapted for seizing and cutting, and the molar surface is wanting. In certain insects the mandibles exhibit more or less evident indications of a secondary division into separate sclerites. In the Machilidae (Fig. 11), for example, they are divided into a proximal and distal piece, and traces of several sclerites are found in *Cetonia*, *Copris* and other Coleoptera. In some cases a flexible plate or *prostheca*, fringed with hairs, is present on the inner border of the mandible and has been incorrectly homologized with a lacinia. Mandibles are wanting in many adult Trichoptera and the vast majority of Diptera, and they are absent or vestigial in almost all Lepidoptera.

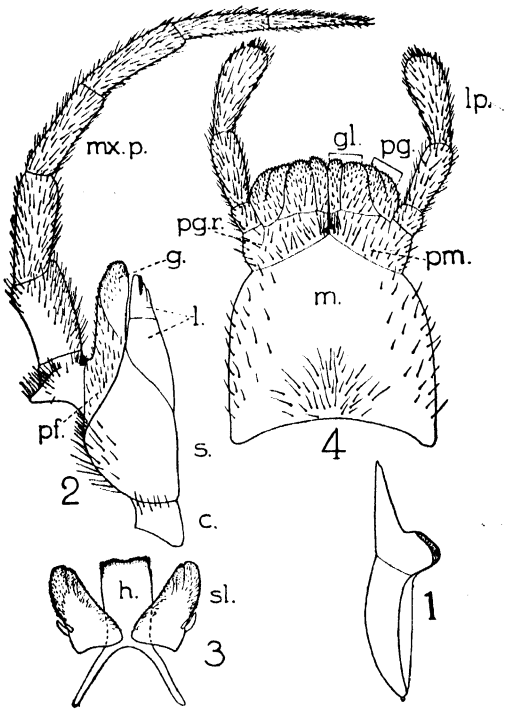


FIG. 11.—Mouthparts of *Petrobius maritimus*

1, Mandible. 2, Maxilla. *pf*, palpifer. 3, Hypopharynx (*h*) and superlinguae (*sl*). 4, Labium. *m*, postmentum. Other lettering as in Fig. 10.

The *maxillae* (Figs. 10–12) are composed of the following sclerites. The *cardo* is the first or proximal piece and, in many insects, is the only portion directly attached to the head. The *stipes* articulates with the distal border of the cardo and bears a lateral (outer) sclerite or *palpifer* and sometimes an inner sclerite, the *subgalea* (or *parastipes*). The palpifer carries the *maxillary palpus* which is the most conspicuous appendage of the maxillae. It is one to seven-segmented and sensory in function. In many insects the subgalea is not evident as a separate sclerite, being either fused with the lacinia or merged into the stipes. Distally the maxilla is composed of two lobes: an outer one or *galea* and an inner one or *lacinia*. The former is often two-segmented and frequently partially overlaps the lacinia after the manner of a hood. The lacinia or blade as a rule is spined or toothed on its inner border and, in cases when it is fused with the subgalea, it has the appearance of carrying the galea. A characteristic muscle, the cranial flexor of the lacinia, runs from the lacinia to the cranial wall and has been used to identify the former in specialized mouthparts (Das, 1937; Imms, 1944). In certain cases (e.g. many Coleop-

terous larvae) each maxilla carries a single lobe or *mala* which in some cases represents the galea and in others the lacinia (Das, 1937). Functionally the maxillae are a pair of accessory jaws, their laciniae aiding the mandibles in holding the food when the latter are extended, as well as assisting in mastication. In many of the higher insects the maxillae are so greatly modified that they no longer retain any evidences of their primitive structure. In piercing insects they are styliform and their palpi atrophied.

The insect maxilla is to be regarded as the highly modified derivative of a walking limb, whose main shaft is represented by the palpus and base by the cardo and stipes. Hansen (1930), and also Crampton (1925), claim that a reduced third element, the palpifer, enters into the formation of the limb base. On this interpretation the galea and lacinia are masticatory lobes, or endites, of the palpifer and stipes respectively. Börner (1921) and Snodgrass (1928) regard the palpifer as a secondarily demarcated portion of the stipes and of little morphological importance. On Snodgrass's theory the galea and lacinia are subdivisions of a single endite of the stipes.

The *labium* (or second maxillae) (Figs. 10, 11, 13, 14, 15) is formed by the fusion of a pair of appendages serially homologous with the maxillae (Crampton, 1925a; 1928). The completeness of the fusion that has taken place varies

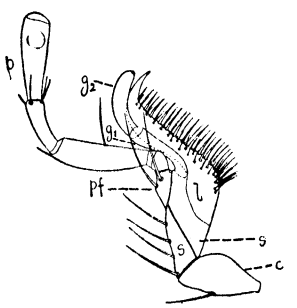


FIG. 12. — Right maxilla (ventral aspect) of a beetle, *Nebria brevicollis*

c, cardo; g_1, g_2, proximal and distal points of galea; *l*, lacinia; *p*, palp; *pf*, palpifer; *s*, *s*, stipes.

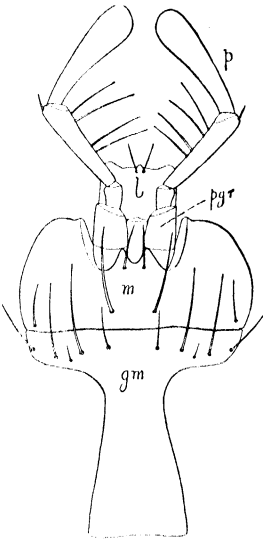


FIG. 13. — Labium (ventral aspect) of *Nebria brevicollis*

gm, gulamentum; *l*, ligula; *m*, mentum; *p*, palp; *pgr*, palpiger.

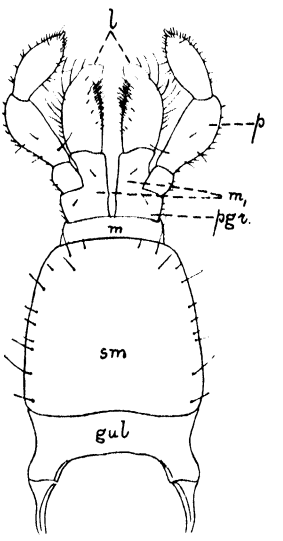


FIG. 14.—Labium of *Forficula* (ventral aspect)

l, ligula; *gul*, gula; *m*, mentum; *p*, palp; *pgr*, palpiger; m_1, prementum; *sm*, submentum.

greatly in different orders of insects, and evidences of the original paired condition are clearly seen among the lower orders. The labium is divided into two primary regions—a proximal *postmentum* and a distal *prementum*, the line of division between the two being the *labial suture*. The muscles of the palpi and the terminal lobes originate within the body of the prementum and consequently lie anterior to the labial suture. The median retractor muscles of the prementum, on the other hand, arise in the postmentum and have their insertions on the proximal margin of the prementum (Fig. 15). The relationships of these muscles, therefore, aid in determining the homologies of the main parts of the labium. The postmentum remains as an undivided

plate in, for example, the Thysanura, Isoptera and some higher orders. In many Orthoptera a distal sclerite or *mentum* is developed immediately behind the labial suture and the proximal area of the original postmental

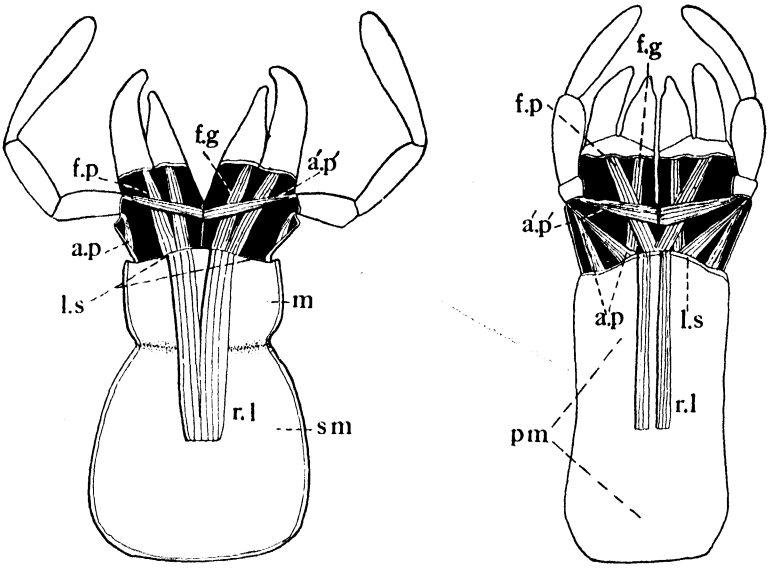


FIG. 15.—Right, labium of *Grylloblatta* (adapted from Walker). Left, labium of *Mastotermes* (original). In both figures the wall of the prementum has been removed to show the musculature

a.p, abductor of palp; *a'.p'*, adductor of palp; *f.g*, flexor of glossa; *f.p*, flexor of paraglossa; *l.s*, labial suture; *m* mentum; *p.m*, postmentum; *r.l*, median retractors of prementum; *sm*, submentum.

plate is termed the *submentum*; the mentum is frequently ill-defined and is without muscle attachments. Near the base of the prementum, on either side, is the *palpiger* which carries the *labial palpus* and often resembles a basal segment of the latter. The labial palpi are composed of from one to four segments and they function as sensory organs. Arising from the distal margin of the prementum are two pairs of lobes which collectively form the *ligula*, viz.: an outer pair or *paraglossae*, and an inner pair or *glossae*. More usually, the latter organs are fused to form a median *glossa* or the prementum may bear a single median lobe to which the general term ligula is applied.

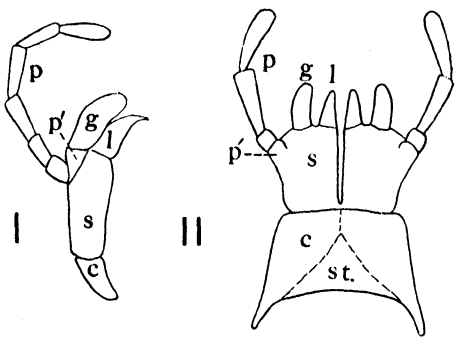


FIG. 16.—Diagram showing homologous parts in maxilla (I) and labium (II)

c, cardo; *s*, stipes; *l*, lacinia; *g*, galea; *p*, palp; *p'*, palpifer (or palpiger in II); *st*, sternum.

In Fig. 16 the homologies of the sclerites of the labium with those of the maxillae are indicated. The glossae and paraglossae are the counterparts of the laciniae and galeae respectively, while the labial palpi are homologous with similar organs of the maxillae. The two lobes of the primitive divided prementum are clearly traceable as the representatives of the stipites which, in most insects, undergo fusion. The only part comparable to united cardines is the postmentum, but it is possible that the median part of the sternum of the labial segment

is incorporated in this sclerite. The true morphological explanation of the postmentum is unsolved and further embryological data are needed. The mentum has frequently been homologized with the stipites, but since the former sclerite is a secondary development it is of little morphological importance and the homology is untenable.

Situated behind the mouth and derived mainly from the mandibular segment of the head (with a possible contribution from the maxillary segment) lies the median hypopharynx (Snodgrass, 1951). This is usually a tongue-like structure and at its base on the lower side there opens the salivary duct. In the Diplura, Collembola, Machilidae and Ephemeropteran nymphs the hypopharynx is 3-lobed, the median lingua bearing a pair of lateral superlinguae probably homologous with the paragnaths of the Crustacea. In the Lepismatidae and Pterygota the hypopharynx is typically a simple lobe with a number of suspensory sclerites but in most Diptera it is a stylet-like structure pierced by the salivary canal and in some cases is used as a piercing organ.

(*d*) Segmentation of the Insect Head

After an insect has emerged from the egg the completed head exhibits but few indications of a segmental origin apart from the fact that it carries paired appendages. There is, however, every reason to believe that the Arthropod head arose by the coalescence of a number of body-segments and a non-segmental anteriorly-placed acron homologous with the Annelid prostomium. Opinions differ on the number and characteristics of the segments involved in the formation of the insect head and most of the hypotheses have been reviewed by Imms (1937) and Weber (1952). The orthodox theory is based largely on embryological evidence, was summarized by Goodrich (1897) and discussed more recently by Tiegs (1940) and Manton (1949). It asserts that the insect head consists of the acron plus 6 segments. The latter may each be recognized embryologically by (i) the presence of a neuromere (paired embryonic ganglia), (ii) the presence of a pair of coelom sacs and (iii) the presence of paired appendages. The segmental composition of the insect head according to this theory is exhibited in tabular form below:

Segment	*Neuromere*	*Coelom sacs*	*Appendages*
1. Pre-antennary	Protocerebrum	Present	Embryonic
2. Antennary	Deutocerebrum	,,	Antennae
3. Intercalary	Tritocerebrum	,,	Embryonic
4. Mandibular	Mandibular ganglion	,,	Mandibles
5. Maxillary	Maxillary ganglion	,,	Maxillae
6. Labial	Labial ganglion	,,	Labium

A few comments on this table are necessary. The pre-antennary segment is clearly defined by its neuromere although the protocerebrum may also comprise the archicerebrum or primitive prostomial ganglion. Pre-antennary coelom sacs and appendages are only known among insects in *Carausius* (Wiesmann, 1926) though, as mentioned below, cavities in the region of the developing labrum are reported in a few cases. Traces of the intercalary segment are found in most embryos, and in *Campodea* (Uzel, 1897) and *Dissosteira* (Snodgrass, 1928) vestiges held to represent the appendages of this segment even occur in the adult. The neuromeres of the mandibular, maxillary and labial segments fuse during development to form the suboesophageal ganglion.

A slight modification of the orthodox theory, also made on embryological grounds, claims the existence of a distinct labral segment in front of the pre-antennary metamere, thus making 7 cephalic segments in all. Coelom sacs are certainly present in the labral region of the embryos of *Carausius* (Wiesmann, 1926), *Pieris* (Eastham, 1930), *Rhodnius* (Mellanby, 1936) and *Locusta* (Roonwal, 1937) and the labrum arises from paired rudiments (held to represent the appendages of the labral segment) in these and some other insects. On the other hand, the labrum is formed from an unpaired rudiment in many other insects, including the Apterygota, *Blattella*, *Acheta* and

Forficula and as the so-called labral coelom sacs may well be derivatives of the preantennal segment the existence of a labral segment cannot be regarded as satisfactorily established.

Other theories of the segmental composition of the insect head are based mainly on anatomical evidence, especially that provided by the cephalic nervous system, but as they cannot readily be reconciled with embryological data they have not found very wide acceptance. The three most important theories are as follows:

1. Hanström (1927–30) concluded from a study of the cephalic ganglia that the protocerebrum and deutocerebrum are secondary derivatives of the ganglion of the acron and that only 4 true segments, corresponding to the intercalary-labial segments of the above table are present, the antennae being regarded as comparable to the prostomial tentacles of Annelids and not as segmental appendages. Snodgrass (1938) follows this view but has been criticized by Manton (1949).

2. Hansen (1930) considered that in addition to the 6 segments recognized in the orthodox theory there is a distinct maxillulary segment lying between the mandibular and maxillary segments and that its small appendages could be recognized in the Apterygota. The anatomical evidence is not very convincing and there is no embryological support for the theory.

3. Henry (1947–48), by tracing the innervation of some cephalic structures, concluded that 6 segments are present, the first three being represented respectively by the labrum, the clypeus and hypopharynx together and an oculo-antennary region of the head broadly equivalent to what is usually called the frons. The remaining three segments are those recognized in the orthodox theory. Ferris (1947) supports this theory which has many resemblances to the views which he developed (Ferris, 1942; 1943) from a study of the exoskeleton of the head.

(*e*) The Cervix or Neck Region

The cervix (Crampton, 1926) is the flexible intersegmental region between the head and the prothorax (Fig. 2). In its membrane are embedded a variable number of small plates termed *cervical sclerites* (Fig. 21). The latter are present in nearly all orders of insects but are best developed in the more primitive groups (Orthoptera, Dermaptera, Isoptera, Odonata, etc.): in the higher orders they occur in a more or less reduced condition. In their least modified form the cervical sclerites consist of paired dorsal, lateral, and ventral plates of which the lateral pair is of special importance. The lateral sclerites usually comprise two plates on either side which are closely hinged together so as to form a fulcrum between the head and prothorax. The distal plate articulates with the occipital condyle of the head, while the proximal plate is hinged to the prothoracic episternum (Fig. 17). Levator muscles arising from the postoccipital rim and from the prothoracic tergum are attached to the lateral cervical sclerites of their side. The contraction of these muscles widens the angle between the two plates of a pair and, in this way, causes the protraction of the head.

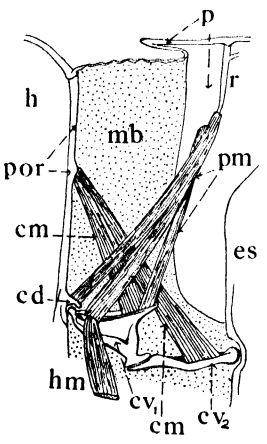


FIG. 17.—Neck and cervical sclerites of a grasshopper (*Dissosteira*)

cd, occipital condyle; *es*, episternum; cephalic (*cm*), protergal (*pm*) and prosternal (*hm*) muscles of cervical sclerites (cv_1, cv_2); *h*, head; *p*, protergum; *por*, postoccipital rim; *r*, ridge of protergum. *From* Snodgrass.

The morphological nature of the neck is highly problematical and the available evidence suggests that something more than an enlarged intersegmental region may be involved. According to Snodgrass (1932) there is some embryological support for the view that the postoccipital rim is a remnant

of the labial segment and that a posterior membranous part of this region together with the anterior part of the prothorax enter into the formation of the neck.

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THE THORAX

(*a*) Segmentation of the Thorax

THE essential morphology of the thorax was first clearly interpreted by Audouin in 1824 who pointed out that it is composed of three segments, the *pro-*, *meso-*, and *metathorax*. This conclusion has received the confirmation of subsequent morphological and embryological research, while the composite-segment theories of Kolbe, Verhoeff and others must be regarded as untenable. In almost all insects each segment bears a pair of legs and, in the majority of adult insects, both the meso- and metathorax carry a pair of wings. In all cases where the legs are wanting, their absence is due to atrophy. This apodous condition is extremely rare among the imagines but it is the rule among the larvae of the Diptera, and also those of certain families of Coleoptera. All hymenopterous larvae, excepting the vast majority of the suborder Symphyta, are similarly devoid of legs. The absence of wings, on the other hand, may be a primitive character as in the Apterygota, but among the Pterygota it is always a secondary feature due to the atrophy of pre-existing organs. The thorax is exhibited in its simplest form in the Thysanura, in certain of the more generalized Pterygota and in the larvae of many orders. In these instances the segments differ but little in size and proportions, but usually with the acquisition of wings, a correlated specialization of the thorax results. The meso- and metathorax become more or less intimately welded together to form a pterothorax and the union is often so close that the limits of those regions can only be ascertained with difficulty. In orders where the wings are of about equal area these two thoracic segments are of equal size (Isoptera, Embioptera, Odonata, etc.). Where the fore wings are markedly larger than the hind pair there is a correspondingly greater development of the mesothorax (Hymenoptera, and also Diptera where the hind wings are absent). In cases where the fore wings are small or not used in flight there is a correlated reduction of the mesothorax (Coleoptera). The prothorax never bears wings and is also variable in its degree of development. Its dorsal region may be enlarged to form a shield as in the Orthoptera, Dictyoptera, Coleoptera and Hemiptera-Heteroptera: in most other orders it is reduced to a narrow annular segment. For general accounts of thoracic morphology see Crampton (1909; 1914), Snodgrass (1909; 1927; 1929) and Weber (1923–27).

(*b*) The Sclerites of a Thoracic Segment

When describing the sclerites and regions of the thorax the prefixes *pro*, *meso* and *meta* are used according to the segment to which there ference applies. Thus the expression protergum refers to the tergum of the prothorax and mesepimeron to the epimeron of the mesothorax. The prefixes *pre* and *post* are also used to designate certain sclerites of any one of the segments

and in such cases the prefixes pro, meso and meta are usually not applied. For example the prescutum may be present on each thoracic segment in front of the scutum.

The **Tergites.**—Primitively it may be supposed (Snodgrass, 1927) that the thoracic terga consisted of three simple segmental plates (the *nota*) between which lay small intersegmental sclerites. In all known insects, however, a secondary segmentation has become established whereby the intersegmental sclerites have become closely associated with the notum in front or with the one behind. In the latter case the intersegmental sclerite forms a narrow band at the front of the notum and is known as the acrotergite. In the former case, the intersegmental sclerite becomes known as the postnotum and is sometimes a conspicuous plate. These transpositions of the intersegmental sclerites of the pterothorax differ in different insects. Thus, in the Apterygota,

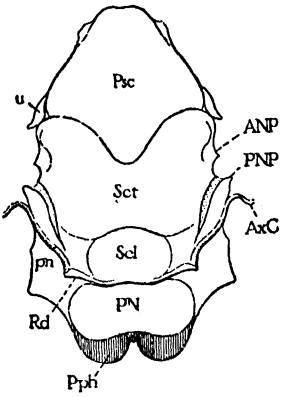


FIG. 18.—Mesotergum of a cranefly showing division of notum into three sclerites (*Psc*, *Sct* and *Scl*) behind which is postnotum (*PN*)

AxC, axillary cord; *ANP*, anterior notal wing process; *PN*, *pn*, postnotum; *PNP*, posterior notal wing process; *Pph*, postphragma; *Psc*, prescutum; *Rd*, posterior reduplication of notum; *Scl*, scutellum; *Sct*, scutum; *u*, lobe of prescutum before base of wing. *After* Snodgrass, *Proc. U.S. Nat. Mus.* 39.

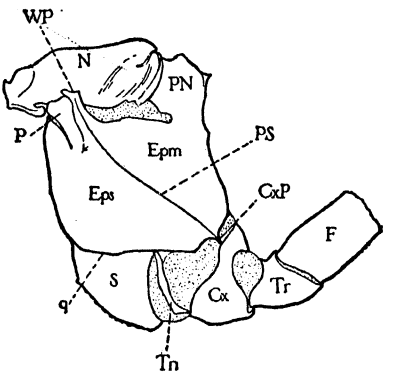


FIG. 19.—Metathorax of a stonefly, left side

Cx, coxa; *CxP*, pleural coxal process; *Epm*, epimeron; *Eps*, episternum; *F*, base of femur; *N*, notum; *P*, episternal parapterum; *PN*, postnotum; *PS*, pleural suture; *q*, sternopleural suture; *S*, sternum; *Tn*, trochantin; *Tr*, trochanter; *WP*, pleural wing process. *After* Snodgrass, *loc. cit.*

the Blattids and the Isoptera and in many immature forms the meso- and metathorax each possesses an acrotergite but no postnotum. In most other orders a postnotum is present in both meso- and metathorax, but in the Orthoptera and Coleoptera the metathorax has acquired two intersegmental sclerites, having both acrotergite and postnotum while the mesothorax has accordingly no postnotum. The notum is typically divided into three sclerites, the prescutum, the scutum and the scutellum (Fig. 18). At the sides of the pronotum in many Lepidoptera are lobe-like structures known as patagia.

The **Pleurites** (Figs. 19–21).—It is now generally considered that the pleural sclerites were derived from the primitive subcoxal segment of the leg which became flattened and incorporated into the pleural region of the body-wall. The dorsal elements of the subcoxa have thus come to form the definitive thoracic pleuron, while a ventral element probably fused with the primitive sternum to form the definitive sternal area. Indications of such subcoxal sclerites are to be found in the small and variable pleural sclerites of the Apterygota, but in the Pterygote insects the pleuron (Figs. 19–21) consists of an anterior sclerite or *episternum* and a posterior sclerite or *epimeron*, the two

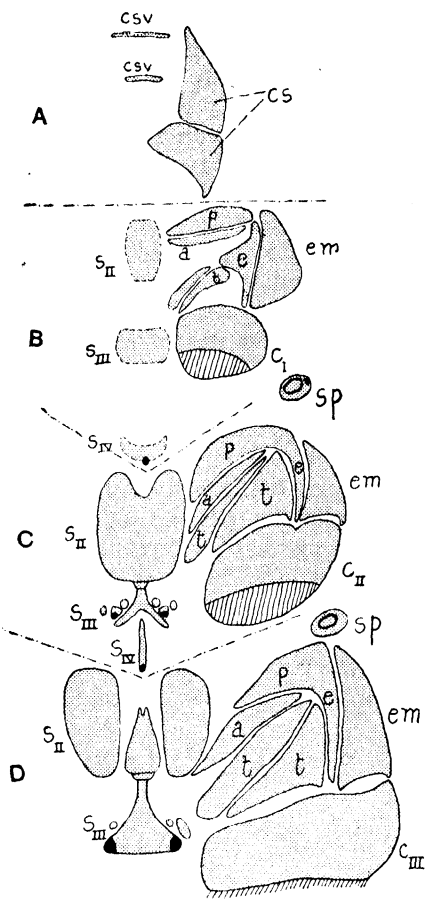


FIG. 20.—Sternal and pleural sclerites of cervix and thorax of *Blatta*

A, Cervix. B, Prothorax. C, Mesothorax. D. Metathorax. *a*, antecoxal piece; cI-cIII, coxae; *cs*, lateral cervical sclerites; *csv*, ventral ditto; *e*, episternum; *em*, epimeron; *p*, precoxal bridge; *sp*, spiracle; *s*II, eusternum; *s*III, sternellum; *s*IV, poststernellum; *t*, *t*, trochantin.

likewise, is sometimes divided into two sclerites by a transverse suture. A recognized terminology applicable to these sclerites does not exist; for the upper plate the name *anepimeron* (or pteropleuron) and for the lower plate the name *katepimeron* may be adopted. When the pleuron as a whole is fused with the sternum the combined sclerite is known as the *pectus*. In many of the higher insects the pleuron is usually connected and fused with the tergum by means of downward prolongations of the prescutum and postnotum.

being separated by the *pleural suture*. In many insects deviations from this simple condition are evident owing to the subdivision of the pleurites into secondary plates, or their fusion with other regions of their segment. The anterior part of the episternum is frequently marked off as a separate plate, the *pre-episternum*, which is mainly present in the lower orders. In many insects (e.g. *Chrysopa*, *Corydalis*, *Tipula*, *Tabanus*) the episternum is divided into an upper and lower sclerite. These two sclerites have been termed the *anepisternum* and *katepisternum* respectively. Not infrequently the lower portion of the episternum is fused up with the sternum, as in Diptera, and the compound plate thus formed is the *sternopleurite* (Crampton) or *sternopleura* (Osten-Sacken). The epimeron,

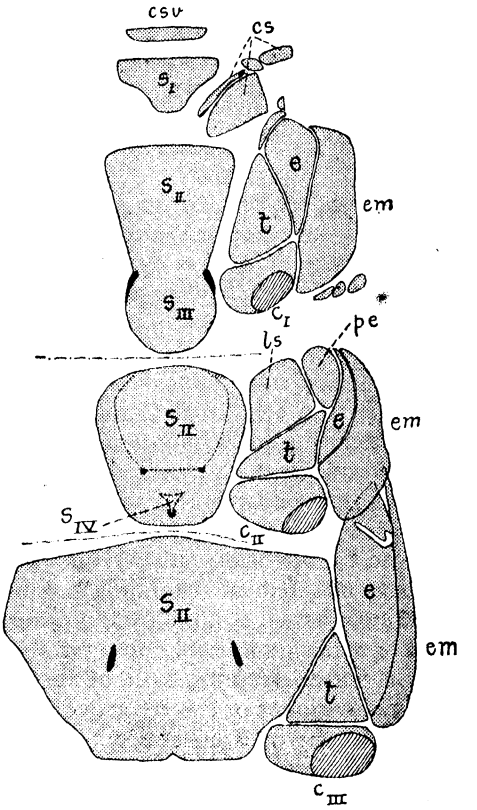


FIG. 21.—Sternal and pleural sclerites o *Forficula*.

pe, pre-episternum; *ls*, laterosternite; s_1, presternum Other lettering as in Fig. 20.

The Sternum.—As in the case of the terga, the sternal region of each segment consists typically of a segmental plate and an intersegmental sclerite, the latter associated with the segmental region in front of it. The segmental plate or eusternum is subdivided into three sclerites, the presternum, basisternum and sternellum and in generalized forms the basisternum is separated from the sternellum by a transverse suture connecting the apophyseal pits—points of cuticular invagination from which arise a pair of furcal arms which form part of the thoracic endoskeleton (p. 60). The intersegmental sclerite is known as the spinasternum (or poststernellum) and is produced internally into a peg-like apodeme which, with the furca, provides areas for the attachment of the ventral longitudinal muscles. Separate laterosternites are sometimes found at the sides of the eusternum and fusion of the sternal and pleural regions may result in the formation of precoxal and postcoxal bridges. While broad sternal plates subdivided as above may be found in many Orthopteroid insects (Fig. 21) there is often considerable specialization of the ventral region. Thus, the sterna may be narrow and extensively desclerotized (as in the Cockroaches), the sutures between the various sclerites may be obliterated and the spinasternum may be lost or its spina consolidated with the eusternum. The apophyseal pits may also become closely approximated, the boundaries between pleuron and sternum may be lost by fusion and a cuticular inflection may be developed along the mid-line of the ventral surface. In an attempt to account for some of the peculiarities of the sternopleural region, Ferris (1940, etc.) has argued that the greater part of the ventral side of the thorax of some insects is derived from pleural structures, but further critical study of his theory is necessary.

(*c*) The Legs

The legs are primarily organs for running or walking and are well represented in their normal condition in a cockroach or Carabid beetle. They exhibit, however, a wide range of adaptive modifications in different families (Fig. 22). Thus in *Gryllotalpa*, the Scarabaeidae and some others the fore legs are modified for burrowing, and in the Mantidae, Phymatidae, etc., for seizing and holding the prey. In certain families of butterflies the fore legs are so much reduced that in these insects there are only two pairs of functional limbs. In the saltatorial Orthoptera, and *Phyllotreta* and other genera of Coleoptera, the hind femora are greatly enlarged in order to accommodate the powerful extensor muscles which are used in leaping. Among the Odonata all the legs are adapted for seizing and retaining the prey and are scarcely, if ever, used for locomotory purposes, while in the Bombyliidae the slender legs are used for alighting rather than walking. In aquatic insects they are often specially adapted as swimming organs. Each leg (Fig. 24) consists of the following parts—*coxa*, *trochanter*, *femur*, *tibia* and *tarsus* together with certain basal or *articular sclerites* and a terminal pretarsus.

The **Basal Articulations of the Legs** (Figs. 19 and 21).—The coxa or proximal segment of the leg articulates with the body by means of the coxal process of the pleuron and with the trochantin when the latter sclerite is present. A ventral, sternal articulation may also occur. The *coxal process* is situated at the ventral extremity of the pleural suture. The *trochantin* is the articular sclerite situated at the base of the coxa in the more primitive orders. It frequently unites with neighbouring sclerites, or it may be divided into a pair of plates. Between the single or divided trochantin and the episternum,

or between the trochantin and the precoxal bridge, there is frequently an inner sclerite or *antecoxal piece*. The homologies of these small basal sclerites in different insects have been much discussed and it is probable that they are derived from an original subcoxa (see below).

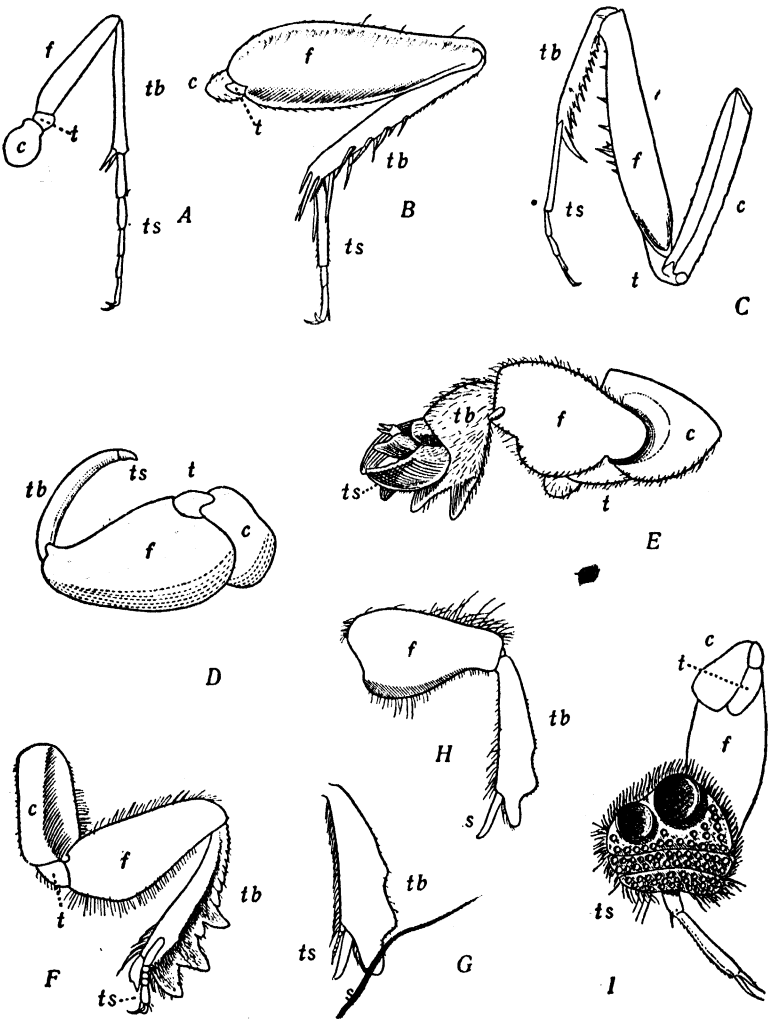


FIG. 22.—Adaptive modifications of the legs

A, *Cicindela sexguttata*; *B*, *Nemobius vittatus*, hind leg; *C*, *Stagmomantis carolina*, left fore leg; *D*, *Pelocoris femoratus*, right fore leg; *E*, *Gryllotalpa borealis*, left fore leg; *F*, *Canthon laevis*, right fore leg; *G*, *Phanaeus carnifex*, fore tibia and tarsus of female; *H*, *P. carnifex*, fore tibia of male; *I*, *Dytiscus fasciventris*, right fore leg of male; *c*, coxa; *f*, femur; *s*, spur; *t*, trochanter; *tb*, tibia; *ts*, tarsus. *After* Folsom, 1923.

The **Subcoxa** is the true basal segment of the primitive leg, but it is either reduced or much modified in all insects. It is only rarely represented by an undivided sclerite as in *Machilis* (Fig. 215) and a few other Apterygota where pleural sclerites are undeveloped. Among the Pterygota, Hansen (1930) regards the trochantin as its sole remnant, but it is more generally conceded that this sclerite is only a small part of the subcoxa, the major part probably having become incorporated into the thoracic wall to form the pleural sclerites

(Snodgrass, 1929). This view is supported by the condition found among Apterygota and in certain immature Pterygota. Thus, in *Magicicada* the large subcoxa shows differentiation into rudimentary pleurites with a small basal piece or *trochantin* (Fig. 23).

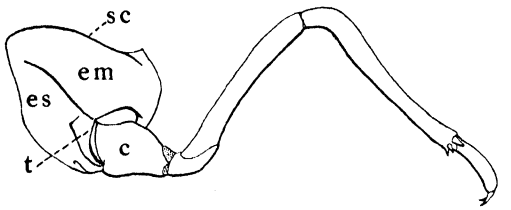


FIG. 23.—Hind leg and pleuron of mature nymph of *Magicicada septendecim*

c, coxa; *em*, epimeron; *es*, episternum; *sc*, subcoxa; *t*, trochantin. *After* Snodgrass.

The **Coxa** has replaced the subcoxa as the functional base of the leg. It is frequently divisible into two lobes by an inflexion of its wall where it articulates with the pleuron. The posterior lobe thus delimited is the *meron* (Larsen, 1945) which is usually the larger part of the coxa. A meron is well developed in *Periplaneta*, the Isoptera, Neuroptera and Lepidoptera.

The **Trochanter** is the second division of the leg: it articulates with the coxa but is usually rigidly fixed to the femur. In the Odonata it is divided into two subsegments and among the parasitic Hymenoptera a second apparent trochanter, derived from the base of the femur, is present (see p. 683).

The **Femur.**—The femur usually forms the largest region of the leg and is especially conspicuous in most insects which have the power of leaping.

The **Tibia.**—The fourth division of the leg is known as the tibia: it is almost always slender and frequently equals or exceeds the femur in length. Near its distal extremity it carries one or more *tibial spurs*. In the Apocritan Hymenoptera the enlarged apical spur of the anterior tibiae fits against a pectinated semicircular pit in the first tarsal segment, and the antennae are passed between these two organs for cleaning purposes.

The **Tarsus** consists primitively of a single segment, a feature which is present in the Protura, Diplura and in some larvae. More usually it is divided into subsegments, typically five in number, but none of these subsegments has acquired muscles and movement of the tarsus as a whole is effected by levator and depressor muscles arising from the apex of the tibia. At its apex the tarsus bears a group of structures forming the *pretarsus* (de Meijere, 1901; Holway, 1935;

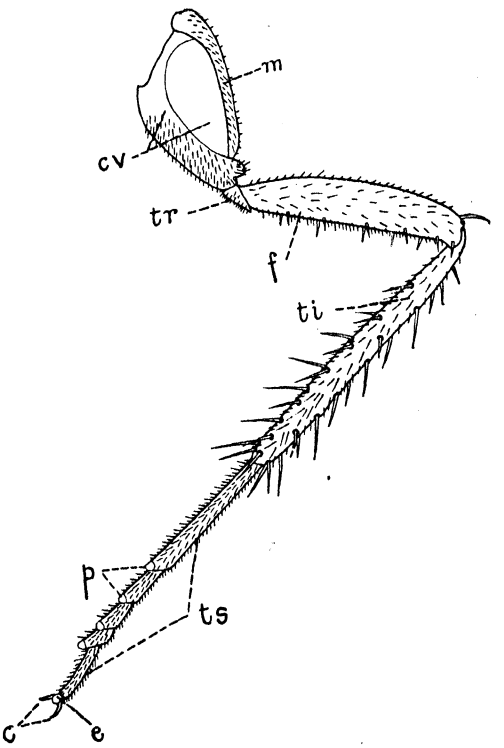


FIG. 24.—A typical leg of an insect (left hind leg of *Blatta*)

cv, coxa vera; *m*, meron; *tr*, trochanter; *f*, femur; *ti*, tibia; *ts*, tarsus; *c*, claws; *e*, arolium; *p*, plantulae.

Dashman, 1953) which represents the terminal segment of the leg. In its simplest condition, seen in Collembola, Protura and many larvae, the pretarsus is prolonged into a single claw. In most insects the claws are paired and between them, on the ventral side, the pretarsus is supported by a median *unguitractor plate* to which the apodeme of the flexor muscle of the claws is attached. In front of and above this plate the pretarsus expands into a median lobe or *arolium* (Fig. 25). Among Diptera there are two lobes or *pulvilli* lying below the claws, often with an arolium between them or, in place of an arolium, the plantar sclerite distal to the unguitractor plate is prolonged into a median bristle or *empodium* (Fig. 26). On the underside of the tarsal segments there are frequently pulvillus-like organs or *plantulae* (Fig. 24). The arolium and pulvilli are pad-like organs enabling their possessors to climb smooth or steep surfaces: the plantulae also have a similar function. Such organs are outgrowths of the parts from which they arise and their cavities contain blood. Various explanations have been offered as to how they function but attachment probably depends on the fact that the structures concerned are covered with tubular tenent hairs, the apices of which are moistened by a glandular secretion. The hairs can be applied very closely to a smooth surface and adhesion occurs, the insect being held by surface molecular forces (Arnhart, 1923; Dahl, 1881–85; Gillett & Wigglesworth, 1932).

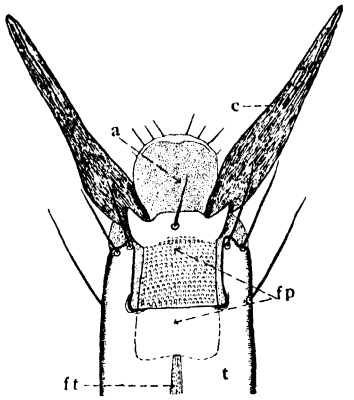


FIG. 25.—Pretarsus of an Orthopteron, ventral view

a, arolium; *c*, claw; *fp*, unguitractor plate; *t*, apodeme of flexor muscle; *t*, tarsus.

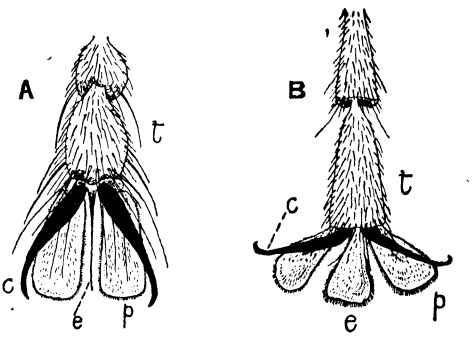


FIG. 26.—Feet of the males of A, *Asilus crabroniformis*; B, *Rhagio notata*

c, claw; *e*, in A, empodium: in B, arolium; *p*, pulvillus *t*, last tarsal segment. *After* Verrall.

Locomotion (Terrestrial). — Many insects are capable of leaping by sudden extension of the hind tibiae (e.g. Orthoptera, Siphonaptera, Halticinae) and some do so with the aid of more specialized structures (e.g. Elaterid beetles, Collembola), but walking is the most usual method of terrestrial locomotion. During this process in hexapod forms the fore legs serve mainly as organs of traction and the middle legs as supporting structures while the hind legs exert a propulsive force. The classical view was that progression occurred in a zig-zag fashion by movement of the legs in two alternating groups, the fore and hind legs of one side and the middle leg of the opposite side being moved forward simultaneously while the insect is balanced on a 'tripod of support' formed by the remaining three legs. In fact, cinematographic analysis (Hughes, 1952) shows that the legs move in sequence, the commonest (but not invariable) order being (i) fore leg, (ii) opposite hind leg, (iii) middle leg. The number of legs on the ground at any instant may be 3, 4 or 5 and the classical alternation of tripod supports is only approached under certain circumstances. Increased speed results from an increased rate of movement of the legs and though there may be a change in the sequence of leg-movements, the pattern of behaviour is fundamentally the same throughout. In insects with only two functional pairs of walking legs (e.g.

Mantidae), movement occurs by alternation of the front leg and the opposite back leg. In the locomotion of caterpillars and some other larvae, movements of the abdomen and its appendages play an important part (Barth, 1937).

(*d*) The Wings

The presence of wings is one of the most characteristic features of insects, and the dominance of the latter as a class is to be attributed to the possession of these organs. Owing to their wide range of differentiation, wings provide one of the most useful characters for purposes of classification. In virtue of its more or less triangular form the wing of an insect presents three margins (Fig. 27): the *anterior margin* or *costa* (*a–b*); the *outer* or *apical margin* (*b–c*) and the *inner* or *anal margin* (*c–d*). Three well-defined angles are also recognizable, viz., the *humeral angle* (*a*) at the base of the costa; the *apex* (*b*) or angle between the costal and outer margins and the *anal angle* or *tornus* (*c*) between the outer and inner margins. Although, in the greater number of insects, the wings appear to be naked, in many cases microscopical examination reveals the presence of fine hairs. On the other hand, in certain groups the wings are obviously clothed. In the Trichoptera and the Dipterous family Psychodidae, for example, they are closely covered with hairs, while in the Lepidoptera the wings are invested with overlapping scales.

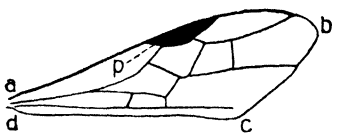


FIG. 27.—Wing of a Hymenopteron (explanation given in the text)

p, pterostigma.

Tillyard (1918a) has made a study of the hairs occurring on the wings of the most primitive groups of the Holometabola. *Microtrichia* are found indiscriminately on the wing-membrane and veins alike. *Macrotrichia* or true setae, which have annular bases of insertion, are found on the main veins and their branches, on the archedictyon (p. 47), less frequently on the wing-membrane and very rarely on the cross-veins. On the disappearance of the archedictyon, or of an individual vein, the macrotrichia may persist on the wing-membrane in their original positions; their presence thereon is regarded by Tillyard as evidence of descent from more densely veined ancestors. By plotting the positions of the macrotrichia present on the wing-membrane in such primitive forms as *Archichauliodes*, *Rhyacophila* and *Anisopus*, and joining them up into a polygonal meshwork, the lost archedictyon can often, to some extent, be reconstructed (Fig. 28).

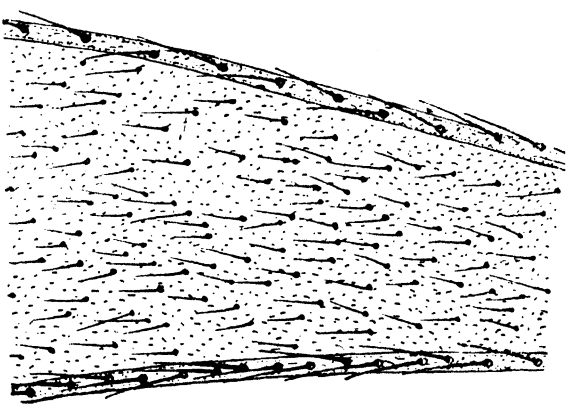


FIG. 28.—Portion of a wing of *Anisopus brevis* showing macrotrichia and microtrichia. *After* Tillyard, *Proc. Linn. Soc. N.S.W.* 43

A conspicuous opaque spot is found near the costal margin of the wing in many insects, and is termed the *stigma* or *pterostigma* (Fig. 27). It is present, for example, in the fore wings of the Psocoptera, and most Hymenoptera, and in both pairs of wings of the Odonata.

The **Basal Attachment and Articular Sclerites of the Wings.**—Each wing is hinged to two processes of the notum of its segment, the *anterior notal*

process and the *posterior notal process* (Fig. 29, A). The wing also articulates below with the *pleural wing process*. The posterior margin of the membrane at the base of the wing is frequently strengthened to form a cord-like structure known as the *axillary cord*. The latter arises, on either side, from the posterior lateral angle of the notum (Fig. 29, A).

Situated around the base of each wing is a variable number of *articular sclerites* which consist of the tegulae, the humeral plate and the axillaries (Fig. 29). The *tegulae* (paraptera of some authors) are a pair of small scale-like sclerites carried at the extreme base of the costa of each fore wing: they are rarely present in connexion with the hind wings. Tegulae are best developed in the Lepidoptera, Hymenoptera and Diptera, being especially large in the first mentioned order. The *axillaries* (pteralia) participate in the formation of the complex joint by which the wing is articulated to the thorax. According to Snodgrass they occur in all winged insects but are much modified in the

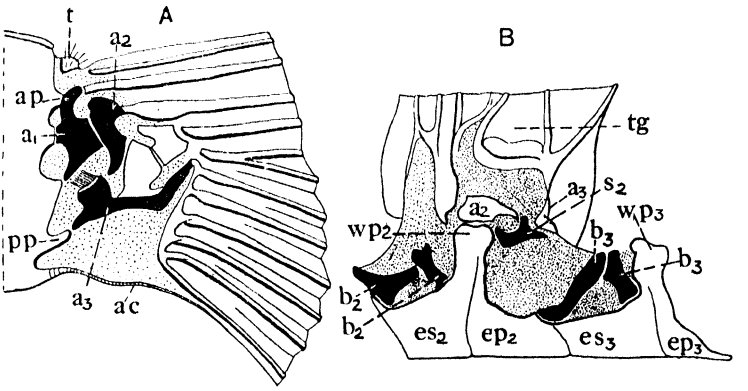


FIG. 29.—Basal articulations of the wings. A. Wing base and tergal articulation. B. Upper part of pleuron of a grasshopper with base of left tegmen (*tg*) upraised

a_1–a_3, axillary sclerites; *ac*, axillary cord; *ap*, anterior notal wing process; b_2, basalar sclerites of mesothorax; b_3, basalar sclerites of metathorax; ep_2, epimeron of mesothorax; ep_3, epimeron of metathorax; es_2, episternum of mesothorax; es_3, episternum of metathorax; *pp*, posterior notal wing process; S_2, subalar sclerite of mesothorax; *t*, tegula; wp_2, pleural wing process of mesothorax; wp_3, pleural wing process of metathorax. Adapted from Snodgrass.

Ephemeroptera and Odonata, presumably because these insects do not flex the wings over the abdomen at rest. As a rule, three of these sclerites are present, but a fourth occurs in the Orthoptera and Hymenoptera. The *first axillary* articulates with the anterior notal process and is associated with the base of the subcostal vein. The *second axillary* articulates partly with the preceding sclerite and, as a rule, partly with the base of the radius (vide p. 45). The *third axillary* usually articulates with the posterior notal process and with a group of anal veins. When a *fourth axillary* occurs it has a double articulation, i.e., with the posterior notal process proximally and with the third axillary distally. For a more detailed treatment of these sclerites vide Snodgrass (1929) and La Greca (1947).

In addition to the foregoing, there are present in many insects small epipleural sclerites which are located below the insertions of the wings (Fig. 29). Although they are regarded as parts of the pleura they may be conveniently referred to here on account of their close association with the wing attachments. These sclerites are separated into two series by the pleural wing process. The anterior or *basalar sclerites* are never more than two in

number, and lie just above the episternum, while the posterior or *subalar sclerite* is almost always single and lies behind the pleural wing process and above the epimeron.

Modifications of Wings.—Although wings are usually present in adult insects a by no means inconsiderable number of species are apterous. This condition is a constant feature of the Apterygota, where it is a primitive character, but in the Pterygota the loss of wings has been secondarily acquired. The parasitic orders Mallophaga, Siphunculata and Siphonaptera are exclusively apterous, and the same applies to the sterile castes of the Isoptera and Formicidae, and to the females of the Coccoidea, Strepsiptera and Embioptera. Among other Pterygota, apterous forms are of more casual occurrence, and often confined to a single sex or species. Thus, in a few moths (*Erranis defoliaria*, etc.), the females alone are apterous, while in the Chalcid genus *Blastophaga* it is the male which has lost the wings. Transitional forms between the apterous and the fully winged condition are found. In the moth *Diurnea fagella*, for example, the wings of the female are lanceolate appendages, but little more than half the length of those of the male, and useless for flight. In the winter moths (*Operophtera*), and in the fly *Clunio marinus*, they are reduced in the female to the condition of small flap-like vestiges.

Throughout the Diptera, and in the males of the Coccoidea, the hind wings are wanting, and are represented only by a pair of slender processes termed *halteres*. Among the Coleoptera, the fore wings are much hardened to form horny sheaths or *elytra*, which protect the hind wings when the latter are in repose. In the genus *Atractocerus*, and the males of the Strepsiptera, the elytra are reduced to the condition of small scale-like appendages. On the other hand, in certain Carabidae and Curculionidae, the hind wings are atrophied and the function of flight is lost. In the Heteroptera the fore wings are thickened at their bases like elytra and, for this reason, are frequently termed *hemelytra*. Among the Orthoptera, Dictyoptera and Phasmida, the fore wings are hardened and of a leathery consistency, being known by many writers as *tegmina*.

The Wing-coupling Apparatus.—There seems little doubt that in the primitive Pterygota the fore and hind pairs of wings moved independently of each other (as in the Neuroptera, Isoptera and Odonata), and that coincidence of motion was a later acquisition consequent upon the development of a wing-coupling apparatus (Fig. 30). Among the Panorpoid orders (Tillyard, 1918) the coupling depends on modifications of the bases of the wings, the fore wing possessing on its posterior margin a small jugal lobe while the anterior margin of the hind wing is produced into a small humeral lobe. In the Mecoptera, both lobes bear a few relatively long bristles, the jugal ones lying on top of the hind wing in flight while the humeral bristles form the frenulum which presses against the under side of the fore wing. In the Trichoptera and some Monotrysian Lepidoptera (Philpott, 1924; 1925), the jugal area is produced into a lobe-like fibula or more elongate jugum which lies on top of the hind wing during flight but may be folded beneath the fore wing at rest. Frenular bristles are absent or small in these insects but there is sometimes a more distally placed series of costal spines (the pseudofrenulum) on the hind wing which functions independently of the jugum by pressing against the anal area of the fore wing (e.g. *Sabatinca*), or a series of interlocking hairs on the basal half of the hind margin of the fore wing and the fore margin of the hind wing (e.g. *Mnesarchaea*). In most higher Lepidoptera, a pseudofrenulum occurs only in some lower families (Braun, 1919), the jugum is almost invariably lost

and the frenulum usually assumes great importance (Braun, 1924). In females it generally consists of a group of stout bristles which lies beneath the extended fore wing and engages there in a retinaculum formed from a patch of hairs near the cubitus. In males the frenular bristles are fused into a single stout structure which is normally held by a curved process from the subcostal vein of the fore wing as well. Finally, in the Papilionoidea and many Bombycoidea, the wings are coupled simply by overlapping basally—the so-called amplexiform method. Among other orders, the Hymenoptera have a

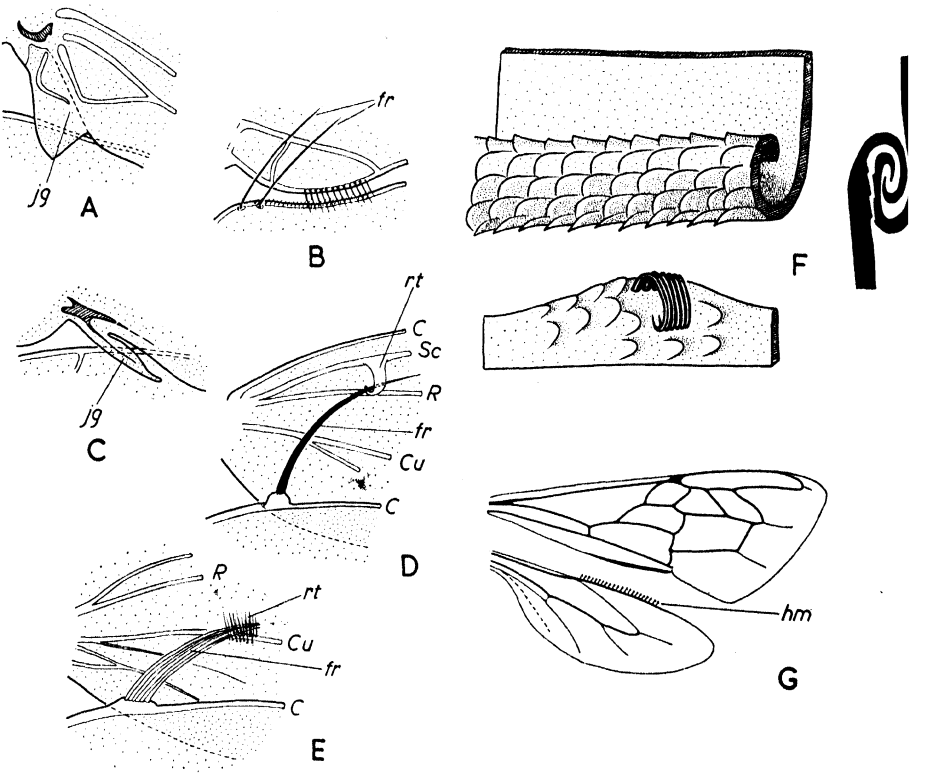


FIG. 30.—Methods of wing-coupling in insects. A. *Rhyacophila* (based on Comstock, 1918). B. *Panorpa*. C. A Hepialid moth (based on Comstock, *l.c.*). D. Male frenate Lepidopteran. E. Female frenate Lepidopteran. F. An aphid, *Drepanosiphon* (*after* Weber, 1930). G. *Apis*

fr, frenulum; *hm*, hamuli; *jg*, jugum; *rt*, retinaculum.

hamulate type of wing-coupling in which a row of small hooks (hamuli) on part of the costal margin of the hind wing catch in a sclerotized fold along the hind margin of the fore wing. In many Hemiptera the wings are held together in flight by various small hooks or folds along the wing-margins (Weber, 1930) while in the Psocoptera the costa of the hind wing is held by a spiny or hooked process of the node where the second cubital vein of the fore wing reaches the margin.

The **Structure and Development of Wings.**—Wings are thin plate-like expansions of the integument which are strengthened by a framework of hollow sclerotized tubes known as *veins* or *nervures*. A wing is composed of upper and lower layers which may readily be separated in an insect which has

just emerged from the pupa. Viewed in transverse section (Fig. 31), the veins are seen to be much more strongly sclerotized than the wing-membrane and each, as a rule, encloses a small central trachea. A fine nerve fibre accompanies the larger veins of many insects (Zacwilichowski, 1931–32) and a degenerate trachea known as 'Semper's rib' is present in Lepidoptera alongside the ordinary trachea within the vein cavity. When an insect emerges from the pupa or nymph, as the case may be, the veins contain blood which has been observed to circulate through them, and even in the fully formed wings the circulation is often still maintained (Yeager & Hendrickson, 1934; Clare & Tauber, 1940).

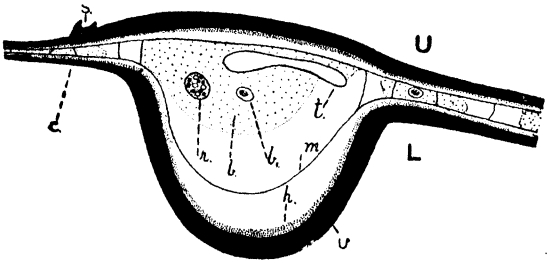


FIG. 31.—Transverse section of a vein and adjacent portion of the wing-membrane of a moth, *Notodonta camelina*

U, upper surface; L, lower surface; *v*, vein; *h*, remains of hypodermis; *t*, trachea; *c*, cuticle; b_1, blood corpuscle and *b*, plasma; *m*, basement membrane; *r*, 'Semper's rib'; *s*, scale socket.

Detailed accounts of the development of the wings are available for the Exopterygote *Pteronarcys* (Holdsworth, 1940; 1942) and for several Endopterygotes (Köhler, 1932; Behrends, 1935; Hundertmark, 1935; Kuntze, 1935; Waddington, 1941) while the older literature is reviewed by Comstock (1918). In insects with an incomplete metamorphosis, the wings develop externally and appear in the early instars along a line where the suture between tergum and pleuron later develops. In most nymphs they are so directly continuous with the tergum that they are normally regarded as postero-lateral outgrowths of that region. The external changes during growth are comparatively slight and consist mainly of an increase in size at each moult. In the Odonata and Orthoptera (*sensu stricto*), however, the wing-pads in the later nymphal instars have twisted about their points of attachment so that the costal margins lie dorsally and the hind wings cover the fore wings. The wings then resume their normal position when the adult emerges. Internally, the developing wing-pad undergoes many histological changes. At first there is merely a thickening of the hypodermis overlain by cuticle. Later, as the saclike evagination develops, the bases of the epithelial cells become drawn out into long processes, so imparting a spongy texture to the tissues of the wing-pad, and the basement membranes of the lower and upper epithelia become apposed for most of their area so as to form the so-called middle membrane (Fig. 32). Blood-filled spaces or *lacunae* soon develop in the wing-pad (appearing in the 2nd instar of *Pteronarcys*, for example) and alter as growth proceeds so that in the later instars the lacunae correspond in arrangement to the veins of the adult wings; the veins, in fact, arise by differential sclerotization of the integument adjacent to the lacunae.

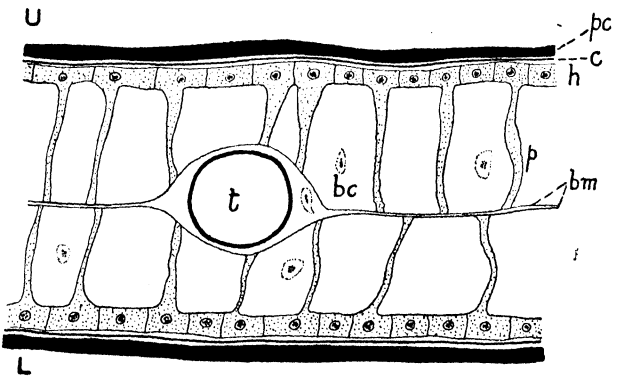


FIG. 32.—Transverse section of a portion of the wing of a pupal insect

U, upper surface; L, lower surface; *pc*, pupal cuticle; *c*, cuticle of developing wing; *h*, hypodermis of wing; *p*, process of hypodermal cell; *bm*, basement membrane; *t*, trachea in cavity of developing vein; *bc*, blood corpuscle.

While each of the principal lacunae is developing, a tracheal branch and a nerve grow into it from the base of the wing, the lacunae apparently offering the paths of least resistance. Though the association between tracheae and lacunae—and therefore between tracheae and subsequent venation—is not always exact, the pattern of nymphal tracheae is often of the greatest value in deciding the homologies of the veins. The generalized arrangement of tracheae is depicted in Fig. 33. Two distinct groups of tracheae enter the wing—a costo-radial group and a cubito-anal group, and while in some forms (Blattidae, Plecoptera and Homoptera) the two groups remain separate, it is more usual for them to be united by a transverse basal trachea. Which of these latter conditions is the primitive one is uncertain (Comstock, 1918; Ander, 1938). It may be noted that tracheae do not precede the cross-veins of the adult wing and that several cases are known where the tracheal and venational patterns differ appreciably. In the final stages of wing-development the hypodermis secretes the wing-membrane and the thickened walls of the veins and the folded adult wings take shape within the cuticle of the last instar nymph. On the emergence of the adult the wing is inflated to its full size by blood-pressure and the cuticle hardens. The hypodermis degenerates and little trace of its cells remains in the fully hardened wings.

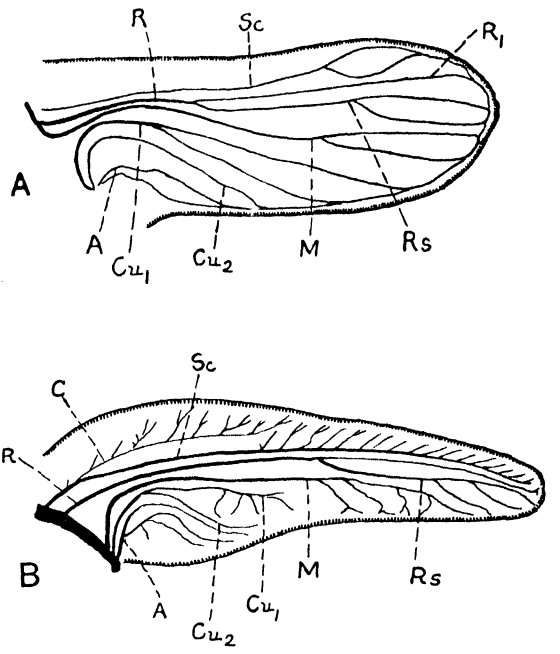


FIG. 33.—Tracheation of developing fore wings of nymphs of A. *Nemoura* (Plecoptera) and B. *Conocephalus* (Tettigoniidae). Adapted from Comstock. (For explanation of lettering, see p. 45)

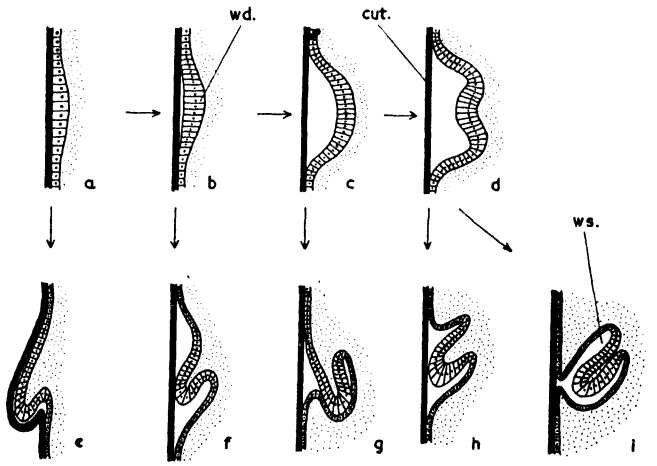


FIG. 34.—Various modes of wing development (*after* Weber, 1933)

a–d denote various early stages, *e–i* denote the corresponding later stages. *e*, free external wing-bud (most Exopterygotes); *f*, free internal wing-bud (many Coleoptera); *g*, reversed wing-bud (Neuroptera, Lepidoptera); *h*, simple sunken wing-bud (Nematocera, some Coleoptera); *i*, stalked wing-bud (Cyclorrhapha); *cut*, cuticle; *wd*, wing-disc; *ws*, wing-sac.

In insects with a complete metamorphosis the wings arise from imaginal buds or thickenings of the hypodermis, usually in the neighbourhood of one of the larger tracheae, and are evident in the very young larva or even the embryo. These buds become enlarged and folded or invaginated in various ways, sometimes forming pocket-like sacs, or *peripodial cavities* (Fig. 34), from the bottom of which the thickened portion of the bud ultimately becomes evaginated. At the same time, the walls of the pocket become extremely thin but retain their connexion with the hypodermis. At a later stage, the evaginated portion elongates and comes to hang downwards; it is this evaginated portion which eventually forms the wing. Internal histological changes, comparable to those occurring in exopterygotes, take place during the prepupal period and the wing-rudiment, as we may term it, becomes pushed out of its pocket and comes to lie just beneath the cuticle. On the assumption of the pupal stage, the wing-rudiments become evident externally along the sides of the body. When the imago emerges, the wings appear as small wrinkled sacs which gradually become distended by blood-pressure, and attain their full development usually several hours afterwards. During their later stages of development the wing-buds become supplied with tracheoles. In *Pieris*, for example, during the 4th larval stadium a series of tracheoles arise as proliferations of the epithelium of the large tracheae associated with the wing-bud. These tracheoles may be termed the larval or provisional tracheoles, and they extend in bundles into the developing lacunae. A little later, the true wing tracheae develop as tubular outgrowths of the large tracheae, and extend into the vein cavities along with the larval tracheoles, which they supplant. During the early pupal stage the latter degenerate and disappear. Although the tracheation of the pupal wings has yielded important data for ascertaining the homologies of the wing-veins of the adults, there is in some orders (e.g. Trichoptera) a wide divergence between the two systems. In such cases, comparisons among the more generalized types and palaeontological evidence may aid in settling the identity of the principal veins.

Venation.—The complete system of veins of a wing is termed its *venation* or *neuration*. The venation presents characters of great systematic importance, but unfortunately the various systems of nomenclature in use are confusing both to the student and the specialist. The establishment of the older systems was made by entomologists whose work was uninfluenced by the modern conceptions of evolution. The result was that the terminology of an individual author was usually only applicable within the limits of the particular order of insects which he studied. This lack of uniformity made it incumbent upon the student to learn the particular nomenclature adopted by the authority whose works he might be studying. It is true, efforts had been made to introduce a common terminology for the venation, which would be uniform throughout the different orders, but, until the work of Comstock and Needham (1898), little success was achieved. By means of an extensive study of the tracheae which precede, and in a general sense coincide with the positions of the veins, these writers have constructed a hypothetical type of venation from which all other types have presumably been derived (Comstock, 1918).

While the researches of Comstock and Needham form the basis for the interpretation of venation, their original conceptions have been modified by the later work of Lameere (1922) and many papers by Martynov and Tillyard. A less exclusive emphasis is now placed on tracheational studies and, in spite of the opposition of Needham (1935), there is a tendency to emphasize the fact that among the lower, generalized orders the wings are longitudinally plicated after the manner of a partially opened fan. Those veins which follow the ridges are termed *convex veins* and those which follow the furrows *concave veins*. These features are well exhibited not only in the early fossil orders but also in the Ephemeroptera and Odonata: in the higher orders they tend to become obscured by flattening of the wing-membrane or the development of second-

ary curvatures imposed by mechanical considerations. The fact that in the lower orders the convex or concave condition is constant for individual veins helps in determining their homologies.

The hypothetical primitive venational pattern recognized here is shown in Fig. 35 which also indicates the nomenclature and abbreviations in common use. The *costa* (*C*) is unbranched and convex while the *subcosta* (*Sc*) is rarely branched and concave. The *radius* (*R*) is typically 5-branched: its main stem is convex and divides into two, of which the first branch (R_1) passes directly to the wing-margin: the second branch or *radial sector* (*Rs*) is concave and divides into four veins (R_2 to R_5). The *media* (*M*) divides into an *anterior media* (*MA*), which is convex and 2-branched (MA_1, MA_2), and a concave *posterior media* (*MP*), which is 4-branched (MP_1 to MP_4). The *cubitus* (*Cu*) divides into two main branches, the first cubitus (Cu_1) being convex and the second cubitus (Cu_2) concave: the first cubitus may subdivide into anterior

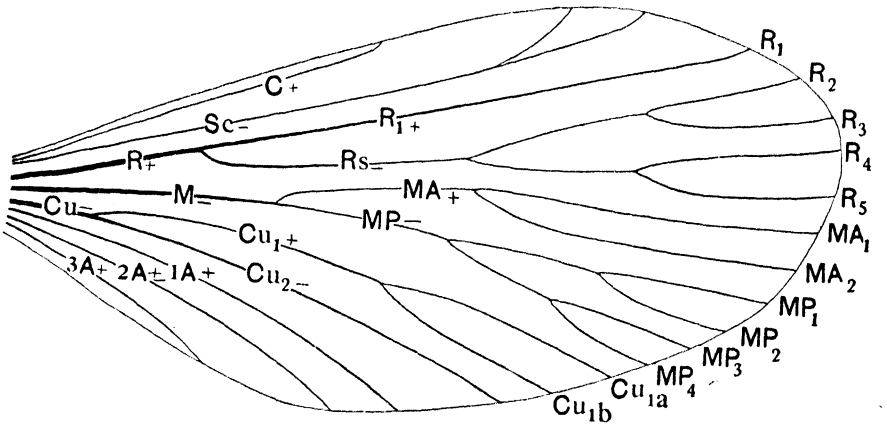


FIG. 35.—Hypothetical primitive type of venation (for reference lettering vide p. 45) (convex veins +, concave veins −)

(Cu_{1a}) and posterior (Cu_{1b}) veins. There follow three *anal veins* (1*A* to 3*A*) which are usually convex, or 2*A* may be concave.

In many insects there are two strongly convex veins, viz.: R_1 and Cu_1, which are easily noted and therefore facilitate the identification of the other veins. A complete media is found in many Palaeozoic fossil insects and in the Ephemeroptera among recent forms. For the most part *MA* atrophies and consequently the media in recent insects is generally *MP*, although it is usually designated by the symbol *M*. The Odonata and Plecoptera, however, are an exception in that they retain *MA* and not *MP*, while further research is needed into the constitution of the media in other Orthopteroid insects. The anal veins are extremely variable and in wings with a reduced anal area one or more are atrophied. On the other hand, in insects with a well-developed anal lobe the anal veins may be freely branched, probably through subdivision of 2*A*. It may be noted that some modern authorities denote by *MA* and *MP* the two main branches of the posterior media, while Cu_1 and Cu_2 are sometimes also known as *CuA* and *CuP* respectively. Forbes (1933) and Snodgrass (1935) have introduced changes in the nomenclature of the cubito-anal veins which do not seem to be widely accepted while Vignon (1929) has an unorthodox modification of the Comstock–Needham system.

Deviation from the primitive venational type has occurred in two ways, i.e., by reduction and by addition. In many insects the number of veins is less than in the hypothetical type, and the reduction has been brought about by the degeneration or complete atrophy of a vein, or of one or more of its branches, or by the coalescence of adjacent veins. Atrophy explains the presence of only a single well-developed anal vein in *Anisopus* (Fig. 36) and other Diptera, while the occurrence in this genus of a single vein R_{2+3}, in the place of the two originally separate veins R_2 and R_3 is due to coalescence. Similarly R_4 and R_5 have coalesced, and the single vein thus formed may be conveniently referred to under the abbreviation R_{4+5}. Coalescence takes place in two ways: the point at which two veins diverge may become gradually pushed outwards nearer and nearer the margin of the wing until the latter is reached, and only a single vein remains evident. In the second method, the apices of the two veins may approximate, and ultimately fuse at a point on the wing-margin: coalescence of this type takes place inwardly towards the base of the wing. The first type is well exhibited in the case of the radial veins of *Anisopus*, while the second method is exhibited in the apical fusion of $1A$ and Cu_1, in *Tabanus* (Fig. 37). The homology of a particular vein is often difficult to determine, and resort has to be made to

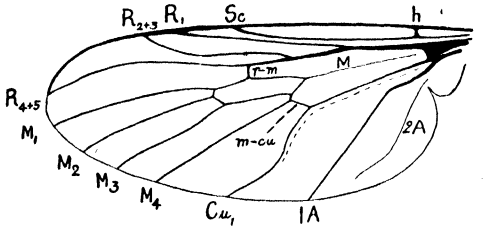


FIG. 36.—Wing of *Anisopus punctatus*. (For explanation of lettering, vide p. 45)

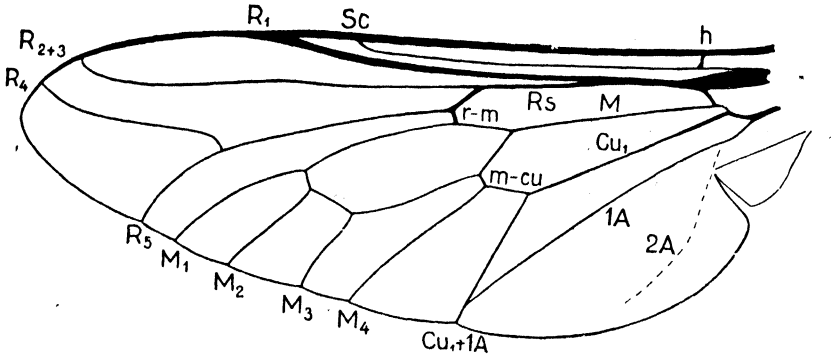


FIG. 37.—Wing of *Tabanus*

comparison with allied forms (including fossils), which exhibit transitional stages in reduction, or to a study of the pupal tracheation.

In cases where an increase in the number of veins occurs, the multiplication of the latter is due either to an increase in the number of branches of a principal vein, or to the development of secondary longitudinal veins, between pre-existing veins. In no instance is there any increase in the number of principal veins present. For a more detailed acquaintance with the various modifications of the wing-veins the textbook of Comstock (1918) should be consulted.

In the wings of certain of the most generalized insects, such as the fossil

Palaeodictyoptera, an irregular network of veins is found between the principal longitudinal veins, but no definite cross-veins are present (Fig. 38). To this primitive meshwork Tillyard (1918a) has given the name *archedictyon*. It appears to have undergone suppression in the Holometabola, though it is very probably homologous with the still existing dense reticulation present in certain orders of Exopterygota such as the Odonata. Needham (1903) from his studies of the wings of the latter order has discussed the transformation of such an irregular network into regular transverse veins, and reference to Fig. 38 is sufficient to explain his views as to the origin of the latter. Transitional stages in the evolution of definite cross-veins may also be observed in wings of the more specialized Palaeodictyoptera and among living Orthoptera, where both irregular and definite cross-veins occur in the same wing. According to Tillyard, however, true cross-veins are later developments; and they are never preceded by tracheae and are almost always devoid of macrotrichia. Veinlets, on the other hand, are primitive and constitute the finer twigs of a principal vein: they are preceded by tracheae and carry macrotrichia (Fig. 39). Whether the archedictyon arose in connexion with preceding tracheae in the wing-rudiment, or independently, is unknown. It is probable, therefore, that homologous cross-veins do

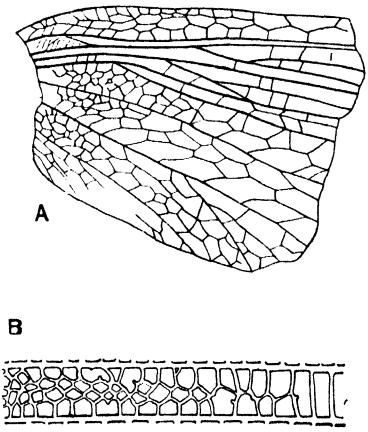


FIG. 38.—A. Portion of a wing of a Carboniferous insect (*Hypermegethes*) showing archedictyon. *After* Handlirsch. B. Diagram illustrating the evolution of regular cross-veins. *After* Needham

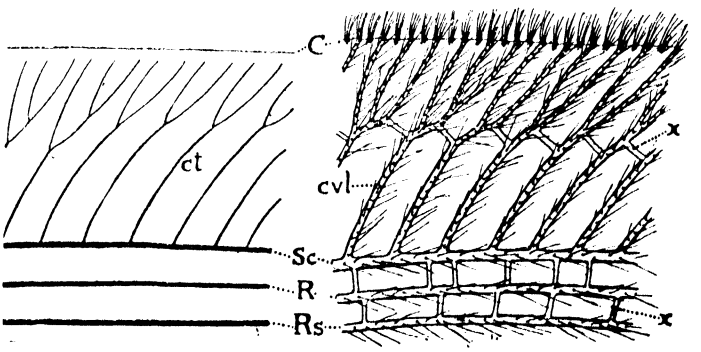


FIG. 39.—Portion of costal area of fore wing of *Psychopsis elegans* with the corresponding tracheation (to the left) of the pupal wing

C, costa; *ct*, tracheae preceding the costal veinlets; *cvl*, costal veinlets; *x*, cross-veins; *R*, radius; *Rs*, radial sector; *Sc*, subcosta. *After* Tillyard, *Proc. Linn. Soc. N.S.W.* 43.

not exist in many orders: their positions, however, in some cases are so constant that analogies, if not homologies, can be traced and similar names are applicable. The following cross-veins are the most important and their symbols are given in brackets.

The *humeral cross-vein* (*h*) extending from the subcosta to the costa, near the humeral angle of the wing.

The *radial cross-vein* (*r*) extending from R_1 to the radial sector (R_s).

The *sectorial cross-vein* (*s*) extending from the stem R_{2+3} to R_{4+5} or from R_3 to R_4.

The *radio-medial cross-vein* (*r–m*) extending from the radius to the media, usually near the middle of the wing.

The *medial cross-vein* (*m*) extending between M_2 and M_3.

The *medio-cubital cross-vein* (*m–cu*) extending from the media to the cubitus.

The veins divide the wings into spaces or *cells*. In the Comstock–Needham system the terminology of the cells is derived from the veins which form their anterior margins. The cells fall into two groups, i.e., basal cells and distal cells. The former are bounded by the main stems of the principal veins, and the latter by the branches of the forked veins. Thus the cell situated behind the main stem of the radius, near the base of the wing, is cell *R*, while the cell behind the first branch of the radius is designated as cell R_1. When two veins coalesce the cell that was between them becomes obliterated. Thus when veins R_2 and R_3 fuse as in *Anisopus* (Fig. 36), the cell situated behind the vein R_{2+3} is referred to as cell R_3, and not cell R_{2+3}, cell R_2 having disappeared. Not infrequently two or more adjacent cells may become confluent owing to the atrophy of the vein or veins separating them. The compound cell is then designated by a combination of the abbreviations applied to the originally separate cells. Thus, a cell resulting from the fusion of cells *R* and *M* is referred to as cell $R + M$. The advantage of this relatively simple system of nomenclature is evident in the case of the so-called discal cell for example. The latter expression has been used in at least four separate orders of insects with reference to a different cell in each instance.

Insect Flight.—Though a satisfactory aerodynamic theory has not yet been developed, normal flight depends on the creation by a propellor-like action of the wings of a zone of low pressure in front of and above the insect and one of high pressure behind and below it, the consequent movement being a resultant of the thrust provided by the insect and forces due to gravity and air-resistance. The skeleto-muscular mechanisms involved in the movements of the wings are outlined on p. 68 but other aspects of flight are discussed here (Magnan, 1934; Chadwick, 1953). Before flight can occur the thoracic flight-muscles must attain a sufficiently high temperature and for this reason some insects carry out preliminary vibrations of the wings before flight, thereby raising the temperature of the muscles to over 30° C., for example, in *Bombus*, and some Lepidoptera (Krogh & Zeuthen, 1941).

Detailed experimental analyses of wing-movements during flight are available for only a few species and probably differ in different insects. Generally speaking, however, in normal flight the wing (or coupled wings) moves in a path such that a point on its surface describes an elongate figure-of-eight with respect to the wing-base, the long axis of the plane of vibration being inclined at an angle to the long axis of the insect (Fig. 40) while the angle at which the surface of the wing is held changes throughout the cycle. The greater part of the propulsive force is generated on the downbeat and the relative sizes of the vertical and horizontal components of this force vary with the angle of the plane of vibration to the horizontal. Thus, in insects which are hovering, the plane of vibration tends to be more horizontal, while the maximum amount of forward movement would be achieved as the plane of vibration becomes vertical. Another mechanism, producing movement in the vertical plane, is indicated by Hollick's (1940) finding that in *Muscina* a reduction in the amplitude of the wing-beat causes the thrust vector to intersect the long axis of the insect's body behind the centre of gravity, so altering the cephalo-caudal couple around this centre. Differences in amplitude between the wing-beats of one side and those of the other cause a lateral turning movement away from the side with the greater amplitude (Stellwaag, 1916). Finally, some insects are also capable of backward flight by shifting the plane of vibration, sometimes so far that the wings actually move upwards on the 'down-beat' (Fig. 40).

There are considerable differences in the speed of different species in flight. *Panorpa communis*, for example, has been recorded to fly at only 0·5 metres per second whereas *Aeshna mixta* can move at 7 metres per second and it is unlikely that any insect exceeds about twice this velocity. The great metabolic activity of insects during flight is indicated by their greatly increased oxygen consumption under these conditions (e.g. Davis & Fraenkel, 1940) and as flight continues uninterruptedly for many hours in some species, a reserve of oxidizable material is required. In *Apis* this is known to be provided by the blood-sugar (Beutler, 1936); in *Drosophila* it consists of glycogen (Williams, Barness & Sawyer, 1943; Wigglesworth, 1949) while in *Eutettix* (Fulton & Romney, 1940) and *Schistocerca* (Krogh & Weis-Fogh, 1951; Weis-Fogh, 1952) it is provided by fat. The complicated movements required in flight are co-ordinated by a number of reflex mechanisms and though much doubtless remains to be discovered in this field a few have been studied in detail. Fraenkel (1932) investigated the reflex stimulation to flight which occurs when the tarsi are deprived of contact with a substratum together with other tactile stimuli to flight perceived by different parts of the body. Continuous flight may also require the stimulus of a moving

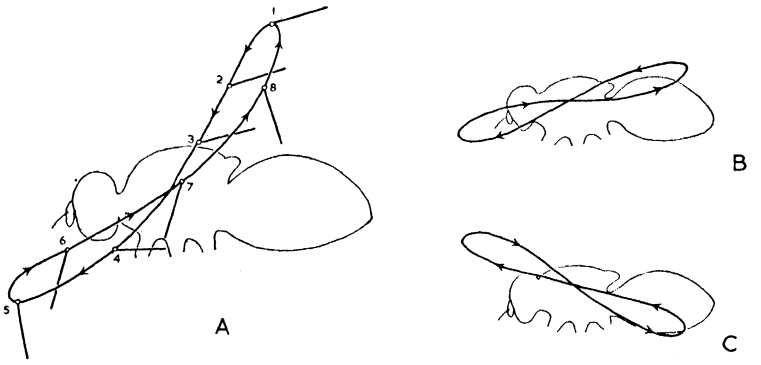


FIG. 40.—Wing movements in insect flight (*partly after* Chadwick, 1953). A, forward flight; 1–8 successive positions of wing. B, hovering. C, backward flight

current of air which in *Schistocerca* is perceived by setae on the head (Weis-Fogh, 1949) and in *Muscina* by the antennae (Hollick, 1940). Other mechanisms ensure an appropriate orientation during flight. Visual stimuli sometimes play a role here and Mittelstaedt (1950) found that Anisopteran dragonflies always fly with the dorsal surface orientated towards a source of light. Reflexes mediated by the antennae were also discovered by Hollick (1940) to modify the path of the wing, and therefore the flight-characteristics, of *Muscina* but the role of the halteres of Diptera and male Strepsiptera in controlling equilibrium during flight is perhaps the best known of these mechanisms (Melin, 1941; Pringle, 1948). Removal of the halteres in *Calliphora* has little or no effect on the beat-frequency, amplitude and duration of flight but markedly affects the stability of the flying insect. The halteres vibrate during flight with the same frequency as the wings but in opposite phase and, by virtue of the relatively heavy terminal knob, they function as gyroscopic organs. Groups of sensilla at the base of the halteres are stimulated by deformations of the integument when the halteres vibrate and the resulting pattern of nervous impulses is modified by the addition of torques due to the turning movements of the fly. The system is apparently most sensitive to movements in the 'yawing' (horizontal) plane, and deviations from the flight-path in this plane can readily be corrected by the fly. There is also some evidence that the halteres act as stimulatory organs, increasing the sensitivity with which the fly reacts to other stimuli during flight (von Buddenbrock, 1919) and in some species removal of the halteres interferes with walking.

For certain physiological properties of the flight muscles, see p. 69.

Origin of Wings.—Two principal theories have been advanced to account for the origin of wings in insects. (1) The *tracheal gill theory* of Gegenbaur which has been upheld by Lubbock, Graber, Lang, Verson,

Woodworth and many others. According to this theory, wings are derived from thoracic tracheal gills, which have lost their original function and become adapted for purposes of flight. Tracheal gills, however, are very inconstant in position, and may be developed from the dorsal aspect of the terga, from the sterna or the pleura, at the apex of the abdomen, on the head and even between the wings. Furthermore, there is good reason to believe that if the tracheal gill theory were upheld, we should have to conclude that the ancestors of winged insects were temporarily aquatic, and thus acquired gills, which subsequently developed into wings when these animals became air breathers for the second time. (2) The alternative theory has been conveniently termed by Crampton (1916) the *paranotal theory*. It is due to Müller (1873–75), and among the supporters of this view are Korschelt and Heider, Packard, Comstock and Needham, Handlirsch and others. It is maintained that wings arose in the first instance as lateral expansions (paranota) of

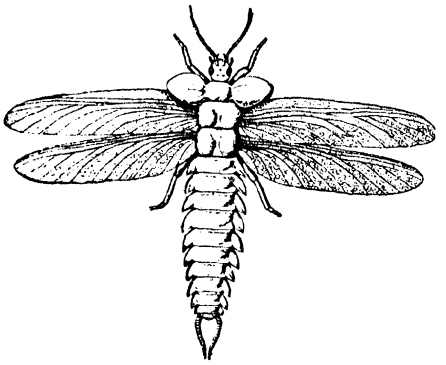


FIG. 41.—A Carboniferous insect (*Stenodictya lobata*) showing prothoracic winglike expansions. From Carpenter, *after* Handlirsch

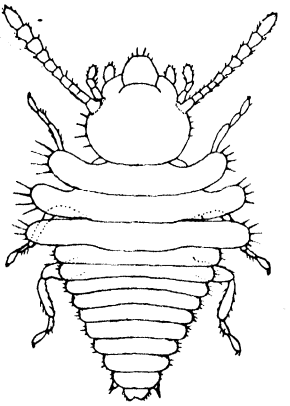


FIG. 42.—A nymph of *Calotermes dilatatus* showing thoracic wing-like expansions. *After* Bugnion, *Bull. Mus. d'Hist. Nat.* 1914

the thoracic terga—a view which is not inconsistent with the facts of wing development among the lower Pterygota. Paranota are found on the prothorax of Palaeodictyoptera (Fig. 41) and other fossil insects. They are also present on nymphs of *Calotermes* (Fig. 42), and in certain Mantids, Lepismatids and Hemiptera, as well as on the abdominal region in various Phasmids. There is, indeed, an inherent tendency towards the development of such structures in diverse groups of insects and in other Arthropods. Furthermore, in at least some cases (e.g. *Lepisma*, Sŭlc, 1927; *Hemiodoecus*, Evans, 1939) the paranotal expansions are supplied with tracheae which are arranged in a pattern somewhat similar to that found in developing wings. During the course of their evolution, it is believed that the tergal expansions became sufficiently large to function somewhat after the manner of gliding planes in insects which possessed a tendency to leap. At a later stage, it is claimed, they acquired direct articulation with the tergal region and developed the power of independent movement.

An extended discussion of these, and other theories which have been put forward to account for the origin of insect wings, is given by Woodworth (1906), Crampton (1916), Sŭlc (1927) and Forbes (1943).

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THE ABDOMEN

(*a*) Segmentation of the Abdomen

THE abdomen (Fig. 2) is composed of a series of segments which are more equally developed than in the other regions of the body. For the most part they retain their simple annular form, the terga and sterna are generally undivided shields, while the pleura are membranous and usually without differentiated sclerites. Each intersegmental sclerite is believed to have fused with the segmental plate behind it. Reduction or special modification of certain of the segments is evident at the anterior and posterior ends of the abdomen, more especially in the latter region, and this specialization increases from the lower to the higher orders. The abdominal segments are sometimes designated *uromeres* and their primitive number as revealed by embryology is eleven, with a terminal non-segmental region or telson. This latter is present in the embryos of certain insects (Fig. 43), but it rarely persists: it is evident, however, in the Protura, while in the few cases where it is found in other insects it is vestigial. The 11th segment is present in the adults of the lower orders where its tergum is represented by the *suranal plate* or *epiproct* above the anus (often fused with the 10th tergum), while vestiges of its sternum are seen in the *podical plates* or *paraprocts* which lie on either side of the anus (Fig. 44). The 10th segment is usually distinct and forms the terminal somite in the higher orders. The Protura differ from all other insects in that the number of abdominal segments increases during post-embryonic development, the young nymphs having only eight segments and a telson. The Collembola are also exceptional in possessing never more than six abdominal segments, either in the embryo or the adult. In most insects the 1st abdominal segment, and more especially its

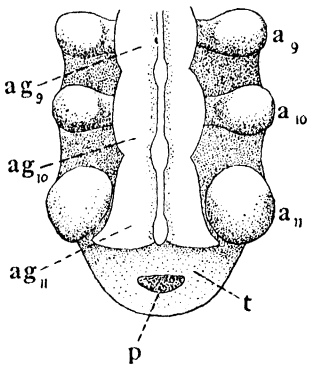


FIG. 43.—Ventral view of last abdominal segments of young embryo of *Gryllotalpa*. From Heymons

a_9 to a_{11}, appendages of 9th to 11th segments and ag_9–ag_{11}, neuromeres of those segments; *p*, proctodaeum; *t*, telson.

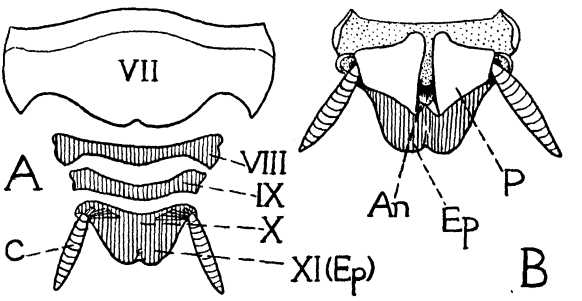


FIG. 44.—Last abdominal segments of *Blatta*. A. Dorsal view. B. Ventral view

An, anus; *C*, cercus; *Ep*, epiproct; *P*, podical plate or paraproct; VII–XI, terga. *After* Snodgrass.

sternum, is reduced or vestigial. Among Apocritan Hymenoptera, however, this segment becomes fused with the metathorax during the change from the larva to the pupa and is known as the *propodeum*, *epinotum*, or *median segment*.

In many Endopterygote insects, more especially certain of those whose eggs are deposited within plant tissues or in other concealed situations, the distal abdominal segments become attenuated and often telescoped, one into the other, to form a retractile tube which is used as an ovipositor. This modification is particularly well exhibited in the Cerambycidae, Cecidomyidae, Trypetidae, Muscidae and other families. A true ovipositor is of an appendicular nature and is dealt with in the next section.

(*b*) Appendages and Processes of the Abdomen

In the embryos of most insects evident rudiments of paired abdominal appendages appear at some stage during development. They are commonly present in relation to each segment, but do not occur on the telson (Fig. 43). A variable number of these appendages may become transformed into organs that are functional during postembryonic life while the remainder disappear. The most conspicuous of the persistent appendages are the *cerci* of the 11th segment, which exhibit wide diversity of form and may even be transformed into forceps, as in the Japygidae and the earwigs. Among the Apterygota the retention of abdominal appendages is a very general feature. They are well exhibited in the Machilidae, where they are present in a reduced condition on the 2nd to 9th segments, and as cerci on the 11th segment. The reduced appendages each consist of a limb-base or *coxite* bearing a distal *stylus* which is sometimes regarded as the vestige of the shaft of a typical walking limb but which may well be a 'coxal epipodite' homologous with the coxal styles of Symphylan or Machilid legs. In many other Thysanura the coxites fuse with the sterna and the styli arise directly from the composite plates so formed (Fig. 45). In most insects, however, the styli disappear and it is probable that the typical abdominal sternum of insects is a plate of composite origin—it is, in fact, a 'coxosternum'. In adult Pterygota the cerci are retained in most of the lower orders but pregenital abdominal appendages are absent and the only other abdominal appendages present are the *gonopods* which enter into the formation of the *genitalia* or external reproductive organs. These are associated with the 8th and 9th segments in the female and with the 9th segment in the male. A completely developed gonopod consists of a coxite bearing a distal stylus, while on its medial border the coxite is produced into a tubular outgrowth or *gonapophysis* (Fig. 46). It may be noted that the term 'gonapophysis' is sometimes also used loosely to denote any genital appendage. The genital aperture is usually located in the membrane immediately behind the 8th or 9th segment.

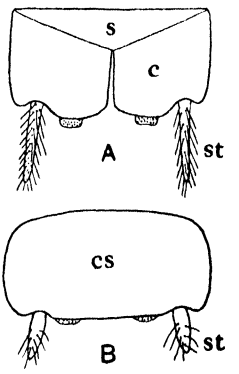


FIG. 45.—Abdominal sterna and appendages of A, *Machilis* and B, *Campodea*

s, sternum; *c*, coxite or limb-base; *cs*, coxosternum; *st*, stylus.

Among immature Pterygote insects, the gills of mayfly nymphs, the abdominal prolegs of Lepidopterous and Symphytan larvae, the terminal appendages of Trichopteran larvae and the gills of Sialoid larvae have all been

regarded as true abdominal appendages (Snodgrass, 1935), but this cannot be regarded as satisfactorily established (Pryor, 1951). Examples of what are certainly secondary abdominal processes include the gills of some other aquatic larvae and nymphs, the pseudopods of Dipterous larvae, the median caudal processes of Thysanura and Ephemeroptera and the copulatory organs on the 2nd abdominal segment of the Odonata.

The *female genitalia* consist typically of three pairs of valves which collectively form the *ovipositor* or egg-laying organ. Their degree of development

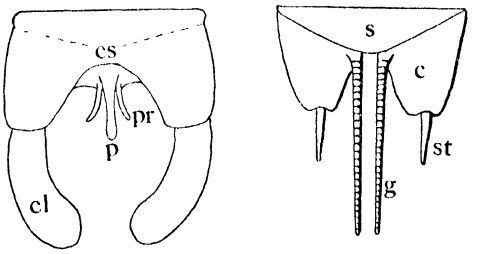


FIG. 46.—Left: Diagram of typical male genitalia. Right: A pair of primitive gonopods

c, coxite; *cl*, clasper; *cs*, coxosternum; *g*, gonapophysis; *p* penis; *pr*, paramere; *s*, sternum; *st*, stylus.

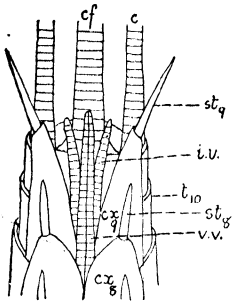


FIG. 47.—Ventral view of the apex of the abdomen of a female *Machilis* showing genitalia

c, cercus; *cf*, median caudal filament; cx_8, cx_9, coxites of 8th and 9th sterna; st_8, st_9, styli; *iv*, *vv*, inner and ventral valves of ovipositor; t_{10}, 10th tergum. *After* Walker, *Ann. ent. Soc. Amer.* 15.

and co-adaptation varies according to the uses to which that organ is subjected. In the Mallophaga and Siphunculata, for example, an ovipositor is absent: in the Dictyoptera its valves are very small and free: in the Tettigoniidae (Figs. 48 and 49) those of one side are held together by tongues and grooves and form, along with their counterparts of the opposite side, an elongate and powerful egg-laying instrument: in most Hymenoptera (Fig. 684) the ovipositor is greatly attenuated and modified for piercing or stinging. A

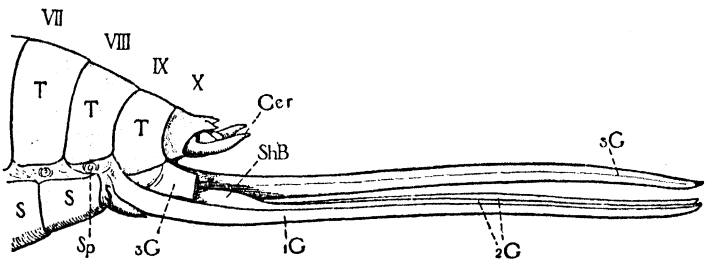


FIG. 48.—Ovipositor of a long-horned grasshopper (*Conocephalus*)

VII–X, terga; *s*, *s*, sterna; *Cer*, cerci; 1*G*, ventral valve; 2*G*, inner valves; *ShB*, bulb-like swelling formed by the fusion of the bases of 2*G*; 3*G*, dorsal valves, the left one is shown as if cut off near its base. *After* Snodgrass, *U.S. Bur. Ent. Tech. Ser.* 18.

typical ovipositor (Fig. 48) consists of (1) a pair of small, anterior valvifers closely associated with the 8th abdominal segment and bearing (2) a pair of anterior (ventral) valves; behind these lies (3) a pair of posterior valvifers to which are articulated (4) a pair of inner (posterior) valves and (5) a pair of dorsal (lateral) valves. The homologies of these structures are not satisfactorily established but it is likely that the anterior valvifers represent the coxites of

the 8th abdominal segment while the ventral valves are formed either from the corresponding gonapophyses or from the styles. The posterior valvifers are probably the coxites of the 9th abdominal segment, the inner valves are the gonapophyses of that segment and the dorsal valves may be the styles or processes of the coxites. In the Thysanura, it may be noted, the gonopods are complete but the coxites and styles do not enter into the composition of the ovipositor, which is formed from two pairs of gonapophyses (Fig. 47).

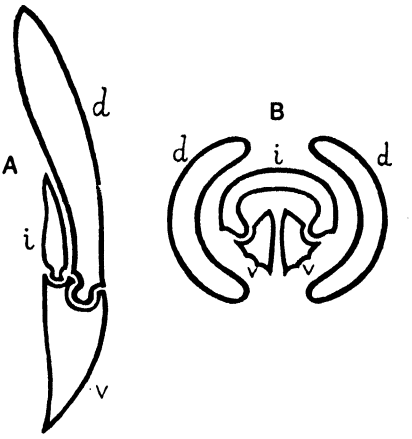


FIG. 49.—Transverse sections of the ovipositor of—A, an orthopteron (*Tettigonia*) *after* Dewitz; B, a hymenopteron (*Sirex*) *after* Taschenberg. The method of interlocking of the valves is shown

d, dorsal valve; *i*, inner valve; *v*, ventral valve.

The *male genitalia* present a wide range of variation and are particularly valuable for separating the genera and species of many groups of insects. When fully developed (Figs. 46 and 50) they consist essentially of a pair of *claspers* which help to grip the female during copulation and between which lies the *aedeagus*. The latter is composed of a *penis* which is usually unpaired (but may be double as in the Ephemeroptera and some Dermaptera) and a pair of more lateral structures which are perhaps best referred to as *parameres*, though this term has been used in several different senses. The homologies of these parts have been the subject of much controversy. The claspers probably represent the coxites and styles of the 9th segment, though in some cases they seem to be composed only of the styles, the coxites having fused with the sternum. Part or all of the aedeagus is held by some authors to be of a secondary, non-appendicular nature but others consider it to be formed by the division of the gonapophyses of the 9th abdominal segment, the two median halves fusing during development to form the penis while the lateral halves constitute the parameres. Yet another view regards it as formed in a similar manner from the gonopods of the 10th abdominal segment. Deviations from the typical structure of the male genitalia are described in the sections dealing with the anatomy of the various orders—they are sometimes supplemented by secondary formations or show various degrees of reduction.

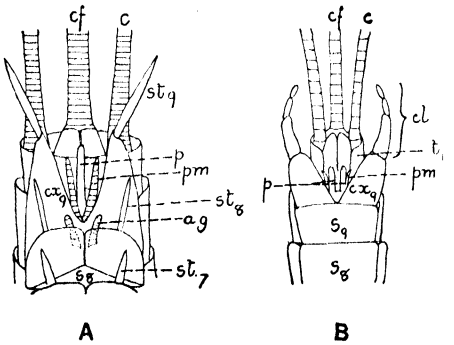


FIG. 50.—Ventral view of the apex of the abdomen of A, *Machilis* and B, an Ephemerid showing male genitalia

ag, accessory genitalia (of 8th segment); *c*, cercus; *cf*, median caudal filament; *cl*, clasper; cx_9, coxite of 9th sternum; *p*, penis (paired in B); *pm*, paramere; s_8 s_9, 8th and 9th sterna; st_7–st_9, 7th to 9th styli; t_{10}, 10th tergum. *After* Walker, *Ann. ent. soc. Amer.* 15.

There is a large literature on the morphological problems presented by the male genitalia. In addition to the more general discussions of Snodgrass (1931; 1933; 1936; 1941), Imms (1937), Qadri (1940), Michener (1944) and Gustafson (1950), there are many specialized papers on development and homologies by, among others,

Pruthi (1924; 1924a; 1925), George (1928), Nel (1930), Metcalfe (1932; 1932a; 1933), Mehta (1933), Peck (1937), Qadri (1949) and Marks (1951).

Literature on the Abdomen and Genitalia

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THE ENDOSKELETON

In certain regions of the body the integument becomes invaginated and greatly hardened, forming rigid processes which serve for the attachment of muscles and the support of certain other organs. This internal framework is termed the *endoskeleton* and its individual parts are known as *apodemes*. The latter arise as invaginations of the body-wall between adjacent sclerites, or at the edge of a sclerite or segment. In some insects the mouths of the invaginations persist throughout life but, more usually, the latter become completely solid through the deposition of cuticular material.

The two most important parts of the endoskeleton are (*a*) the tentorium and (*b*) the endothorax, but endoskeletal structures may be developed in almost any part of the body where muscles are attached.

(*a*) The Tentorium (Figs. 51, 52) (Hudson, 1945–51)

This name is given to the endoskeleton of the head and, in generalized Pterygote insects, it is composed of two or three pairs of apodemes which coalesce at their bases. The functions of the tentorium are—(1) to afford a basis for the attachment of many of the cephalic muscles and, at the same time, to give rigidity to the head; (2) to lend support to the brain and fore intestine; (3) to strengthen the points of articulation of certain of the mouth-parts. The apodemes which enter into the formation of the cephalic endoskeleton are termed the *anterior*, *posterior* and *dorsal arms of the tentorium* according to their positions. The inner ends of these arms fuse with each other and the median skeletal part thus formed is termed the *body of the tentorium*.

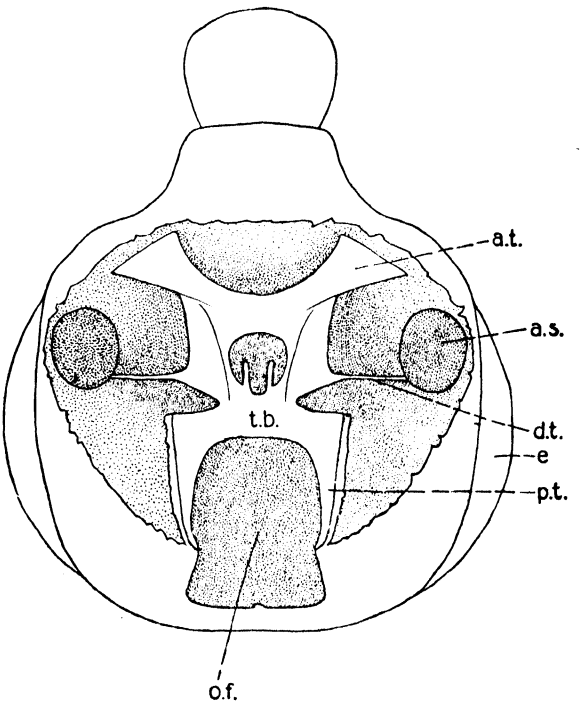


FIG. 51.—Head of *Blatta* with the greater part of frontal wall dissected away to show the tentorium

a.s, antennal socket; *a.t*, *d.t*, *p.t*, anterior, dorsal and posterior arms of tentorium; *e*, compound eye; *o.f*, occipital foramen; *t.b*, body of tentorium.

The **anterior arms of the tentorium.**—The invaginations which form these apodemes usually lie on either side of the clypeo-frontal suture, when the latter is present, and just above the condylar articulations for the mandibles. While in most insects they are manifested externally as mere pits, in many Diptera they are in the form of intracranial tunnels.

The **posterior arms of the tentorium.**—These apodemes are derived from ingrowths situated at the ventral ends of the postoccipital sutures and generally in close relation with the occipital foramen. In some prognathous types they tend to lie more forward on the ventral wall of the head (vide p. 21).

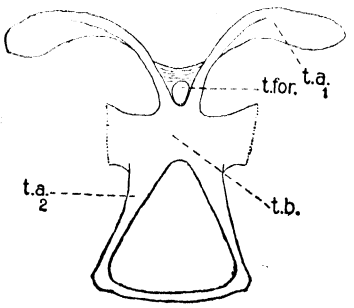


FIG. 52.—Tentorium of a winged termite

t.a$_1$, *ta*$_2$, anterior and posterior arms; *t.b*, body of tentorium; *t.for*, tentorial foramen.

The **dorsal arms of the tentorium.**—These arise not as integumental invaginations but as outgrowths either from the body of the tentorium, or from the bases of the anterior arms. They pass upwards and outwards often to become attached to the head wall near the antennae or eyes. They are generally present in Orthoptera, but in some cases (e.g. *Blatta*) they are tendon-like, while they are often undeveloped in other orders.

The **body of the tentorium.**—This is a median plate which is often large and its shape varies to some extent in conformity with that of the head: thus, in the soldiers of many termites it is elongate, while in the workers it is a relatively narrow band.

It may be noted that the Diplura, Collembola and Protura do not possess a true tentorium (Snodgrass, 1951); it appears in a primitive form in the Machilidae and in certain Lepismatidae it has assumed the typical Pterygote structure.

(*b*) **The Endothorax** (Figs. 53, 54)

Under the term endothorax is included the endoskeleton of the thorax. It is composed of invaginations of the tergal, pleural and sternal regions of a segment and these several apodemes may be conveniently termed the *endotergites*, the *endopleurites* and the *endosternites* respectively.

The **endotergites** or **phragmata** (Snodgrass, 1929) arise as transverse infoldings of the intersegmental sclerites (see p. 32) and as their main function is to provide increased areas of attachment for the dorsal longitudinal muscles they are best developed in winged insects, especially those that fly actively. There are normally three phragmata associated with the intersegmentalia between the pro-, meso- and metathorax and the 1st abdominal segment, but owing to the varied transpositions of the

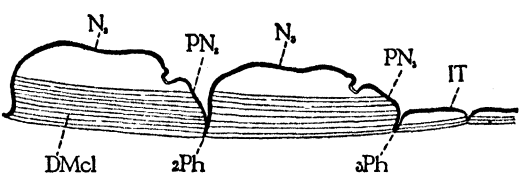


FIG. 53.—Longitudinal section through the dorsal part of the meso- and metathorax and base of the abdomen of a stonefly (*Alloperla*)

DMcl, dorsal longitudinal muscles; *IT*, 1st abdominal tergum; *N*$_2$, mesonotum; *N*$_3$, metanotum; *PN*$_2$, *PN*$_3$, postnotum of meso- and metathorax; *2Ph*, *3Ph*, phragmata. *After* Snodgrass, *Proc. U.S. Nat. Mus.* 39.

intersegmental sclerites (p. 32) the relations of the phragmata to the definitive segmentation differ in different groups of insects. Thus, they are sometimes situated at the front of the segment, between the acrotergite and prescutum and sometimes at the back of a segment, behind the postnotum. Phragmata occupying these two positions have been referred to as pre- and postphragmata respectively and both may be carried by either the meso- or metathorax of some insects; no phragma is ever borne by the prothorax.

The **endopleurites** or **lateral apodemes** are infoldings between the pleurites. In a typical wing-bearing segment of most insects there is a single apodeme on either side formed by infolding along the pleural suture and known as the *pleural ridge*. It terminates in the wing process above, the coxal process below, and often bears an inwardly projecting *pleural arm*. The endopleurites are well developed in the Odonata where, according to Berlese, there are five pairs.

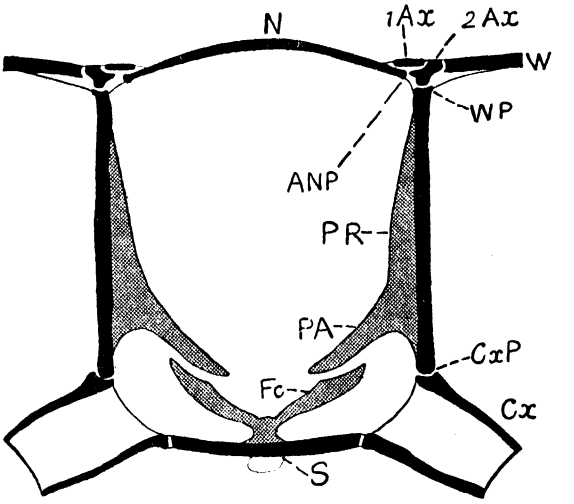


FIG. 54.—Diagram of a section across a wing-bearing segment

ANP, anterior notal wing process; *1Ax*, *2Ax*, 1st and 2nd axillary sclerites; *Cx*, coxa; *CxP*, coxal process of pleuron; *Fc*, furca; *N*, notum; *PA*, pleural arm; *PR*, pleural ridge; *S*, sternum; *W*, wing; *WP*, wing process of pleuron. *After* Snodgrass, *Proc. U.S. Nat. Mus.* 36.

The **endosternites** are typically formed of a pair of apophyses arising from pits on the eusterna between the basisternum and sternellum. Frequently, however, there is also an ingrowth of the sternum near their origin so that they are carried inwards and the whole forms a Y-shaped structure, the *furca*, whose internal arms may become fused with the pleural arms or are connected with them by short muscles. In many generalized insects there is also a median, unbranched apodeme or *spina* which arises from the intersegmental spinasternum. In the higher orders, the spina is lost or consolidated with the furca. In the Odonata the endosternites are paired, and are inclined so far inwards, towards the median line, that they almost meet over the nerve cord. In the honey bee those of the prothorax fuse to form a supraneural bridge, and the combined meso- and metathoracic endosternites together form a second bridge of a similar character.

(*c*) The Abdominal Endoskeleton

In the abdomen apodemes are developed for the purposes of giving firm bases of origin to certain of the more important muscles. Most of the terga usually present internal ridges or phragmata, as in the thorax, giving attachment to the chief longitudinal muscles. On the ventral aspect sternal apophyses are commonly present and in some cases highly developed. Specialized apodemes may be developed in connexion with the ovipositor and the male copulatory organs.

Literature on the Endoskeleton

N.B. There is little special literature dealing with the endoskeleton. Reference may be made to the following and to the more general papers listed under the sections dealing with the three main regions of the body.

Hudson, G. B. (1945–51). Studies in the comparative anatomy and systematic importance of the Hexapod tentorium. I–IV. *J. ent. Soc. sthn. Africa*, **8**: 71–90, 10 figs.; **9**: 99–110, 7 figs.; **11**: 37–49, 8 figs.; **14**: 3–23, 12 figs.

Snodgrass, R. E. (1929). The thoracic mechanism of a grasshopper and its antecedents. *Smithson. Misc. Coll.*, **82**: 111 pp., 54 figs.

—— (1951). *Comparative studies on the Head of Mandibulate Arthropods.* Ithaca, N.Y., 118 pp., 37 figs.

THE MUSCULAR SYSTEM

THE muscles of insects are, for the most part, translucent and either colourless or grey, but the wing muscles frequently exhibit a yellow, orange or brown tinge. Unlike vertebrate muscles, the fibres of both the somatic (skeletal) and splanchnic (visceral) muscles of insects are clearly cross-striated, though it has been asserted that unstriated fibres occur in the heart and the peritoneal layer of gonads and gut. Insect muscles differ fundamentally from those of the Annelida not only in histological structure, but also in the fact that they are never incorporated with the layers of the body-wall to form a dermo-muscular tube.

In the case of most of the somatic muscles, and those of the appendages in particular, one of the extremities of a muscle is attached to a relatively stationary skeletal part and the other is attached to the region or organ which is movable. The attachment to the stationary base is the *origin* and that to the movable part is the *insertion* of the muscle. In many instances the fibres of a muscle are directly fixed into the parts which serve as the origin and insertion. In others sclerotized cords, bands or integumentary invaginations known as *apodemes* intervene between the points of attachment and the actual muscle as, for example, in the muscles of the mandibles.

(*a*) Histology of the Muscles (Fig. 55)

The somatic muscles are fibrous structures, each fibre comprising a number of longitudinally directed myofibrils or sarcostyles embedded in a nucleated matrix, the sarcoplasm, which may form a peripheral sheath or sarcolemma. Each myofibril is composed of contractile protein chains differentiated longitudinally into a number of regions which, because they occur at the same level in adjacent fibrils, give to the whole fibre its characteristic cross-striated appearance (Fig. 55). In the simplest case, each fibril is composed of alternating light (isotropic) and dark (anisotropic) portions, so that the fibre shows an alternation of light and dark discs. In others, the light disc of the fibre is traversed by a dark line—the telophragma or Krauss's membrane—which was thought at one time to be a discrete septum dividing the fibre into sarcomeres but which, like the other structures mentioned below, has also been interpreted as an optical effect at the junction of zones of different refractile properties. In yet a third type of fibre there is also present in the middle of the dark disc a paler stripe (the median disc or Hensen's line) which, in a fourth type, is traversed by a dark line (the mesophragma) while one or more accessory discs run across the light disc. When a muscle is stimulated to contract (normally by receipt of a motor impulse from the central nervous system), its component fibres shorten through a reduction in the length of the anisotropic parts of the fibrils.

Several types of muscle fibres are found among different insects (Fig. 55).

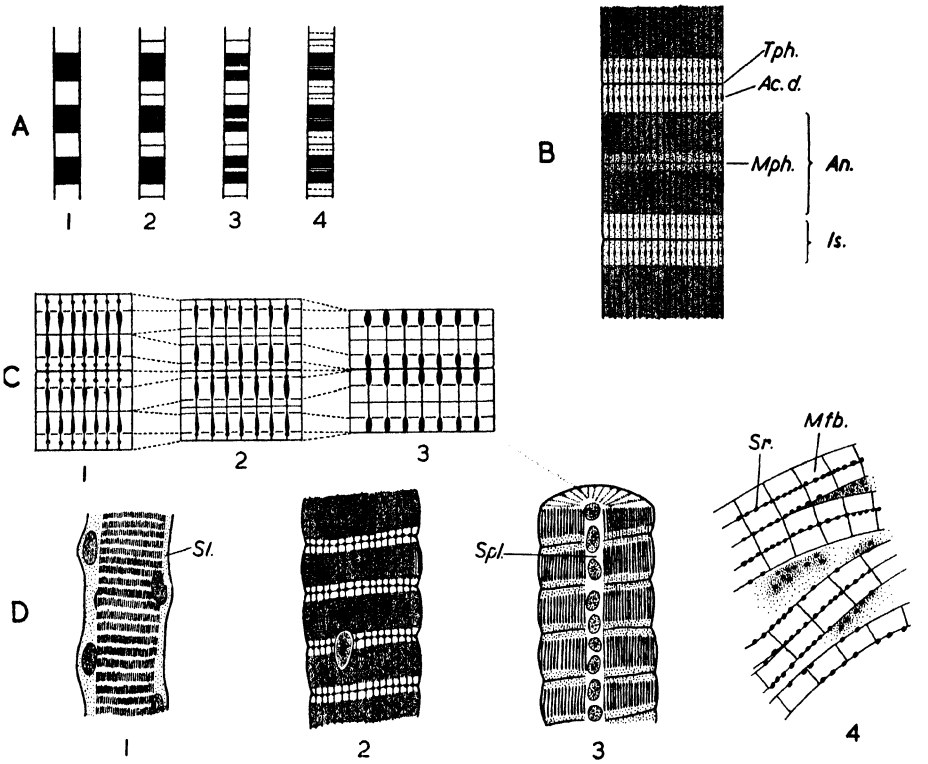


FIG. 55.—Histology of insect muscle. A. Various types of cross-striation in individual myofibrils (*after* Plate). B. Diagram of striated fibre. C. 1–3, stages in fibre contraction, showing reversal of striation. D. Types of insect muscle: 1, from larva of *Apis*; 2, from leg of *Melolontha*; 3, tubular muscle from *Apis* leg; 4, fibrillar flight muscles of *Apis* (B–D *after* Snodgrass, 1925)

Ac.d, accessory disc; *An*, anisotropic zone; *Is*, isotropic zone; *Mfb*, myofibril; *Mph*, mesophragma; *Sl*, sarcolemma; *Spl*, sarcoplasm; *Sr*, sarcosome.

Thus, in many larvae and among Apterygota the sarcostyles are surrounded by a thick layer of sacroplasm containing the nuclei (Snodgrass, 1925). This same general type of fibre is present in the leg and abdominal muscles of beetles and other insects, only the sarcoplasm is greatly reduced and the sarcostyles are usually more numerous. Among adult Hymenoptera and Diptera the fibres are tubular in character with the sarcostyles disposed radially around a central core of sarcoplasm in which are embedded the nuclei (Kielich, 1918; Snodgrass, 1925). The indirect wing muscles of the bee and other insects have exceptionally large fibres which are readily separated apart and the sarcolemma is usually wanting, while the nuclei are either peripheral or embedded in the body of the fibre (Jordan, 1919–20; Morison, 1927–28). Such fibres have a rich tracheal supply and lying in regular rows between the sarcostyles are deeply-staining bodies or sarcosomes which represent sites of cytochrome localization (Levenbook, 1953).

The visceral muscles of insects exhibit a totally different structure from those of vertebrates and, in their striated appearance and frequent tendency to branching, they bear a resemblance to cardiac muscle (e.g. Maziarski, 1927–31). The detailed structure of insect muscle and its interpretation are dealt with in papers by Janet (1895), Jordan (1919–20), Morison (1927), Cremer (1934), Loreti (1940, 1940a) and Korn (1943).

The nature of the attachment of muscles to the cuticle has been much discussed (Richards, 1951). In all cases it appears that the sarcolemma of the muscle is continuous with the basement membrane of the hypodermis. In certain instances the muscle abuts against unmodified hypodermal cells but more frequently the site of attachment is marked by fibrillar, non-striated

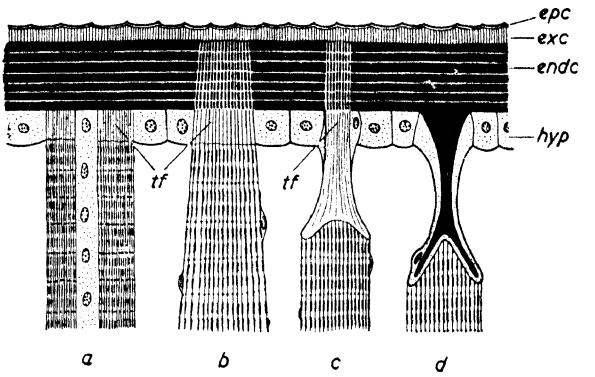


FIG. 56.—Diagram illustrating types of connexions between muscles and cuticle (*after* Weber, 1949)

endc, endocuticle; *epc*, epicuticle; *exc*, exocuticle; *hyp*, hypodermis; *tf*, tonofibrillae.

structures (tonofibrillae) which extend through or between the hypodermal cells and often also traverse the procuticle (Fig. 56). The tonofibrillae closely resemble the cuticular fibrils formed at the attachments of chordotonal organs to the cuticle and are probably not directly continuous with the myofibrils though the two sets of structures may interlace at their junction and the whole system presumably serves to anchor the muscles more firmly to the integument. The chemical nature of the tonofibrillae is uncertain, but they may be intra-hypodermal cuticular formations.

(*b*) Arrangement of the Muscles (Myology) (Figs. 57 and 58)

In general arrangement the muscular system corresponds with the segmentation of the body and is exhibited in its least modified condition in some Apterygota, the lower Pterygota and many larvae. The number of muscles is generally very great and may even reach about 2,000 in larvae of the Lepidoptera. With few exceptions, the somatic muscles are paired, thereby conforming to the general bilateral symmetry of the body, and the names of the muscles generally indicate their origins and insertions, or their functions. The splanchnic muscles, on the other hand, usually exhibit no such symmetry and, as they do not come under the general category of myology, they are dealt with in the sections devoted to the different internal organs.

Although detailed studies of the musculature of several types of insects are available, the homologies of the various muscles are often difficult to determine and no uniform terminology has been evolved. The points of attachment of apparently homologous muscles also vary to some extent in different insects, and the subject of comparative myology is not sufficiently advanced for general treatment. The principal muscles of orthopteroid insects, taken as typical of the lower forms, are emphasized below, but to deal adequately with all those present would encroach upon more space than is

available and demand a wealth of illustration. On account of the musculature exhibiting its most generalized condition in the abdomen, the myology of this region will be considered first and the cephalic muscles last.

A. The **Abdominal Muscles.**—The principal muscles of a typical abdominal segment may be grouped into the following series, simplified and altered somewhat from Snodgrass (1935).

(*a*) LONGITUDINAL.—These may be divided into (*a*) *tergal* and (*b*) *sternal* longitudinal muscles. In each case they run between the intersegmental folds or antecostae of successive segments. Acting together, the two groups serve as retractors by telescoping the abdomen. Acting alone, the sternal muscles curve the abdomen downwards and the tergals straighten it or bend it upwards.

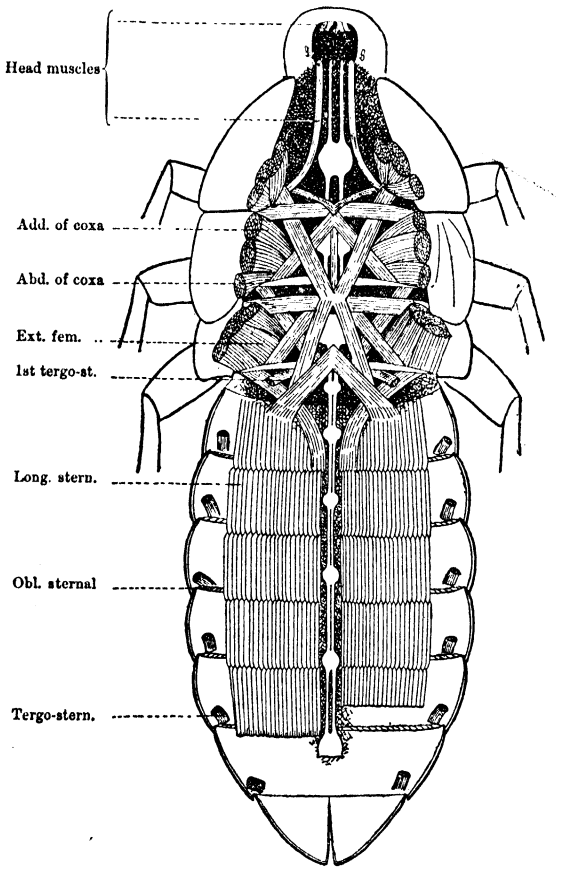


FIG. 57.—Muscles of the ventral wall of a cockroach, with the nerve-cord. *After* Miall and Denny

(*b*) LATERAL.—These typically run dorsoventrally and are both inter- and intrasegmental in position. They are usually *tergosternals*, but when distinct pleurites are present there may also be *tergopleural* and *sternopleural* muscles. By contraction they tend to compress the segment and are therefore important in respiratory movements.

(*c*) TRANSVERSE.—These lie internal to the longitudinals on both ventral and dorsal sides and are better known as the muscles of the dorsal and ventral diaphragms (see p. 151).

In addition there are special muscles concerned with the movements of the genitalia, cerci and spiracles.

B. **Thoracic Muscles.**—The muscles of a typical alate segment are set out below, following a simplified version of Snodgrass's (1935) scheme, but it should be noted that the prothorax differs in the absence of some flight-muscles.

(*a*) LONGITUDINAL. As in the abdomen, these are divisible into *tergal* and *sternal* groups, the former being important indirect flight-muscles.

(*b*) DORSOVENTRAL. Two main groups occur here, the *tergosternals*, which are the principal levators of the wing (acting anatagonistically to the longitudinal tergals) and the *tergocoxal* muscles, which act as the tergal promotors and remotors of the leg.

(*c*) PLEURAL. Three sets of pleural muscles may be distinguished. The *tergopleural* muscles are very variable in development and include the axillary muscles; the *pleurosternals* are short fibres linking the pleural and sternal apophyses while the *pleurocoxals* act as abductors of the coxae.

(*d*) STERNAL. These include two muscle groups. The *sternocoxals* are the sternal promotors and remotors of the leg while the *lateral intersegmental* muscle runs from the sternum to the pleuron or tergum of the succeeding segment and is best developed in larval forms.

(*e*) INTRINSIC LEG MUSCLES. In addition to the various extrinsic leg-muscles mentioned above, whose function it is to move the whole limb, there are also muscles lying within the segments of the leg. They include the levator and depressor of the trochanter, tibia and tarsus and the levator of the pretarsus.

As well as these, there are the spiracular muscles and the epipleural muscles, the latter inserting on the subalare and basalare.

C. **Cephalic Muscles.**—The principal muscles of the head may be divided into (*a*) cervical muscles, (*b*) muscles of the mouthparts, and (*c*) muscles of the antennae.

(*a*) The CERVICAL MUSCLES. —These control the movements of the head and are classified into levators, depressors, retractors, and rotators according to their function. They take their origin from the prothorax and cervix and are inserted into the tentorium and epicranium.

(*b*) The MUSCLES OF THE MOUTHPARTS. —Associated with the labrum are (Cook, 1944):

1. The *labral compressors*, running between the dorsal and ventral surfaces of the labrum.

2. The *posterior* labral muscles which run from the tormal sclerites of the labrum to the wall of the head.

3. The *anterior labral* muscles (retractors) which run from the anterior margin of the labral base to the wall of the head.

The mandibular muscles (Snodgrass, 1950) include:

4. The *dorsal abductors* which originate on the upper lateral part of the epicranium and insert each on an apodeme connected with the outer, basal region of the mandible.

5. The *dorsal adductors* have an extensive origin on the posterodorsal part of the head and each inserts on an apodeme connected with the inner, basal region of the mandible.

6. The *ventral adductors* are present only in the Apterygotes and some lower Pterygotes.

The principal maxillary muscles are as follows:

7. *Dorsal basal* muscles arising on the dorsal part of the head and forming the *anterior* and *posterior rotators* of the cardo and the *cranial flexor of the lacinia.*

8. *Ventral basal muscles* which are inserted on the cardo and stipes and which originate on the tentorium in most Pterygotes and on the hypopharyngeal apodemes in the Apterygotes.

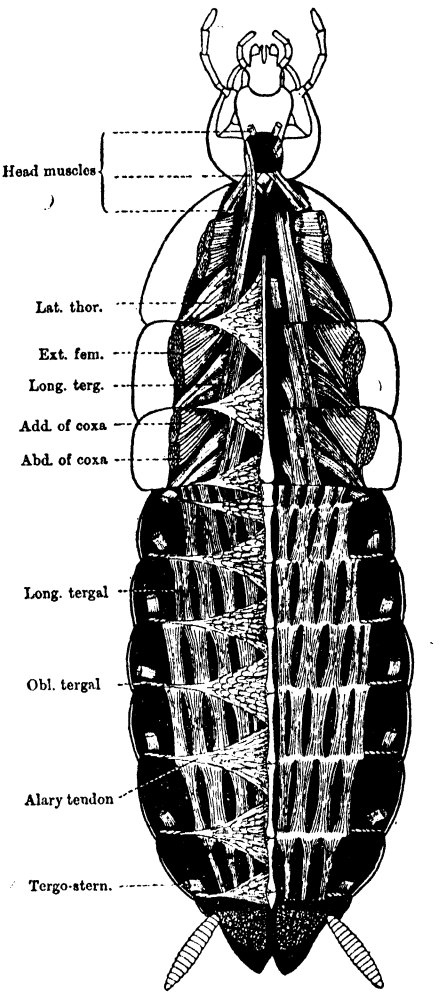


FIG. 58.—Muscles of the dorsal wall of a cockroach, with the heart and pericardial tendons. *After* Miall and Denny

9. *Stipital muscles.* These all originate on the stipes and include the *levator and depressor* of the palp, the *flexor* of the galea and the *stipital flexor of the lacinia.*

10. The *intrinsic palp muscles.*

The muscles of the labium are:

11. *Extrinsic labial muscles.* These arise on the tentorium or cranial wall and insert on the prementum. They correspond to the ventral basal muscles of the maxilla.

12. *Median labial muscles.* When present, these run from the back of the prementum to the postmentum and have no homologues in the maxilla.

13. *Labial salivary muscles.* There are usually two pairs, arising on the prementum and converging on the labial wall of the salivarium near the opening of the salivary duct.

14. *Muscles of the endites and palps.* From the prementum there run the *levator* and *depressor* muscles of the palps and a *flexor* of each glossa and paraglossa. These are homologues of the stipital muscles of the maxilla but it should be noted that the glossae possess no muscles corresponding to the cranial flexors of the laciniae.

15. *Intrinsic palp muscles.*

Inserted on the suspensorium of the hypopharynx there are typically the *hypopharyngeal adductors of the mandible* and two pairs of *frontal* muscles (the so-called 'retractors of the mouth angles').

(*c*) MUSCLES OF THE ANTENNAE (Imms, 1939).—These are:

1. *Extrinsic antennal muscles.* A *levator* and, usually, two *depressors* are inserted on the base of the scape. They arise from the dorsal and anterior arms of the tentorium or from the dorsal arm alone or from the wall of the head.

2. *Intrinsic antennal muscles.* In all insects with normally developed antennae there is a pair of muscles arising in the scape and inserted on the base of the pedicel. In the Collembola and Diplura similar muscles also occur in all other segments except the last, but in the Thysanura and Pterygota the flagellar segments are devoid of muscles.

D. **Muscles of Flight.**—The flight of insects has been alluded to on p. 48 and the muscular mechanisms involved have been discussed by Stellwaag (1910), Ritter (1911), Snodgrass (1927, 1930) and others.

The flight movements are effected by two sets of muscles—*indirect muscles* and *direct muscles* (Figs. 59, 60). The *indirect muscles* are usually the largest in the body,

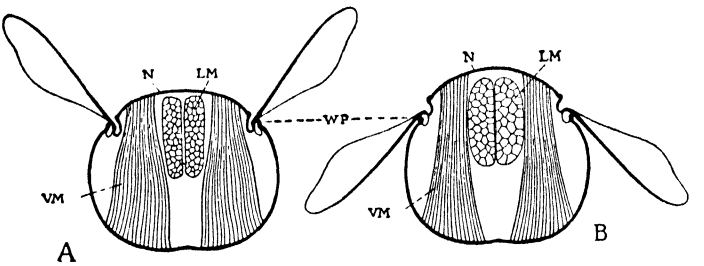


FIG. 59.—Diagrammatic cross-section of thorax of a bee through pleural wing process *WP*

A, wings thrown upward by depression of tergum *N* caused by contraction of vertical muscles *VM*. B, wings thrown downward by elevation of tergum *N* caused by contraction of longitudinal muscles *LM*. *After* Snodgrass.

and are attached to the thorax and not to the wing-bases. In most insects they consist of two groups of muscles: (1) a pair of dorsoventral muscles by whose contraction the tergal region of the thorax is depressed, with the result that the wings are forced upwards owing to the peculiar nature of their articulation with the thorax; (2) a pair of longitudinal muscles by whose contraction the tergal region becomes arched upwards which results in the wings being forced downwards. The rapid alternate contraction of these two groups of muscles consequently raises and lowers the wings by their action upon the dorsal wall of the thorax. The *direct muscles* (Fig. 60) are typically the epipleural and axillary muscles and generally consist of four pairs—(*a*) the 1st anterior extensor arising usually from the sternal region and attached to the basalar sclerite (p. 39); (*b*) the 2nd anterior extensor arising from the rim of the coxa, just in front of its pleural articulation, and similarly inserted into the basalar sclerite; (*c*) the posterior extensor arising from the rim of the coxa, just behind its pleural articulation, and inserted into the subalar sclerite; (*d*) the flexor arising from the pleural ridge and inserted into the 3rd axillary sclerite. While the indirect muscles are alternately elevating and depressing the wings, the forward and backward movements of the latter are effected by muscles (*a*), (*b*) and (*c*), while muscle (*c*) also aids in depressing the wing. These same muscles, furthermore, bring about the turning of the wing on its long axis. The complete mechanics of the wing during flight is a complex process. During the downstroke the wing is pulled downwards and forwards

while its anterior margin is deflected and its posterior area upraised. During the upstroke the wing is pulled upwards and backwards while the posterior area, at the same time, is deflected. The flexor muscle is concerned with whatever folding the wing undergoes during flexion and in drawing the wing towards the side of the body.

Though it is often asserted (Lendenfeld, 1881; Snodgrass, 1927) that the wings of the Odonata are moved solely by direct muscles, the work of Clark (1940) shows that both direct and indirect muscles are involved, though the former are far more important than in other insects.

In addition to works cited above, the following include some of the more important descriptions of musculature: Barth (1937), Bauer (1910), Carbonell (1947), Das (1937), Dirkes (1928), DuPorte (1920), Forbes (1914), Ford (1923), Korn (1943), La Greca (1939), Leverault (1939), Maki (1935; 1936; 1938), Maloeuf (1935), Marquardt (1939), Morison (1927–28), Samtleben (1929), Snodgrass (1942), Voss (1905) and Weber (1928; 1935).

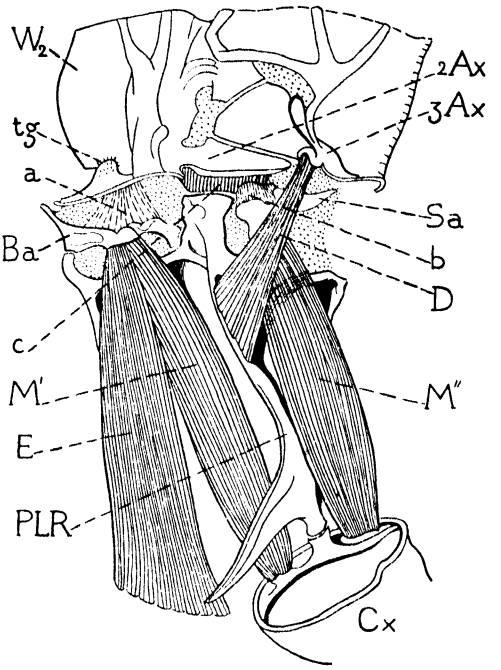


FIG. 60.—Direct wing muscles of mesothorax of a grasshopper

2Ax, 2nd axillary sclerite and *c*, its ventral plate; *3Ax*, 3rd axillary sclerite; *Ba*, basalar sclerites; *Cx*, coxa; *D*, flexor muscle; *E*, 1st anterior extensor muscle; *M'*, 2nd anterior extensor muscle; *M''*, posterior extensor muscle; *PLR*, pleural ridge; *Sa*, subalar sclerite; *tg*, tegula; W_2, fore wing, turned upward. Adapted from Snodgrass, 1930.

Physiology of Muscular Tissue.—With the notable exception mentioned below, the physiological properties of insect muscles do not differ greatly from those of vertebrate skeletal muscle, such features as absolute muscular power, chronaxie and the characteristics of the simple contraction (twitch) being of a similar order in the two groups. Though relatively little is known of the biochemistry of muscular contraction in insects, the available evidence (Gilmour, 1953) indicates that, as in other animals, the complex protein actomyosin undergoes contraction at the expense of energy derived from the dephosphorylation of adenosine triphosphate. The energy of the latter system is then immediately replaced by the breakdown of a phosphagen—arginine phosphate, as in most invertebrates—and this in turn is resynthesized at the expense of glycolysis. The resulting pyruvic acid is finally oxidized to water and carbon dioxide through a tricarboxylic acid cycle.

Some insect muscles are capable of both a relatively rapid twitch and a slower, sustained tonic contraction, the two types of response being mediated by separate nerve fibres (Pringle, 1939). Electrical stimulation of isolated muscles produces a twitch which lasts not less than about 0·1 seconds and while such a response may form an adequate basis for certain movements, the relatively long duration of the twitch cannot easily be reconciled with the exceedingly rapid contractions of the indirect flight musculature which may approach 1,000 cycles per second (Chadwick, 1953). Heidermanns (1931) suggested that the flight-muscles are in a state of partial tetanus during flight and in forms like *Aeshna*, with a relatively slow rate of wing-beat, this may provide the complete explanation. It does not, however, cover the case of

Calliphora, where Pringle (1949) has shown that the frequency of contraction of the indirect flight-muscles is not determined by the central nervous system but is directly controlled by the loading on the muscles. This author suggests that the muscles are stimulated by low-frequency impulses from the central nervous system to respond directly to stretching. The resulting twitch is of a duration controlled by the conditions of loading and contraction causes direct stimulation of the antagonistic muscles. The rhythm resulting from repetition of this cycle is therefore myogenic and continues for as long as the muscles remain excited by the inflow of the low-frequency nervous impulses. A similar mechanism operates in the rapid contractions of the tymbal muscle of cicadas.

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THE NERVOUS SYSTEM

I. The General Nervous System

Introduction.—The nervous system, in insects as in other animals, serves as an elaborate connecting link between the sense-organs, which respond to the numerous diverse stimuli provided by the environment, and the effector organs (muscles, glands, etc.) through which the organism reacts to these stimuli in a co-ordinated fashion. The tissues of which it is composed consist of non-nervous, supporting *neuroglia* and the nervous tissue proper which is highly specialized for the rapid conduction of electro-chemical nervous impulses. The essential element of the nervous tissue is the individual nerve-cell or *neurone* which may assume various forms but normally gives off a number of protoplasmic processes which serve to put it in contact with other nerve-cells (by a synaptic junction) or with sensory structures or effector organs. One or more of these processes is usually more highly developed than the others and forms a long conducting fibre or *axon* which generally ends in a group of fine branching fibrils, the number of axons enabling the neurones to be classified as uni-, bi- or multipolar. Functionally, the neurones belong to one of three groups: sensory (afferent) neurones convey impulses inwards from the sense-organs (p. 84), motor (efferent) neurones convey them outwards to the effector organs and association (internuncial) neurones serve as links between the other two types. Over most of the nervous system the neurones are grouped together into nervous centres or *ganglia* (Fig. 61) while the axons from these aggregated cells either form the fibre-tracts of the ganglia or run out, grouped together, as nerves. Neuroglial cells support the ganglia and nerves and they are surrounded by a more homogeneous *neural lamella*, the latter apparently playing a special role in insects (Hoyle, 1953) by forming a barrier between the potassium ions of the haemolymph and the neurones. The axons are generally described as non-medullated (cf. Vertebrates) but surrounding the cytoplasm of the axon is a sheath composed of oriented lipoprotein molecules not unlike myelin (Richards, 1943; 1944). In transverse section, the individual axons are seen to vary considerably in diameter, the motor axons, which are usually fewer in number, sometimes attaining a diameter entitling them to be considered as giant fibres (Power, 1948).

Anatomically it is convenient to divide the insect nervous system into (*a*) the central nervous system, (*b*) the visceral nervous system and (*c*) the peripheral nervous system, but it must be remembered that all three parts are connected with each other.

(*a*) The Central Nervous System

This constitutes the principal divison of the nervous system and is composed of a double series of ganglia which are joined together by means of

longitudinal and transverse strands of nerve fibres (Fig. 61). The longitudinal cords are termed *connectives* and they serve to join a pair of ganglia with those which precede and succeed it. The transverse fibres or *commissures* unite the two ganglia of a pair. Typically there is a pair of ganglia in each segment of the body, but the members of a pair are usually so closely united that they appear as a single ganglion, the commissure being no longer evident. The connectives may be separated and distinct throughout the body as in *Machilis* and *Corydalis*, or in the thorax only as in the Orthoptera, Coleoptera and many lepidopterous larvae, but usually they are so closely approximated as to appear as a single longitudinal cord. In many cases the ganglia of adjacent segments coalesce to form *ganglionic centres*. Two of the latter are always present in the head, and varying degrees of coalescence of the thoracic and abdominal ganglia are revealed by a comparative study of the nervous system in different orders of insects (Brandt, 1880a, etc.).

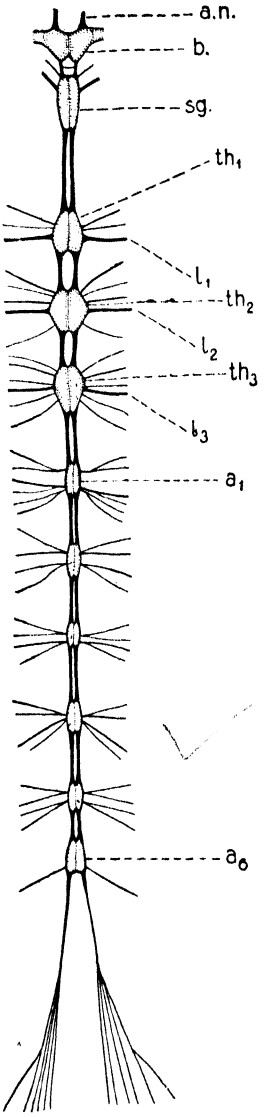


FIG. 61.—Central nervous system of *Forficula*

a.n, antennary nerve; *b*, brain; *sg*, suboesophageal ganglion; th_1–th_3, thoracic ganglia; l_1–l_3, nerves to legs; a_1–a_6, 1st and terminal abdominal ganglia.

Seen in transverse sections, a typical ganglion is invested by a syncytial membrane or epineurium which also secretes the neural lamella. Beneath the epineurium are groups of neurones forming the cortex of the ganglion and enclosing a central medullary substance or neuropile. The neurones are for the most part unipolar and are chiefly evident by their nuclei, the cytoplasm being of relatively small amount. The neuropile is formed by the fine twigs of the axons, held together by a variable amount of neuroglia: when viewed in sections the neuropile presents a punctured appearance owing to the twigs being cut across in large numbers.

The central nervous system is divisible into the brain or cerebral ganglion, the suboesophageal ganglion and the ventral nerve-cord.

1. The BRAIN (Figs. 62–64) lies just above the oesophagus between the supporting apodemes of the tentorium. It is the dorsal ganglionic centre of the head; its nerve-cells are almost entirely association neurones and it is formed by the coalescence of the first three neuromeres in the embryo. This threefold division is maintained in the completed organ which is divided into corresponding regions which are designated the *protocerebrum*, the *deutocerebrum* and the *tritocerebrum* respectively, though the division is not always apparent externally. Among the chief modern writings on the structure of the brain are those of Gejvall (1936), Jawlowski (1936), Malmsten (1939), Hanström (1940), Power (1943), Ehnbohm (1948) and Goossen (1949).

The PROTOCEREBRUM represents the fused pair of ganglia of the preantennary segment. It forms the greater part of the brain and innervates the

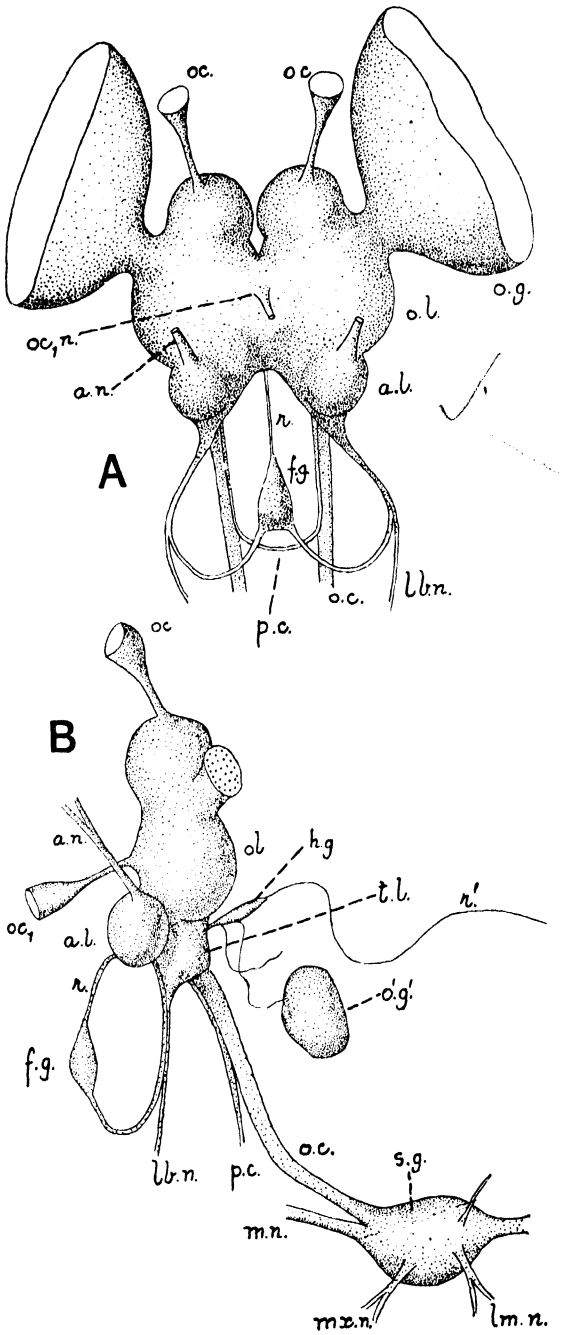


FIG. 62.—Brain and suboesophageal ganglion of a locust (*Melanoplus*)

A, frontal view; B, lateral view. *a.l*, antennary lobe; *a.n*, antennary nerve; *f.g*, frontal ganglion; *h.g*, hypocerebral ganglion; *lb.n*, labral nerve; *lm.n*, labial nerve; *m.n*, mandibular nerve; *mx.n*, maxillary nerve; *oc*, lateral ocellus; oc_1, median ocellus; oc_1n, root of nerve to median ocellus; *o.c*, para-oesophageal connective; *o.g*, optic ganglion; *o'.g'*, oesophageal ganglion; *o.l*, optic lobe; *p.c*, postoesophageal commissure; *r*, recurrent nerve (continued in B as the stomatogastric nerve *r'*); *s.g.*, suboesophageal ganglion; *t.l*, tritocerebral lobe. *After* Burgess, *2nd Rep. U.S. Ent. Comm.*

compound eyes and ocelli. The protocerebrum is divisible into (1) the protocerebral lobes and (2) the optic lobes and the detailed account of their structure given below is based on accounts by Viallanes (1885–88).

(1) The *protocerebral lobes* are fused together along the median line to form a bilobed ganglion. The two lobes are interconnected by a median commissural system termed the *central body*, towards which fibres converge from various parts of the brain. In addition to the central body there are two smaller commissures, viz. the anterior and posterior dorsal. The *anterior dorsal commissure* passes in front of and above the central body. The *posterior dorsal commissure* is a Π-shaped fibre-tract lying behind the former commissure. The most conspicuous formations in the protocerebral lobes are the *mushroom* or *stalked bodies* (corpora pedunculata) which are important association-centres. Each mushroom body rests on the surface of the protocerebrum and is divisible into an outer and an inner lobe. These lobes are each formed of a peripheral layer of nerve cells and a central fibrous tract, the latter being deeply indented to form the *calyx*. The fibres are produced downwards to form the stalk and the two stalks of a mushroom body coalesce further inwards, thus giving rise to the main peduncle which is inserted deeply in the medulla. In the region of the brain between the mushroom bodies, are four small *ocellar lobes* from each of which an *ocellar nerve* takes its origin. The two outer nerves supply the paired ocelli, while the two inner nerves unite just outside the brain to form a single nerve supplying the median ocellus.

(2) The *optic lobes* (*optic ganglia* or *optic tract*) form a complex region of the brain and their degree of development is in direct relation with that of the compound eyes. Each lobe (Zawarsin, 1914; Bretschneider, 1921; Cajal & Sánchez, 1915) consists of three principal zones or tracts of nerve tissues which are connected by a similar number of layers of nerve fibres (Figs. 64 and 89). The *ganglionic layer* or *plate* (*periopticon*) is the zone nearest the eye and is connected with the inner ends of the ommatidia (vide p. 102) by the *layer of post-retinal fibres*. The middle zone is termed the *external medullary mass* (*epiopticon*) and is connected with the ganglionic plate by means of the *external chiasma* which is formed by the crossing of nerve fibres. The inner zone is the internal medullary mass (*opticon*); the latter is united with the preceding zone by means of the *internal chiasma*. The nerve fibres of this layer cross completely in a manner similar to those of the external chiasma. The fibres of the *optic nerve* issue from the inner aspect of the internal medullary mass and divide into anterior and posterior bundles, which pass to the centre of the protocerebrum.

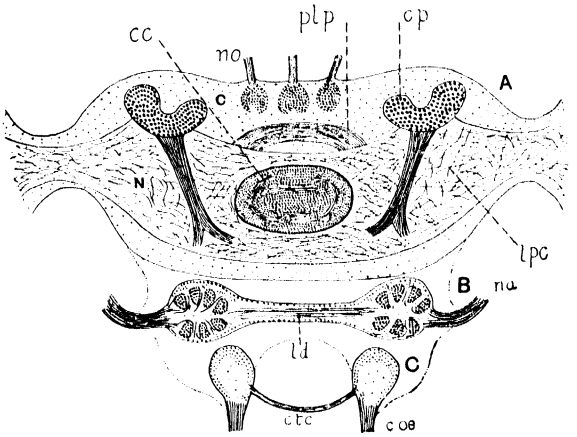


FIG. 63.—Generalized diagram of the three pairs of ganglia forming the brain

A, protocerebrum; B, deutocerebrum; C, tritocerebrum (cortical (cellular) layer); *N*, neuropile. Other lettering as in Fig. 64.

The DEUTOCEREBRUM represents the fused ganglia of the antennary segment. It is chiefly composed of the paired *antennary* or *olfactory lobes* which are prominent swellings situated on the anteroventral aspect of the brain and innervate the antennae.

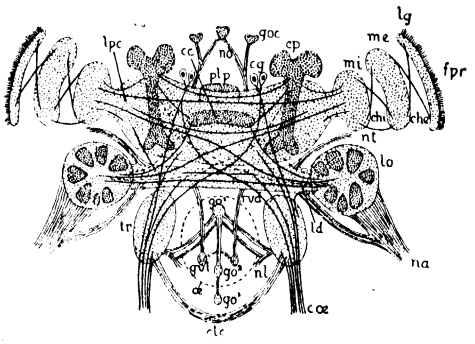


FIG. 64.—Diagram of the brain and visceral nervous system of a cricket (much of the cortical layer has been omitted)

cc, central body; *cg*, ganglion cells; *che*, external chiasma; *chi*, internal chiasma; *coe*, para-oesophageal connective; *cp*, mushroom body; *ctc*, postoesophageal (tritocerebral) commissure; *fpr*, post-retinal fibres; *goc*, ocellar ganglion; go_1, hypocerebral ganglion; go_2, go_3, unpaired visceral ganglia; *gul*, oesophageal ganglion; *ld*, dorsal lobe of deutocerebrum; *lg*, periopticon; *lo*, olfactory (deutocerebral) lobe; *lpc*, protocerebral lobe; *me*, epiopticon; *mi*, opticon; *na*, antennary nerve; *nl*, labral nerve; *no*, ocellar nerve; *nt*, tegumentary nerve; *oe*, outline of oesophagus; *plp*, posterior dorsal commissure; *rvd*, root of oesophageal ganglion; *tr*, tritocerebrum. *After* Viallanes, *Ann. Sci. Nat.* 1893.

The so-called *dorsal lobe* is chiefly represented by a transverse fibrous tract situated above the antennary lobes and serving to connect the latter together. Each half of the dorsal lobe is connected with the protocerebral lobe of the opposite side by means of a chiasma and the antennary lobe is connected with the mushroom body of its side and the central body by the *optico-olfactory chiasma*. Arising from the deutocerebrum are four pairs of nerves as follows: the *antennary nerves* are the longest and most important, and are the sensory nerves of the antennae though in some cases the motor fibres mentioned next are also present in the same nerve; each has two roots, one of which is derived from the antennary lobe of its side and the other from the dorsal lobe. The *accessory antennal nerves* issue from the antennary lobes and are the motor nerves of the appendages concerned. The *tegumentary nerves* are a pair of slender strands arising from the dorsal lobe and passing to the vertex.

The TRITOCEREBRUM is formed by the ganglia of the third or intercalary segment of the head. It is divided into two small widely separated lobes which are attached to the dorsal lobe of the deutocerebrum and receive nerve fibres from the latter. The tritocerebral lobes are joined together by means of the *postoesophageal commissure* which passes immediately behind the oesophagus. They also give origin to (1) the *para-oesophageal connectives* or *crura cerebri* which unite the brain with the suboesophageal ganglion, and (2) the *labro-frontal nerves*. Each of the latter consists of two bundles of fibres, one of which passes to the labrum as the *labral nerve*, and the other forms the root of the frontal ganglion.

2. The **Suboesophageal Ganglion** is the ventral ganglionic centre of the head and is formed by the fusion of the ganglia of the mandibular, maxillary and labial segments. It gives off paired nerves supplying their respective appendages.

3. The **Ventral Nerve-Cord** consists of a series of ganglia lying on the floor of the thorax and abdomen. They are united into a longitudinal chain by means of a pair of connectives which issue from the posterior border of the suboesophageal ganglion. The first three ganglia are situated one in each of the thoracic segments, and are known as the thoracic ganglia; the remainder lie in the abdomen and form the ganglia of that region.

The *thoracic ganglia* control the locomotory organs. Each ganglion gives off two pairs of principal nerves, one of which supplies the general musculature of the segment and the other innervates the muscles of the legs. In the meso- and metathorax an additional pair of nerves is present which controls the movements of the wings.

The *abdominal ganglia* are variable in number; in *Machilis* and in many larvae there are eight ganglia in the abdomen but as a rule there are fewer. The first abdominal ganglion frequently coalesces with that of the metathorax and the terminal ganglion is always composite. The latter is a ganglionic centre formed by the fusion of at least three primitive ganglia. Each abdominal ganglion gives off a pair of principal nerves to the muscles of its segment.

The histological structure of the ganglia of the ventral chain has been studied by Zawarsin (1924a).

(*b*) The Visceral Nervous System

The visceral or sympathetic nervous system is divided into (1) oesophageal sympathetic, (2) ventral sympathetic and (3) caudal sympathetic systems.

1. The OESOPHAGEAL SYMPATHETIC (or STOMATOGASTRIC) NERVOUS SYSTEM is directly connected with the brain and innervates the fore and middle intestine, heart and certain other parts. It is dorsal in position, lying above and at the side of the fore intestine and its structure is described in a wide variety of types by Cazal (1948), two common arrangements being shown in Fig. 65. Typically, a small triangular *frontal ganglion* lies above the oesophagus, a short distance in front of the brain. Anteriorly it gives off a *frontal nerve* which passes to the clypeus, and a pair of lateral roots connect the frontal ganglion with the tritocerebrum. Posteriorly the frontal ganglion gives off a *recurrent nerve* which extends along the mid-dorsal line of the oesophagus and, passing just beneath the brain, expands a short distance behind the latter centre into a *hypocerebral ganglion*. The recurrent nerve leaves the hypocerebral ganglion in the form of a median or paired lateral oesophageal nerves and passes

backwards to the hinder region of the fore intestine, where it (or each branch) terminates in a *ventricular* or *stomachic* ganglion. The latter innervates the adjacent region of the fore and middle intestine. A pair of *oesophageal* or *pharyngeal ganglia* (also known as *corpora cardiaca*) lies on the oesophagus just behind the brain and each ganglion is joined with the hypocerebral ganglion. They are also connected with the protocerebrum, and it is probable that the corpora cardiaca include both nervous and endocrine secretory cells. Connected with them by nerves are the non-nervous corpora allata, with

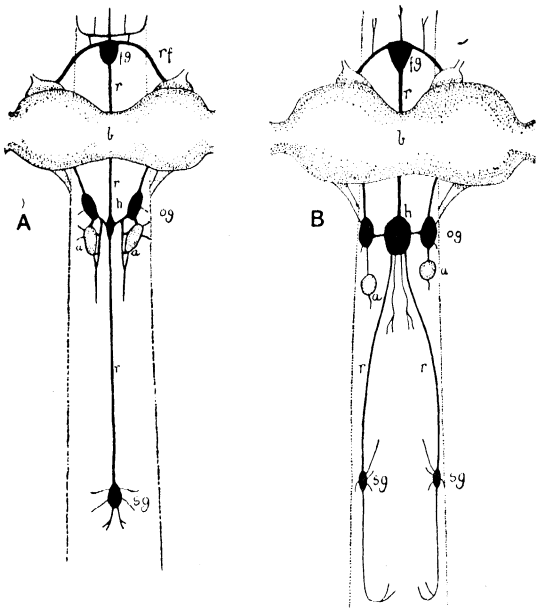


FIG. 65.—Semi-diagrammatic figures of two prevalent types of sympathetic nervous system (in black)

A, with a single recurrent nerve and stomachic ganglion; B, with paired recurrent nerves and ganglia. The fore intestine is represented by the dotted lines. *a*, *a*, corpora allata; *b*, brain; *fg*, frontal ganglion; *h*, hypocerebral ganglion; *og*, oesophageal ganglion (right); *r*, recurrent nerve; *rf*, root of frontal ganglion; *sg*, stomachic ganglion.

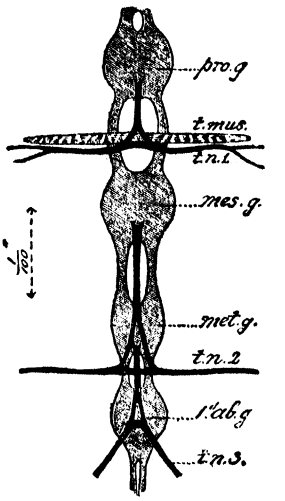


FIG. 66.—Thoracic ganglia and portion of sympathetic nervous system of a *Chironomus* larva

pro.g, *mes.g*, *met.g*, thoracic ganglia; *1ab.g*, 1st abdominal ganglion; *t.mus*, transverse muscle; tn_1–tn_3, sympathetic nerves. *After* Miall and Hammond.

important endocrine functions (see p. 175). Among variations on this generalized Pterygote plan may be mentioned the connexion of the frontal ganglion with the protocerebrum by a median *nervus connectivus*, the regression of the hypocerebral ganglion and varying degrees of fusion between the hypocerebral ganglion, the corpora cardiaca and the corpora allata, culminating in the condition found in the larvae of Cyclorrhaphan Diptera where all three fuse to form a composite structure known as Weismann's ring which encircles the aorta just behind the brain (Thomsen, 1951). In the Apterygota, the stomatogastric system is variable and usually reduced, but a frontal ganglion is always present and the Lepismatidae approach the Pterygote condition.

(2) The VENTRAL SYMPATHETIC NERVOUS SYSTEM (Fig. 66), when typically developed (Zawarsin, 1924), consists of a pair of transverse nerves associated with each ganglion of the ventral nerve-cord, and each pair is connected with the ganglion preceding it by a median longitudinal nerve. The transverse nerves pass to the spiracles of their segment and dilate into one or more small ganglionic enlargements along their course.

(3) The CAUDAL SYMPATHETIC NERVOUS SYSTEM arises from the compound posterior ganglion of the abdominal nerve-cord and supplies the reproductive system and posterior part of the gut.

(*c*) The Peripheral Nervous System

Strictly speaking, this includes all the nerves radiating from the ganglia of the central and sympathetic systems. Most accounts of it are fragmentary, dealing only with the innervation of particular organs and some peripheral nerves have been described above in connexion with the ganglia from which they arise. Particular interest, however, attaches to the peripheral sensory nervous system (Fig. 67). This is an exceedingly delicate plexus of sensory neurones of two main types. The first kind are bipolar neurones which differentiate from hypodermal cells and acquire distal connexions with cuticular

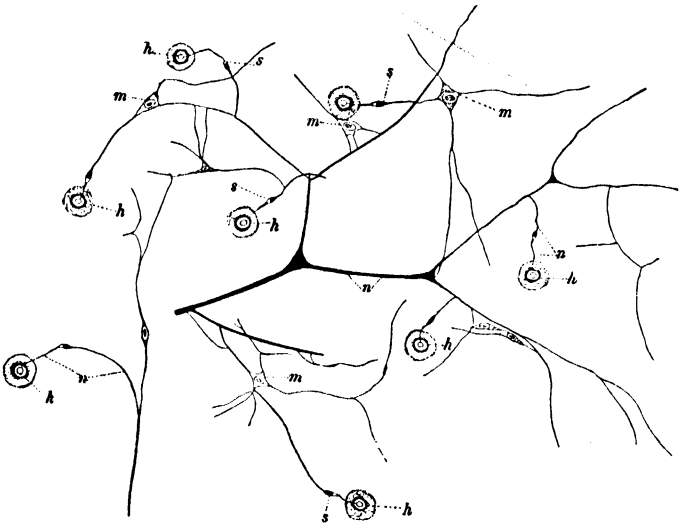


FIG. 67.—Portion of the peripheral sensory nervous system of a silkworm

h, *h*, bases of sensory hairs; *s*, *s*, bipolar nerve cells; *m*, *m*, multipolar nerve cells; *n*, *n*, nerves. *After* Hilton, *Amer. Nat.* 36.

sensory hairs and proximal ones with the central nervous system. The second type includes the multipolar neurones which occur immediately beneath the integument—where they may form an elaborate network—or on the surface of muscles and the wall of the gut. The distal processes of these cells ramify over the surfaces which they innervate while their centripetal connexion is to the ganglia of the central system. For further details of the peripheral sensory system see Zawarsin (1912; 1912a; 1916), Orlov (1924), Rogosina (1928), Rehm (1939), and Wigglesworth (1953).

II. Modifications of the Nervous System

There are many grades of cerebral development in insects, some at least of the observable differences being clearly correlated with the complexity of the insect's sensory equipment or behaviour. Thus, the volume of the brain is 1/174th of the body volume in *Apis* and 1/280th in *Formica*, but only 1/3290th in *Melolontha* and 1/4200th in *Dytiscus*. Again, the optic lobes are developed in proportion to the size of the eyes and the antennary lobes re-

lated to the development of the organs and senses connected with them. Internally, the mushroom bodies attain their greatest size and complexity in Hymenoptera with elaborate behaviour. Jonescu (1909) has shown that structural differences in the brains of drone, worker and queen bees appear to be correlated with the degree of development of the special instincts and activities of the three forms. Von Alten (1910) has compared the ratio of the size of the mushroom bodies to the brain as a whole obtaining, in this way, a kind of brain index. On the basis of such numerically expressed relationships in the Hymenoptera, the sawflies come lowest in the scale, the social

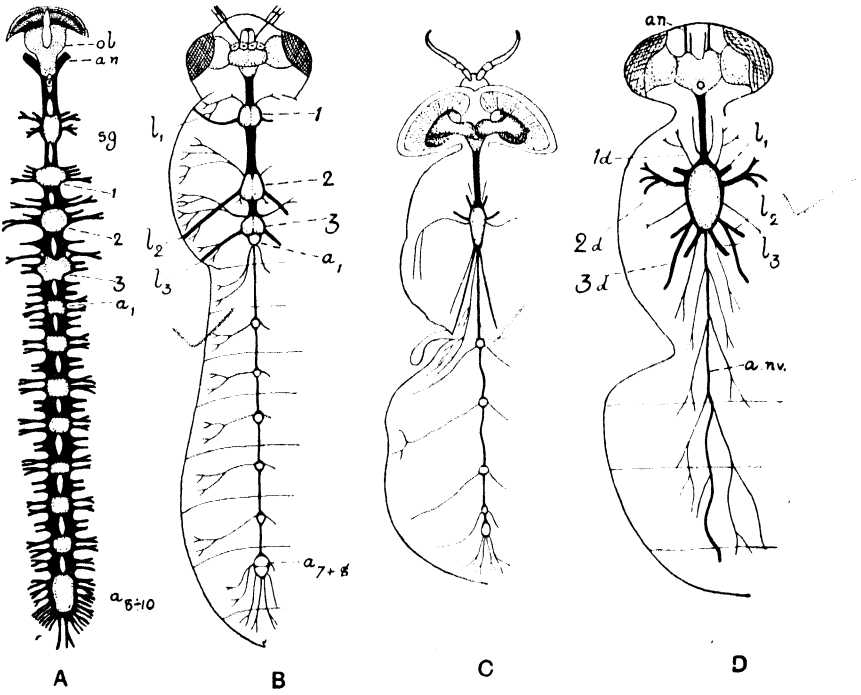


FIG. 68.—Schematic figures of the central nervous system showing degrees of concentration, based upon various authors

A, *Machilis* (Oudemans); B, *Chironomus* (Brandt); C, *Stratiomyia* (Kunckel d'Herculais); D, *Musca* (Hewitt). 1–3, thoracic ganglia; a_1, a_{7-8}, a_{8-10}, abdominal ganglia; *an*, antennary nerve; *ol*, optic lobe; *sg*, suboesophageal ganglion; l_{1-3}, nerves to legs; 1*d*–3*d*, dorsal thoracic nerves; *a.nv*, abdominal nerve-cord.

Hymenoptera highest, while the solitary bees occupy an intermediate position. For similar studies see also Thompson (1913) and Goossen (1949).

In the ventral nerve-cord (Fig. 68), the most generalized condition occurs in the Thysanura, many larvae and some lower Pterygotes where the suboesophageal ganglion, three thoracic and eight abdominal ganglia are separately visible, the most posterior being a composite ganglion. Most Orthopteroid insects, Mecoptera, Trichoptera and Hymenoptera show only a little more concentration than this, but the metathoracic ganglion commonly fuses with the first 1–3 abdominal ones and the 7th and subsequent abdominal ganglia form a compound centre. The other orders show various increasing degrees of fusion, often reaching extremes. Thus, in many Heteroptera, the suboesophageal and prothoracic ganglia are distinct but all the others have fused together. In many Sternorrhynchan Homoptera and higher Diptera, only the suboesophageal ganglion and a single compound thoracico-abdominal

ganglion are to be seen while in the Coccoidea, Aphidoidea and some Coleopteran larvae all the ventral ganglia (including the suboesophageal) are united in a single centre. Data amplifying these generalizations will be found in papers by Brandt (1879–82), Pflugfelder (1937) and Nesbitt (1941).

III. Physiology of the Nervous System

A detailed treatment of this topic cannot be attempted here and reference should be made to physiological works (see especially Ten Cate (1931), Welsh & Shallek (1946), Bullock (1947) and Roeder (1953)).

The study of nervous activity by methods of electrical stimulation and recording is now a well-established technique and though very few major nervous pathways have been explored in this way in insects (Pumphrey & Rawdon-Smith, 1937; Roeder, 1948) the general physiological properties of insect nervous tissue have been found to resemble those of vertebrates. Conduction of the nervous impulse occurs at rates of the order of 5 metres per second and several types of synapse occur, exhibiting a wide degree of variation in the phenomena of summation and adaptation. The neuromuscular junction is formed either by fine ramifications of the nerve fibre within or over the surface of the muscle fibrils or takes the form of an endplate (Marcu, 1929) and transmission across this junction differs somewhat from that among vertebrates in its greater stability to the action of drugs and fatigue. A double motor innervation has been described in some muscles (see p. 69). The nerves, synapses and neuromuscular junctions of insects appear to be relalatively insensitive to changes in the concentrations of cations in the external medium (Roeder, 1948a; Hoyle, 1953) and they fail to react to many drugs, including acetylcholine. The latter fact causes some uncertainty as to the mechanism of synaptic transmission in insects, though acetylcholine and cholinesterases have been extracted from insect ganglia and the effects of anticholinesterases in insects resemble those seen in vertebrate nerve preparations. An interesting feature is the spontaneous asynchronous electrical discharge which has been recorded from the isolated nervous systems of several species (e.g. Adrian, 1931). This arises in the ganglia and apparently provides a background of nervous activity which assists in maintaining muscle tonus and which may be modified by the inflow of sensory impulses.

Though insect behaviour has, in more recent times, been subjected to detailed experimental analysis (e.g. Fraenkel & Gunn, 1940; Tinbergen, 1951), the nervous mechanisms involved have as yet hardly been explored. Such results as exist are based mainly on changes in the performance of relatively simple reflexes following surgical interference with parts of the nervous system. The principal conclusion is that each segment of the body, with its ganglion, is capable of a considerable degree of autonomous reflex behaviour, these local segmental reflexes being co-ordinated by intersegmental mechanisms and modified by impulses from the cephalic centres so as to create an organized pattern of behaviour. Centralization of function is therefore less well developed than in the vertebrates. Local segmental reflexes are clearly shown, for example, in the respiratory movements of the gills of *Cloeon* nymphs (Alverdes, 1926) where the activity of each pair of gills is under the control of the corresponding abdominal ganglion but the latter are themselves regulated by inhibitory and stimulatory centres located respectively in the 2nd and 6th abdominal ganglia. Again, the legs of isolated thoracic segments are capable of some reflex movements on stimulation but

normal movement requires intersegmental co-ordination which, in *Periplaneta* (Ten Cate, 1941), depends partly on impulses originating in the prothorax and partly on those from proprioceptive sense-organs in the legs. There may also be a non-specific facilitating action of one segment on another, since local reflexes are not so well-marked in isolated segments. Local reflexes are also involved in reproductive movements—the isolated abdomen of a female silk-worm moth can be fertilized and lay eggs, while in mantids the copulatory movements of the male and movements of the ovipositor can be made after decapitation. The maintenance of a tonic contraction in some segmental muscles can also be due partly to local reflexes. The cephalic centres (brain and suboesophageal ganglion) mediate local reflexes concerned with the antennae, mouthparts and cephalic sense-organs but they also exercise some general control over the thoracic and abdominal ganglia, serving to raise or lower the state of excitation of the local reflexes. Each half of the brain (Roeder, 1937) has connexions on the same side with lower centres through which it helps to maintain the general tonus of the body muscles and others by which it exerts an inhibitory action on centres in the suboesophageal ganglion. There is also a system of crossed inhibitory connexions whereby each half of the brain regulates the activity of the opposite side. Tonic immobility (akinesis) apparently depends mainly on cerebral inhibition. The suboesophageal ganglion tends generally to excite the locomotor centres and when the inhibitory action of the brain on these suboesophageal centres is removed, insects may respond to slight stimuli by walking restlessly. On the other hand, in male mantids the suboesophageal ganglion has an inhibitory action on the copulatory reflexes (Roeder, 1935).

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THE SENSE ORGANS AND PERCEPTION

THE sense organs or receptors (Demoll, 1917; Snodgrass, 1926; Eltringham, 1933a; von Buddenbrock, 1952) are those structures whereby the energy of a stimulus arising outside or, less obviously, within the insect, is transformed into a nervous impulse which, after transmission to one of the central ganglia, usually results in a change in the behaviour of the insect or in the maintenance of some existing activity. Proof that a given organ is a receptor has, in some cases, been obtained by electrical recording of the nervous impulse which follows stimulation but in most cases receptors have been studied only through observations on the insect's behaviour and occasionally a sensory function

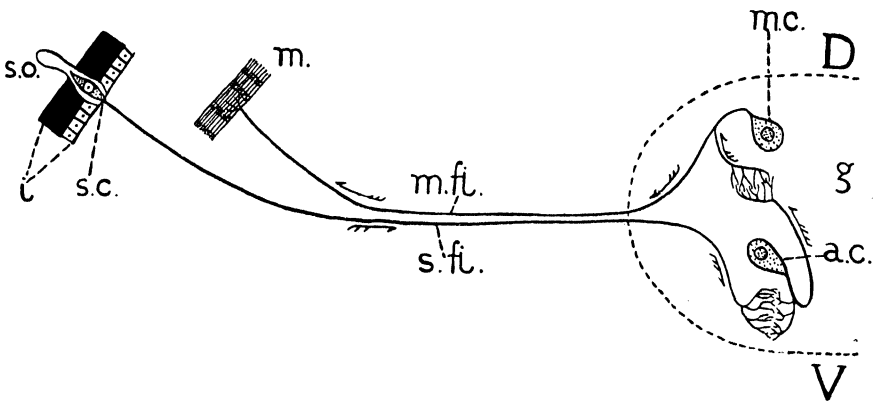


FIG. 69.—Diagram of the reflex mechanism of the nervous system of an insect. One half of a ganglion, *g*, of the ventral nerve-cord is represented in outline

D, dorsal aspect; *V*, ventral aspect. A motor (*m.fi*) and a sensory fibre (*s.fi*) of a lateral nerve are shown; *i*, integument; *s.o*, sense organ; *s.c*, sensory neurone; *m*, muscle; *a.c*, association neurone; *m.c*, motor neurone. (The course traversed by a stimulus, received by the sense organ, is represented by arrows.)

has been ascribed solely on the basis of structure and anatomical relations. The connexion between a receptor and the effector organs which change or maintain activity is often represented as a relatively simple reflex arc (Fig. 69) though it is probable that even the simplest behavioural act involves the co-ordination of many variable conducting paths whose functional activity depends on the quality of the stimulus and the physiological state of the receptor and nervous system.

Sense organs are associated especially with the integument and each organ or *sensillum* (pl. *sensilla*) typically comprises: (*a*) a structure—cuticular and/or hypodermal—through which the stimulus is amplified or directed or translated into other mechanical or chemical changes (not always adequately analysed as yet) and (*b*) one or more sensory neurones responding to the modified stimulus resulting from (*a*) by nervous activity. In the simplest cases, however, the neurone may end distally in fine ramifications among

apparently unmodified epithelial cells or be produced into a simple process surmounted by cuticle which is hardly, if at all, specialized. The sensory neurones of insects are usually regarded as *primary sense cells* since they are produced centripetally into axons which enter a ganglion and end in contact with association neurones. Secondary sense cells, i.e., ectodermal structures innervated by deep-lying sensory neurones similar to those in the spinal ganglia of vetebrates, are apparently absent in the Insecta (but see Schön, 1911; Vogel, 1923 and p. 106). So far as is known the nerve-impulses leaving the sensory neurones are qualitatively similar in all the different types of receptors and the specificity which these organs exhibit (i.e. the fact that some respond only to light, others to sound, etc.) often depends mainly on the character of the transforming structures mentioned above.

According to the broadest aspects of their function, receptors may be divided into two classes. These are (*a*) *Exteroceptors*, perceiving stimuli which arise in the external environment and (*b*) *Interoceptors* which are excited by stimuli arising within the body and of which the *proprioceptors* (those organs influenced by changes in the position of the body or its parts) are an important group. Here, however, it is more convenient to consider the insect sense organs according to the sense which they subserve, under five main headings:

1. Mechanoreceptors.
2. Auditory Organs.
3. Chemoreceptors.
4. Temperature and Humidity Receptors.
5. Visual Organs.

It may be noted that the auditory organs are actually only a specialized type of mechanoreceptor while humidity perception may ultimately prove reducible to one of the other mechanisms.

1. **Mechanoreceptors.**—The members of this diverse group have the common property that they are excited by processes involving the mechanical deformation of some part of the receptor (Dethier, 1953). As such they may mediate the sense of touch, including contact with solid objects or currents of air or water; they may also respond to mechanical stresses set up in the cuticle and so function as proprioceptors, including the specialized organs of equilibrium; and, as mentioned above, in certain cases they respond to the displacement of air-particles and so act as sound receptors. Three main structural types of mechanoreceptor may be distinguished:

(*a*) **Articulated sensory hairs** (Fig. 70). Each sensory hair comprises the usual trichogen and tormogen cells which secrete respectively the hair and its socket (p. 12) together with a bipolar neurone which is produced distally into a scolopoid body (scolopale) which may be cuticular and is in close contact with the base of the hair (Schneider, 1923; Sihler, 1924; Hsü, 1938). Such hairs are widely distributed over the insect body, especially on the antennae, tarsi and cerci and are usually tactile organs, being stimulated to produce a nervous impulse on movement of the hair in its socket (Pumphrey, 1936). Grouped together in the form of hair-plates (Pringle, 1938) they may occur near the joints of the appendages and act as proprioceptors since they are displaced when one segment of the limb moves against the adjacent one.

(*b*) **Campaniform sensilla.** These are comparable in structure to the innervated hairs (Fig. 71). Forms intermediate between the two types are known in *Drosophila* mutants (Lees, 1942) and two specialized hypodermal cells and a bipolar neurone are associated with each campaniform sensillum,

though Hsü (1938) considers that the cells are difficult to homologize. Otherwise, this type of sensillum consists of a dome-shaped cuticular structure often oval in surface view and slightly elevated above or depressed below the general level of the cuticle while the longer axis of the dome may be marked

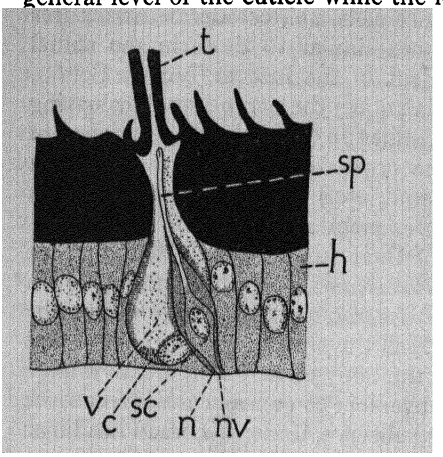


FIG. 70.—Simple tactile hair from the cercus of *Gryllus campestris* (cuticular parts deep black)

c, trichogenous cell; *h*, hypodermis; *n*, neurilemma; *nv*, nerve fibre; *sc*, sense cell and its process *sp*; *t*, base of hair; *v*, vacuole. From Sihler.

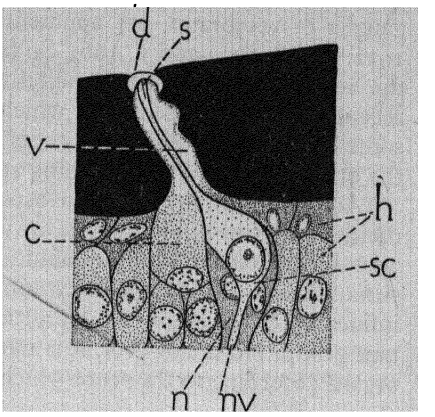


FIG. 71.—Campaniform sensillum from the cercus of *Blatta orientalis*

c, trichogenous cell; *d*, dome-like covering; *h*, hypodermis; *n*, neurilemma; *nv*, nerve fibre; *s*, scolopale; *sc*, sense cell; *v*, vacuole; (integument deep black). From Sihler.

by a thickened ridge or a line of thinner cuticle. The distal process of the sensory neurone forms a rod-like structure (scolopale) which is inserted into or touches the cuticular dome. For various modifications see Hochreuther (1912), McIndoo (1914–15) and Newton (1931). Campaniform sensilla occur on many regions of the body—cerci, wings, basal parts of appendages, etc.—and are often grouped together into functional units. Pringle (1938) has shown electro-physiologically that in the palps and legs of *Periplaneta* they act as proprioceptors: stresses in the cuticle are thought to be resolved into a movement of the central part of the dome which stretches or compresses the rod-like distal part of the neurone.

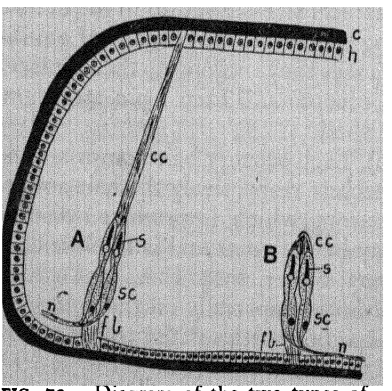


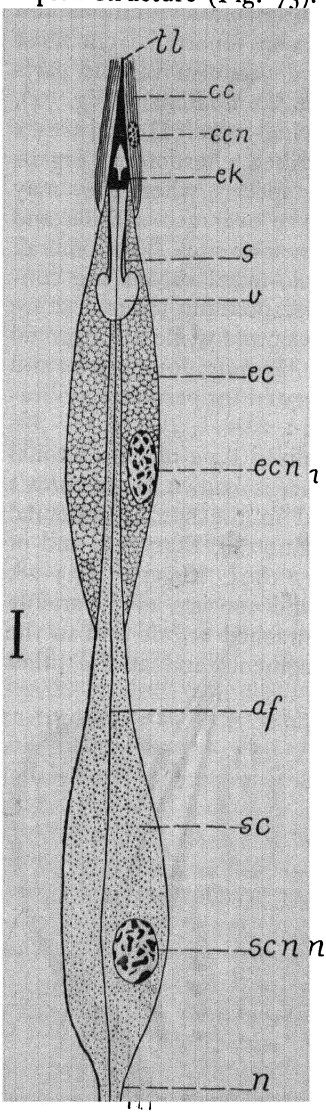
FIG. 72.—Diagram of the two types of scolopophores

A, integumental; B, subintegumental. *c*, cuticle; *h*, hypodermis; *cc*, cap cell; *s*, scolopale; *sc*, sensory cell; *fb*, fibrillar binding tissue; *n*, nerve.

(*c*) **Chordotonal organs (scoloparia)**. These are usually compound structures composed of a number of specialized sensilla (*scolopophores* or *scolopidia*) which each contain a relatively conspicuous sensory rod (*scolops* or *scolopale*). Berlese (1909) regarded each scolopophore as derived from a campaniform sensillum by elongation of the parts and withdrawal into the body, but Eggers (1923) suggests an origin from an elongate bipolar neurone with a peculiar distal fibrillar attachment to the cuticle. Each chordotonal organ consists typically of a spindle-shaped bundle of scolopophores attached at each end to the integument, but less frequently the

distal attachment is absent and the organ ends freely in the body-cavity. The two types may be distinguished respectively as *integumental* and *sub-integumental* chordotonal organs (Fig. 72).

Each scolopophore (Eggers, 1923–28; Debaisieux, 1936–38) has a complex structure (Fig. 73). A bipolar neurone, produced basally into a fibre of the chordotonal nerve, is drawn out distally into a slender prolongation enclosed by an *envelope cell* and a *cap cell*. The scolopale is formed within the envelope cell and its cavity communicates basally with a liquid-filled vacuole. Viewed in transverse section the wall of the scolopale is composed of a number of ribs: in the simple type of sensillum studied by Hess (1917) there are seven ribs at each end of the scolopale, each rib being divided in the intermediate part. Distally the scolopale is almost always thickened to form the *end-knob*, and the entire scolopale is bathed in a fluid medium in which it is free to move. The cap cell appears to be a modified hypodermal cell and in the integumental type of scolophore it forms the elongate strand attaching the distal end of the sensillum to the body-wall. The opposite end of the sensillum is attached to the cuticle by strands of connective tissue (the 'fibrillar binding substance' of Schwabe, 1906) which is prolonged over the group of sensilla to ensheath them. An axial fibre or group of neurofibrils from the chordotonal nerve traverses the length of each sensillum to join the end-knob of the scolopale.



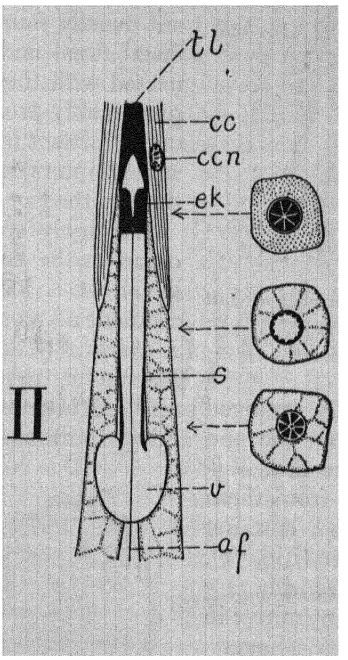


FIG. 73.—I. A scolopophore of the integumental type from a Cerambycid larva

II. Apical portion of a scolopophore, more highly magnified, together with transverse sections

After Hess, *Ann. ent. Soc. Amer.* 10.

af, axial fibre; *cc*, cap cell; *ccn*, nucleus of cap cell; *ec*, envelope cell and its nucleus *ecn*; *ek*, end-knob; *n*, nerve fibre; *s*, scolopale; *sc*, nerve end-cell and its nucleus *scn*; *tl*, terminal ligament; *v*, vacuole.

Because of their association with tympanic membranes in auditory organs

(q.v.), the chordotonal sensilla were at one time regarded solely as sound receptors acting as resonant elements resembling stretched strings. It is now known that they are stimulated by tension and are used for various purposes including proprioception and the perception of internal pressure changes, mechanical vibrations and sound. They have been reported from most orders of insects and occur in various parts of the body such as the abdomen (Fig. 74), appendages and wing-bases. Debaisieux (1936–38) has described chordotonal organs in the legs of many species, where they may consist of from one to over 200 sensilla and are usually found in four sites. The femoral, distal tibial and tibio-tarsal organs are connected with the corresponding joints and are presumably proprioceptors while a subgenual organ (absent from *Machilis*, *Rhagonycha* and some Diptera) is adapted for perceiving vibrations of the leg.

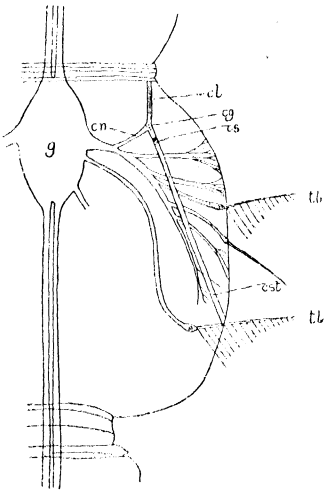


FIG. 74.—Right half of 8th body-segment of the larva of *Chaoborus*

cg, *cs*, chordotonal organ and its terminal prolongation *cst*; *cl*, basal ligament; *cn*, chordotonal nerve; *tb*, tactile setae; *g*, ganglion of ventral nerve-cord. *After* Graber.

A highly specialized type of chordotonal organ in the antenna is known as *Johnston's organ*. It is located in the second antennal segment of most, if not all, Pterygota and of *Lepisma* (Child, 1894; Eggers, 1923–28; Debauche, 1936) and consists of a variable number of radially arranged sensilla. These are attached at one end to the membrane between the 2nd and 3rd antennal segments and at the other to the wall of the 2nd segment, the axons from them running back and entering the antennal nerve (Fig. 75). The individual sensilla are apparently most primitive in Odonate nymphs (Eggers, 1923) and the organ is developed to differing degrees in the different groups of insects. It reaches its greatest complexity in male Chironomids and Culicids and it appears that the other chordotonal organs and campaniform sensilla in the antenna are reduced in proportion to the size of Johnston's organ. The latter is stimulated by movements of the antennal flagellum and therefore acts not only as a proprioceptor but also enables the insect to perceive air-currents, contacts with solid objects and, in the Gyrinidae, vibrations of the water-surface

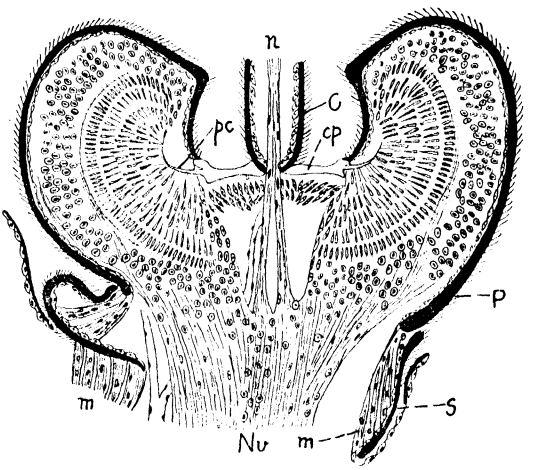


FIG. 75.—Longitudinal section of the base of the antenna of a male mosquito (*Chaoborus*) showing Johnston's organ

s, scape; *p*, pedicel; *cp*, conjunctival plate and its process *pc*; *C*, base of clavola; *Nv*, antennary nerve; *n*, nerve to clavola; *m*, antennal muscles. *After* Child, 1894.

on which these beetles swim. It is also a sound-receptor in Culicidae (see below).

Before leaving the topic of mechanoreceptors, mention must be made of the organs of equilibrium. Orientation of the insect with respect to gravitational or other forces acting on it may be accomplished partly through a variety of sense organs making use of proprioceptors or tactile sensilla, sometimes organized in special ways. In the simplest cases, the ordinary proprioceptors may suffice (with the aid of visual stimuli) to maintain normal orientation. In *Notonecta*, the antenna, bearing specialized tactile hairs, is pressed against the surface of a large air-bubble lying behind the head and can register movements in the position of the bubble due to changes in the orientation of the insect (Weber, 1930). In *Nepa* and *Aphelocheirus* (Thorpe & Crisp, 1947) orientation is achieved partly through more specialized structures responding to differences in hydrostatic pressure and developed in association with some of the abdominal spiracles but again depending fundamentally on mechanoreceptors. Orientation during flight is accomplished in the higher Diptera through the halteres, whose receptor structures include several groups of campaniform sensilla (p. 85). Static sense organs composed of a hollow *statocyst* containing movable bodies (*statoliths*) which impinge on tactile hairs are apparently absent from terrestrial insects but occur in the terminal abdominal segments of some Tipulid larvae (Grobben, 1876; von Studnitz, 1932) and Palmén's organ in the cephalic tracheal system of Ephemeropteran nymphs may also function in this way (Wodsedalek, 1912). The function of Graber's organ, a peculiar structure in the hind abdominal segments of Tabanid larvae, is uncertain; though its form suggests that it might be a static sense organ, experimental support for this is lacking.

2. **Auditory Organs.**—Though noises may be transmitted through liquid and solid media, little is known of their reception by insects in such cases and for the present purpose it is convenient to regard sound as consisting of air-disturbances of low intensity, irrespective of whether they fall within the range of human hearing (Pumphrey, 1940). Such disturbances produce both a local pressure increase and a displacement of air-particles away from the source of the sound, but it is probable that all insect auditory organs act as displacement receptors. They are, in fact, mechanoreceptors which differ from tactile sense organs only in that they respond to disturbances of much lower intensity and further study may well reveal receptors of an intermediate character. In spite of their underlying similarity, three types of sound receptors may be recognized:

(*a*) **Tympanal organs.** These are paired structures always composed of a thin cuticular membrane, the *tympanum*, associated with tracheal air-sacs

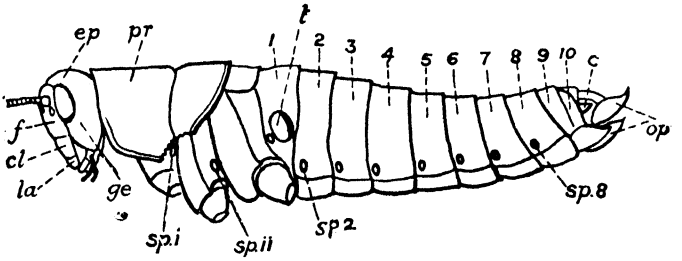


FIG. 76.—Lateral view of a locust with wings and legs removed showing tympanum
After Carpenter.

and chordotonal sensilla. They occur in the Orthoptera (Acridoidea, Tettigonioidea and Grylloidea), the Cicadidae and some Lepidoptera (Noctuidae, Geometridae, Cymatophoridae, Uraniidae, Pyralididae, etc.).

In the Acridoidea there is a tympanal organ on each side of the first abdominal tergum, with an externally visible tympanum surrounded by a cuticular ring (Figs. 76, 77). Internally (Schwabe, 1906), a group of numerous scolopophores, forming a swelling known as Müller's organ, is applied to the inner surface of each tympanum and is connected by the auditory nerve to the metathoracic ganglion. Two sclerotized processes and a pyriform vesicle filled with a clear liquid are intimately associated with Müller's organ; they probably serve to transmit the tympanal vibrations to the sensilla. The first abdominal spiracle is situated near the anterior margin of the tympanum and gives off an air-sac which is applied to the under surface of that membrane. Two other air-sacs arise from the ventral tracheal trunk on each side of the 2nd abdominal segment and lie internal to and in close contact with the first-mentioned sac.

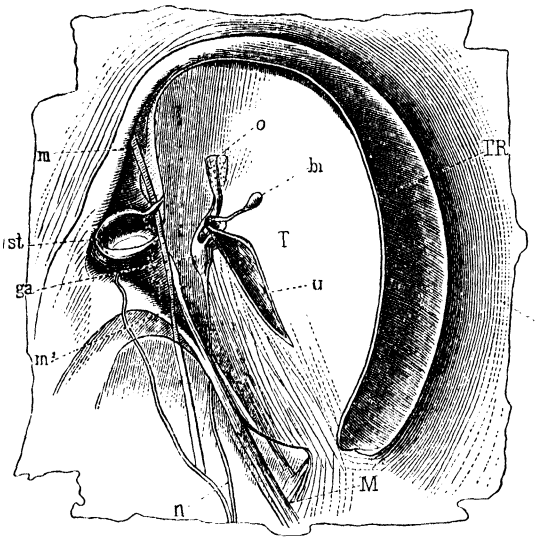


FIG. 77.—Tympanum of a locust (*Calliptamus*) viewed from within

T, tympanum with its border *TR*; *bi*, pyriform vesicle; *o*, *u*, horn-like processes; *ga*, Müller's organ; *n*, auditory nerve; *st*, spiracle; *M*, tensor muscle of tympanum. *After* Graber.

In the Tettigonioidea and Grylloidea there is often a pair of tympanal organs at the base of each fore tibia (Figs. 78–80). In many genera they are easily seen, but in others each organ is concealed by a cuticular fold and comes to lie in a cavity which communicates with the exterior by a slit-like opening (Fig. 80).

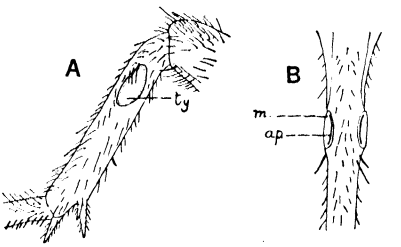


FIG. 78.—Left fore tibia of *Acheta domesticus* seen from the outside showing tympanum *ty*

B. Portion of fore tibia of *Tettigonia viri-dissima*, frontal view

m, membrane covering tympanum; *ap*, aperture into tympanal chamber.

These organs attain great complexity of structure and most of what is known concerning them is due to the researches of Graber (1876), von Adelung (1892) and Schwabe (1906). In *Decticus verrucivorus* the tympanal organs are of the concealed type (Figs. 79 and 80). The trachea supplying the leg is greatly modified and, on entering the tibia, it becomes inflated and divides into an anterior and a posterior branch, which reunite below the auditory organ. Each trachea is closely applied to the tympanum of its side, which thus has air on both its aspects: the open air on the outer surface, and the air of the trachea on its inner surface. It is noteworthy that these tracheae

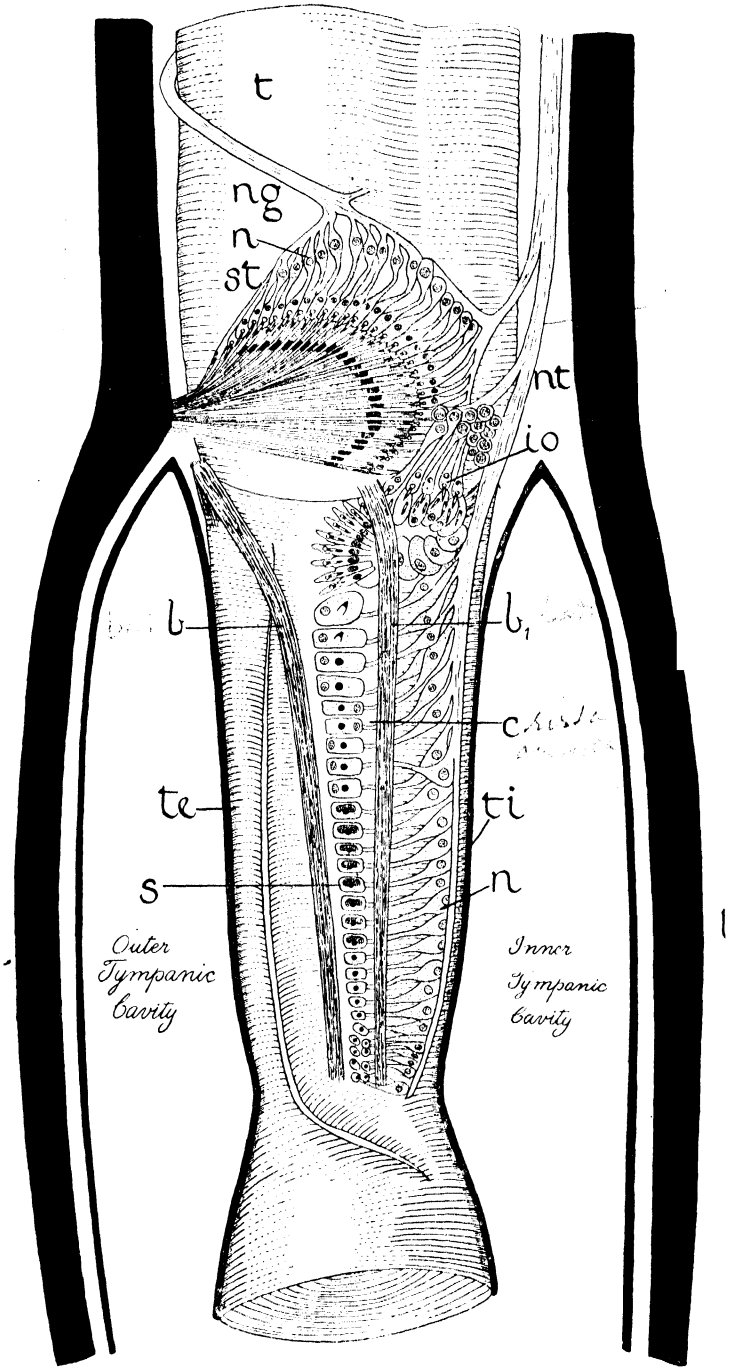


FIG. 79.—Longitudinal section of the fore tibia of *Decticus*

c, crista acustica with its supporting bands *b* and b_1; *io*, intermediate organ; *le*, *li*, outer and inner aspects of tibia; *n*, nerve cells; *ng*, subgenual branch of crural nerve; *nt*, tympanal nerve; *s*, scolopalia; *st*, supratympanal organ; *t*, main trachea; *te*, *ti*, outer and inner tympana. Redrawn from Schwabe, *Zoologica*, 1906.

communicate with the exterior by a special orifice on either side, in close proximity to the prothoracic spiracle, and these orifices are only present in

species with tympanal organs. In a transverse section of the tibia (Fig. 80) it will be observed that the two tracheae occupy the area between the tympana. There is an extensive outer chamber in the leg (above the tracheae, as seen in the figure) and a corresponding inner chamber below. The outer chamber contains the supratympanal organ together with leucocytes and adipose cells. The *supratympanal organ* is placed a short distance above the tympana, and is composed of a number of scolopophores of the integumental type, whose cap cells are attached to the integument of the leg. Immediately below this organ, on its outer side, there is a smaller sensory

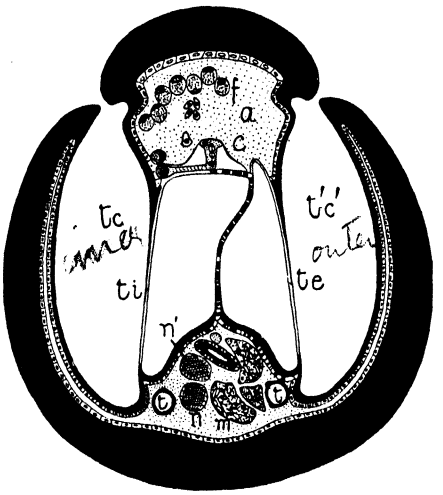


FIG. 80.—Transverse section of the fore tibia of *Decticus* passing through the crista acustica (*c*)

a, anterior blood space; *f*, fat-body; *m*, muscles; *n* tarsal nerve; *n'*, tibial nerve; *t*, tracheae; *tc*, *t'c'*, inner and outer tympanic cavities; *ti*, *te*, inner and outer tympana. Redrawn from Schwabe.

structure which is termed the *intermediate organ*: it is composed of scolopophores of the subintegumental type. On the outer face of the anterior trachea is a third chordotonal organ—the *crista acustica* (*organ of Siebold*). It is an elongated ridge or crest composed of a large number of scolopophores of the subintegumental type, which gradually decrease in size towards the distal extremity of the tibia. There are two principal nerves in the tibia—the tibial nerve and the tympanal nerve—both arising from the prothoracic ganglion. The supratympanal organ is supplied by a branch from each of those nerves, while the two remaining organs are innervated by the tympanal nerve.

Tympanal organs also occur in individuals of both sexes in some Hemiptera, notably the Cicadidae. In these insects Vogel (1923a) has shown that the cavity of the operculum of the sound-producing organ is bounded posteriorly by a true tympanum named the 'mirror'. The percipient part of this organ consists of

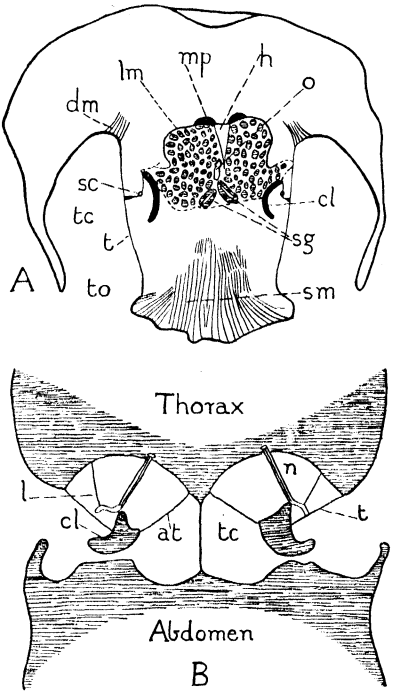


FIG. 81.—Tympanal organs of Lepidoptera. A. Vertical section across base of abdomen of a Geometrid moth. B. A diagrammatic horizontal section across base of thorax and abdomen of a Noctuid moth

at, accessory tympanum; *cl*, cuticular lamella; *dm*, dorsal muscle of tympanum; *h*, heart; *l*, ligament supporting chordotonal organ; *lm*, longitudinal muscles; *mp*, mesophragma; *n*, chordotonal nerve; *o*, oesophagus; *sc*, scolopalia; *sg*, salivary gland; *sm*, sternal muscles; *t*, tympanum; *tc*, tympanic chamber; *to*, external opening of tympanic chamber. Adapted from Eggers and v. Kennel.

a group of about 1,500 chordotonal sensilla stretching like a ligament across a kind of auditory cavity. In many families of Lepidoptera conspicuous tympanal organs are also present on either side of the metathorax or at the base of the abdomen. These organs have been chiefly investigated by Eggers (1919), Kennel and Eggers (1933) and Gohrbrandt (1937). Each organ consists of an internal vesicle invested by tracheal epithelium and lodged in a cavity formed by an invagination of its segment. The cavity communicates with the exterior by an opening which is guarded by an integumentary fold. Just within the opening is the glistening tympanic membrane and, closely associated with it, is a pair of chordotonal sensilla connected with a special tympanic nerve from the metathoracic ganglion. Whereas in Geometrid moths the tympanal organs are lodged in the abdomen, in Noctuid moths they are situated in the thorax and, lying more deeply within the tympanic vesicle, there is an accessory tympanum which appears to function as a resonator (Fig. 81).

Tympanal organs are described by Hagemann (1910) in *Corixa* and its allies on either side of the mesothorax, in close relation with the second pair of spiracles.

To judge from the structure of the tympanal organs, it would appear that sound waves impinging on the tympanum cause it to vibrate and these movements stimulate the chordotonal sensilla. The earliest experimental proof of the auditory function of tympanal organs is due to Regen (1909, etc.), working with *Pholidoptera* and *Gryllus*. He showed that various responses to artificial sounds or natural stridulation were lost after extirpation of the organs. Later methods of electrical recording (Wever & Bray, 1933; Pumphrey & Rawdon-Smith, 1936) showed the occurrence of impulses in the nerves from stimulated Orthopteran tympanal organs and excitation by artificial sounds showed that they respond to vibrations from 250 to 45,000 cycles per second, the threshold intensity varying throughout the frequency spectrum but with the greatest sensitivity between 5,000 and 20,000 cycles per second. The most interesting feature, however, is that electrical discharge in the nerve is not synchronous with the frequency of a pure-tone stimulus of uniform intensity but when the stimulus undergoes amplitude modulation the nervous responses synchronize with the modulation frequency (Pumphrey & Rawdon-Smith, 1939); the frequency of the 'carrier wave' is immaterial provided it falls within the auditory range. To the insect relying on such a tympanal organ, therefore, sounds are discriminated by the rhythmic variations in intensity which make up the modulation pattern and not by variations in pitch. Such a mechanism of differentiation corresponds with the demonstration (Pierce, 1948) that Orthopteran stridulation consists of high-frequency sounds modulated in different ways.

Much less is known of the mode of action of tympanal organs in orders other than the Orthoptera but the Cicadidae probably resemble them in the importance of amplitude modulation (Pringle, 1953). In at least some Lepidoptera there is experimental evidence that they perceive sound with the tympanal organs (Eggers, 1928) but the latter may also be proprioceptors.

(*b*) **Auditory hairs.** Minnich (1925, 1936) has shown in many Lepidopterous larvae that responses to sound are mediated by hair sensilla which react to low frequencies. Pumphrey & Rawdon-Smith (1936) found that hairs on the cerci of some Orthoptera act as displacement receptors of sound vibrations having a frequency of less than about 3,000 cycles per second and that,

at least in the lower parts of the range, the impulses in the cercal nerves synchronize with the frequency of the stimulus.

(*c*) **Johnston's organ.** Roth (1948) has shown that in males of *Aedes aegypti*, sound waves can set in motion the hairs on the antennal flagellum and this in turn causes movements of the whole flagellum which stimulate the sensilla of Johnston's organ. The insects readily respond by this mechanism to frequencies between about 300 and 500 cycles per second, and less readily to lower frequencies. See also Risler, 1953.

3. **Chemoreceptors.**—The physiology of the chemical senses and the receptors involved are discussed by Dethier & Chadwick (1948), Frings & Frings (1949) and Dethier (1953). Since many different structural types of

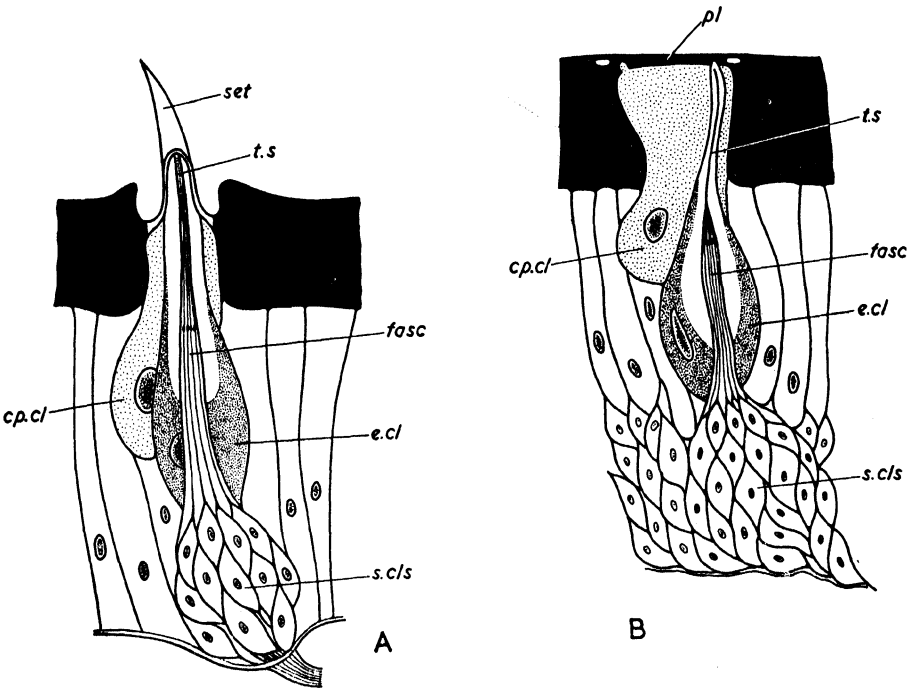


FIG. 82.—Two types of Chemoreceptor (*after* Snodgrass, 1935). A. Thin-walled chemoreceptor seta. B. Placoid sensilla of *Apis* antenna

cp.cl, cap cell; *e.cl*, envelope cell; *fasc*, fascicle of sense-cell processes; *pl*, outer plate; *s.cls*, sense-cells; *set*, thin-walled seta; *t.s*, terminal strand of sense-cell processes.

receptor are implicated (e.g. Hsü, 1938) and they are often clustered together in such a way that extirpation experiments do not always show conclusively which type of chemical sense they mediate, it is most convenient to describe the chemoreceptors first and then to discuss the different kinds of sensory reactions. All types of chemoreceptors are characterized by the possession of cuticle which is at least partly thin-walled (though never perforated) and are innervated by one or a group of bipolar neurones, whose associated distal processes contain small refringent bodies. They may be regarded as derived from sensory hairs (Wacker, 1925) and the following types have been recognized (Figs. 82 and 83):

(*a*) **Sensilla trichoidea olfactoria.** These are thin-walled hairs which have been described from the tarsi and labella of *Tabanus* (Frings & O'Neal, 1946), the tarsi

of *Pyrameis* and *Musca* (Eltringham, 1933; Hayes & Liu, 1947) and the antennae of several species (Vogel, 1923; Prüffer, 1929; Wigglesworth & Gillett, 1934; Dethier, 1947a). The *sensilla chaetica* are similar, but shorter and stouter hairs.

(*b*) **Sensilla basiconica** and **styloconica.** These are peg-like or cone-like organs only distinguished from the olfactory trichoid sensilla by the more thick-set appearance of the projecting part. They occur particularly on the antennae of many species (Vogel, 1921; Warnke, 1931; Valentine, 1931; Wigglesworth, 1941; Dethier, 1947a) and are also reported from the palps of *Hydrophilus piceus* (Ritter, 1936) and *Agriotes* larvae (Crombie & Darrah, 1947) and the antennae and palps of *Periplaneta* (Glaser, 1927) and Lepidopterous larvae (Dethier, 1937). Basiconic sensilla grouped together and sunk in a pit occur in the antennae of Muscids (Liebermann, 1925) and other Diptera and the palps of butterflies (Hsü, 1938). They have also been described from various other parts of the body, including the hypopharynx and the epipharyngeal surface of the labrum.



FIG. 83.—Cuticular parts of coeloconic sensillum (A) and ampullaceous sensillum (B) (*after* Snodgrass, 1935)

(*c*) **Sensilla coeloconica.** These differ from basiconic sensilla in that the cuticular process is sunk below the general level of the integument. In some cases the organ is very deeply sunk and connected with the surface by an elongate tube—the so-called *sensilla ampullacea.* They have been described from the antennae of various Coleoptera (Hochreuther, 1912; Warnke, 1931), Lepidoptera (Bohm, 1911; Prüffer, 1929) and Hymenoptera (Schenk, 1903).

(*d*) **Sensilla placodea** (pore-plates). This rather distinctive form of sensillum consists of a thin cuticular plate, approximately circular or elongate-oval in shape, beneath which lies a cap cell and an envelope cell, the latter penetrated by bundles of distal processes from the bipolar neurones. These processes coalesce in a terminal strand which ends in the pore-plate. Sensilla placodea have been studied in the antennae of many insects such as Aphididae (Flögel, 1905), Coleoptera (Hochreuther, 1912; Warnke, 1931), *Apis* and other Hymenoptera (Vogel, 1923; Wacker, 1925; Snodgrass, 1925) and Lepidopterous larvae (Dethier, 1937). They are particularly numerous on the last eight segments of the antennae of *Apis mellifera* males.

The modern tendency seems to be to distinguish three categories of chemical sense—a general chemical sense and those of smell and taste. The distinctions between these seem to be relatively clear in terrestrial insects, but further studies of chemoreception are required in aquatic species and those inhabiting such moist environments as soil or plant tissues.

(*a*) **Common chemical sense.** This may be recognized as leading to an avoiding reaction to high concentrations of irritant substances (e.g. chlorine, ammonia and the vapours of essential oils). It has been little studied, but persists after the removal of olfactory receptors and the sense organs responsible, though not satisfactorily identified, seem to occur on all parts of the body.

(*b*) **Olfactory sense (smell).** The sense of smell is stimulated by low concentrations of the vapours of substances which are relatively volatile at ordinary temperatures, though such a definition is satisfactory only in species from dry surroundings. Olfactory stimulation has been intensively studied through the search for attractant and repellent substances in economic entomology (Dethier, 1947), but while behavioural aspects of the problem have received much attention, little is known of the mode of perception beyond the identification in a few cases of receptors on the palps and antennae (placoid sensilla in *Apis*; basiconic, coeloconic and trichoid sensilla in other cases). The olfactory threshold is very low for some substances. Thus, skatol at a

concentration of 0·003 mgm. per litre of air can attract *Geotrupes* (Warnke, 1931) and in the well-investigated case of *Apis mellifera* reacting to the odours of essential oils the thresholds are similar to those of man with a close qualitative similarity between the olfactory senses of the two species (von Frisch, 1919). Many factors such as age, sex, nutritional status and previous conditioning, as well as temperature, humidity and the rate of air-flow, are known to affect olfactory thresholds and in some cases a reversal of response may occur naturally during the life of the insect or be induced experimentally. For example, the newly-emerged females of *Pimpla ruficollis*—a parasite of the Pine-shoot Moth, *Evetria buoliana*—are repelled by the essential oils of pine, but when sexually mature they become attracted by them and return to the pines where their hosts are available for oviposition (Thorpe & Caudle, 1938). Again, Thorpe (1939), by larval conditioning, has induced *Drosophila* adults to react positively to the normally repellent odour of peppermint oils.

One of the most interesting features of olfactory responses is their considerable specificity and the role played by specific attractants in the life of the insect. Biologically, such odours may be classified as: (i) Sexual attractants, (ii) Recognition odours, (iii) Oviposition attractants and (iv) Food attractants.

(i) *Sexual attractants.*—It has long been known that certain male moths (especially Lasiocampidae, Bombycidae and Saturniidae) are attracted by the scent of virgin females of their own species and assemble in their vicinity. Similar reactions have been recorded for other groups of insects (Richards, 1927; Dethier, 1947). In some cases the odour is perceived at a great distance—over 2 miles is reported for the Gipsy Moth, *Lymantria dispar*, by Collins & Potts (1932). The chemical identity of the sexual attractants is not fully established and though many pure organic compounds attract males they are not definitely known to be secreted by the females.

(ii) *Recognition odours.*—Social insects appear to be able to detect members of their own species, caste or colony by olfactory means (McIndoo, 1917), ants and honey bees, for example, reacting amicably to members of their own colony but attacking strangers. Certain ants perceive odour trails left by their companions and so orientate themselves in foraging (e.g. Carthy, 1951). Salt (1937) has shown that the Chalcidoid egg-parasite *Trichogramma* recognizes previously parasitized host eggs by olfactory means.

(iii) *Oviposition attractants.*—The deposition of eggs in places suitable for their further development is often the result of the female insect being attracted by scents from the oviposition site. Many parasitic insects, for example, are attracted to their hosts in this way (e.g. Thorpe & Jones, 1937). Insects with saprophagous larvae are attracted by odours such as ammonia, skatol, etc., arising from the bacterial decomposition of organic materials (see examples in Dethier, 1947).

(iv) *Food attractants.*—Phytophagous insects are frequently attracted to their host-plants by the smell of the essential oils there (McIndoo, 1926; Dethier, 1947; etc.). This attraction may, however, only occur when the insect is very close to the plant—as shown for some Lepidopterous larvae by Dethier (1937) and for *Leptinotarsa* by Chin (1950)—and stimuli of taste and sight are probably also involved in host-selection by phytophagous insects.

(*c*) **Gustatory sense (taste).** This is defined by a response to relatively high concentrations of the stimulant, which, in liquid form (normally as an aqueous solution) comes into contact with the receptors. The latter have not usually been identified with certainty but they are probably basiconic and short trichoid sensilla and are known to occur on the antennae in some Hymenoptera, on the surfaces of the preoral food cavity and mouthparts of many insects, on the ovipositor of a few forms and on the tarsus and distal parts of the tibia in many Lepidoptera, Diptera and in honey bees (Frings & Frings, 1949). Experimental work on the sense of taste has consisted largely of behavioural studies of the acceptability or otherwise of various pure chemi-

cal substances (Dethier, 1953). There are wide differences in the taste-thresholds of different substances with a given species and for different species with the same substance. Considerable variations in threshold may also occur when one species is responding to a single substance, sometimes depending on which group of receptors is being stimulated. Generally speaking, the well-investigated behaviour of *Apis* (von Frisch, 1934), *Phormia* and *Calliphora* indicates that most sugars are acceptable, some—such as fructose, glucose, fucose, sucrose and maltose—being perceived at relatively low concentrations, while others like galactose, mannose and arabinose require higher concentrations to evoke a response. A wide variety of other substances, including acids, salts, alcohols, esters, amino-acids and oils, are all rejected if the concentration is sufficiently high but dilute solutions of acids and salts are sometimes preferred to water or dilute sugar solutions. Data for other insects tend to confirm these generalizations, though many exceptions are known. Thus, Thorpe *et al.* (1947) found that larvae of *Agriotes* spp. responded by biting movements to animal proteins, a fat and the sodium salts of some fatty acids as well as to sugars, while the host specificity of many phytophagous insects seems to depend partly on the presence of specific gustatory attractants in the plant (e.g. Chin, 1950).

Attempts to deduce something of the mode of action of gustatory stimulants by comparing their biological activity with their physico-chemical properties have not yet yielded results of a very fundamental character, though Frings (1946) found that various series of salts stimulated receptors on the mouthparts of *Periplaneta americana* in proportion to the mobility of the cations while Dethier & Chadwick (1950) found that for many organic compounds, the effectiveness in producing a rejection response in *Phormia* was inversely proportional to the solubility of the substance in water.

4. **Humidity and Temperature Perception.**—The great biological importance of these two environmental variables and the fact that they interact in controlling desiccation is sufficient reason for their treatment under a distinct heading.

(*a*) **Humidity.** Many insects react to differences in humidity and detailed behavioural studies have been made for a few species (e.g. *Tenebrio molitor* by Pielou & Gunn (1940) and Gunn & Pielou (1940); *Agriotes* larvae by Lees (1943); *Tribolium castaneum* by Willis & Roth (1950)). Some insects orientate themselves by the vapour from a distant source of water while in other cases the insects, by avoiding high or low humidities, tend to congregate in a preferred zone. There are indications that the humidity preferred by some species is similar to that in their natural habitat (Shelford, 1913) but behaviour is also known in some cases to be affected by the water-balance of the insect (e.g. Bentley, 1944; Roth & Willis, 1951a). Humidity receptors have been tentatively identified in *Pediculus* as peculiar tuft-like cuticular sensilla (Wigglesworth, 1941) and in many species as basiconic, trichoid and placoid sensilla (see summary in Roth & Willis, 1951). In some cases it seems that different receptors mediate the responses to dry and moist air. Whether the humidity receptors act like mechanical hygrometers through hygroscopic deformation of the cuticle or by some other mechanism dependent upon evaporation or whether there is a specific chemoreceptive response to water-vapour is not yet known.

(*b*) **Temperature perception** (Herter, 1953). Heat may be transferred to or from an insect by radiation, convection or conduction and also by evaporation or condensation. Only the first three methods are important as

stimuli to behaviour changes and experimental assessments of their relative importance have been made in some cases (Fraenkel & Gunn, 1940). Responses to radiant heat alone have been shown in few insects. *Schistocerca gregaria* displays a postural orientation to the sun's rays which, though partly a visual response, seems principally to depend on radiant energy (Fraenkel, 1930) and Slifer (1951) considers that similar behaviour in *Locusta migratoria* may involve peculiar segmentally arranged thermoreceptors on the head, thorax and abdomen. Many examples are known of blood-sucking insects which move towards a near source of heat provided by their mammalian hosts or an artificial body of similar temperature. The basis of this reaction is not always clear, but probably convective transfer of heat in the air is the directing stimulus rather than radiation and the antennae are the perceptive organs, though the actual receptors have not been identified with certainty (Wigglesworth & Gillett, 1934; Wigglesworth, 1941). Temperature receptors on the antennae, maxillary palps and tarsi are discussed by Gebhardt (1953). Many experimenters have exposed insects in an apparatus providing a gradient of temperature and found that they tend to congregate in a preferred zone (e.g. mainly from 24–32° C. for *Stomoxys calcitrans*; Nieschulz, 1934). Krumbiegel (1932) found that different races of *Carabus nemoralis* have preferenda correlated with the temperatures characteristic of the districts which they inhabit and in some species the zone depends on the previous history of the specimens. Not all experiments with a temperature gradient are satisfactory since the method fails to distinguish between convective and conductive transfer and humidity variations within the apparatus are not always eliminated.

5. **Vision and Visual Organs.**—Responses to light (though not necessarily to the same wavelengths that are perceived by the human eye) are mediated by (*a*) *Dermal receptors*, (*b*) *Dorsal ocelli*, (*c*) *Lateral ocelli* or *stemmata* and (*d*) *Compound eyes*. Typically, the imago possesses both compound eyes and dorsal ocelli though the latter are frequently absent, notably in wingless forms (Kalmus, 1945); lateral ocelli occur only in Endopterygote larvae (but see p. 106). Reduction or loss of photoreceptors is common among species which live habitually in dark situations (e.g. endoparasitic and cavernicolous insects and those inhabiting the nests of termites or ants or burrowing in soil or plant tissues). It is also characteristic of many ectoparasites (Mallophaga, Siphunculata, Siphonaptera, most Pupiparan Diptera).

(*a*) **Dermal light sense.** Several insects (Lepidopterous larvae, *Periplaneta*, *Tenebrio* larvae) react to light even after the eyes and ocelli have been removed or covered with opaque material. The general body surface appears to be sensitive to light and localized receptors have not been identified.

(*b*) **Dorsal ocelli.** The dorsal ocelli are innervated from the ocellar lobes which are located in the protocerebrum, between the mushroom bodies. When typically developed they are three in number disposed in a triangle. In the Plecoptera they are borne on the frons, and in certain other insects the median ocellus is situated on the frons, while the paired ocelli are located in the suture between that region and the vertex. In the more specialized orders the ocelli are usually situated on the vertex. In the Blattoidea they are either absent or, with very few exceptions, represented only by degenerate structures known as fenestrae. In the Siphonaptera Hanström (1927) considered that the paired ocelli, when present, occur on the sides of the head, the compound eyes having disappeared completely in this group. Wenk (1953), however, doubts this interpretation.

The median ocellus exhibits evidence of a paired origin since the root of the nerve supplying it is double, whereas the nerve-roots of the other ocelli are single. In some insects (e.g. Odonata, *Bombus*) the median ocellus exhibits a bilateral structure which is never found in the remaining ocelli.

The dorsal ocelli vary greatly in the details of their structure in various insects (see e.g. Hesse, 1901; Caesar, 1913; Link, 1908), but they exhibit certain common essential features and the following parts can be distinguished (Fig. 84).

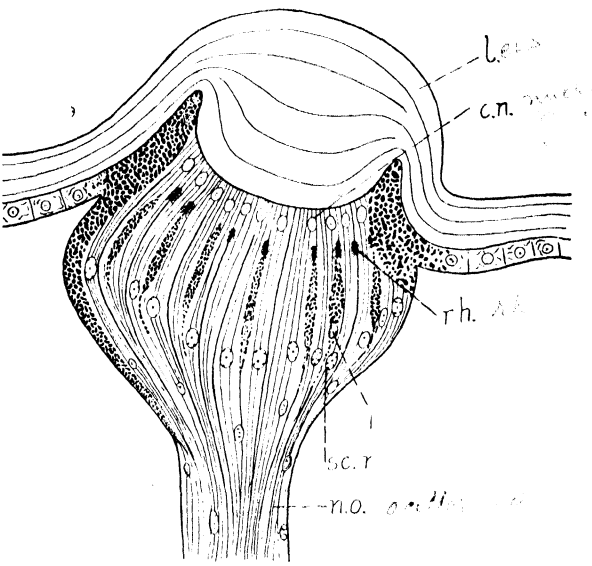


FIG. 84.—Section through an ocellus of *Aphrophora spumaria*

c.n, nucleus of corneagen cell; *l*, lens; *n.o*, ocellar nerve; *pc.n*, nucleus of pigment cell; *rh*, rhabdom; *sc.n*, nucleus of retinulae. *After* Link, *Zool. Jb. Morph.* 1908.

(i) *The cornea.*—The name cornea is given to that portion of the cuticle which is arched or raised to form the external investment of the ocellus. In this region the cuticle is more transparent than elsewhere and usually becomes thickened to form a more or less spherical body known as the *lens*. In rare instances (Ephemeroptera, Fig. 85) the cornea is arched but not thickened and the lens is formed by a mass of polygonal cells lying beneath the corneagen layer (vide Hesse, 1901; Seiler, 1905).

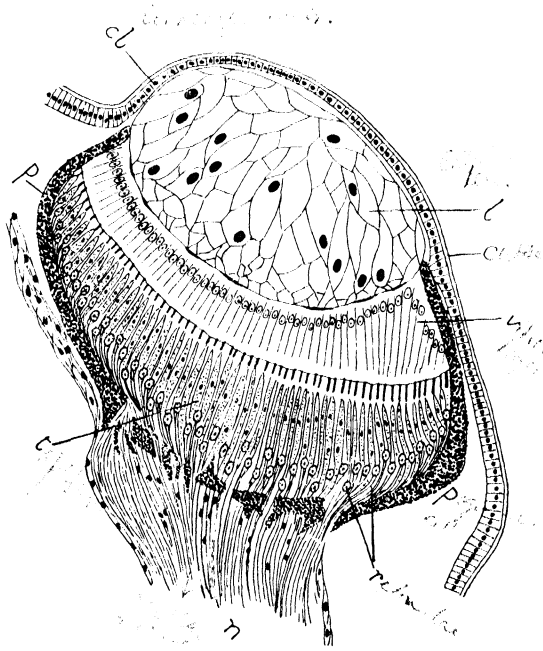


FIG. 85.—Section of the median ocellus of *Cloeon*

c, cuticle; *cl*, corneagen layer; *l*, cellular lens; *v*, vitreous layer; *r*, retinulae; *t*, tapetum; *p*, pigment ; *n*, ocellar nerve. *After* Hesse, 1901.

(ii) *The corneagen layer.*—This layer is directly continuous with the hypodermis but differs in being composed of colourless transparent cells which secrete and afford support to the lens. In some insects its cells become elongated and grouped together to form the *vitreous body* which supplements the lens in its function.

(iii) *The retina.*—The retina is composed of *visual*

cells which are sensory neurones, each being in direct connexion with a fibre of the ocellar nerve. The visual cells are associated together in groups of two, three or more cells, each group being termed a *retinula*, which surrounds a longitudinal optic rod or *rhabdom*. The latter is produced along the inner junctions of the component cells of a retinula, and varies in form according to the number of those cells present.

(iv) *Pigment cells*.—In some ocelli there are accessory cells loaded with pigment situated between the retinulae, or the pigment may be contained within the visual cells themselves. In deeply pigmented ocelli the margin of the lens and the proximal ends of the visual cells are enveloped in a dense layer of pigment forming the *iris* which is only interrupted by the fibres of the ocellar nerve.

The functions of the dorsal ocelli are not entirely clear. Though the lens is optically capable of forming an image, it does so at a level far below the retina (Parry, 1947) and form-perception is therefore impossible. Blackening of the dorsal ocelli reduces the speed with which some insects respond to stimulation of the compound eye by light and they are therefore regarded as 'stimulatory organs' which, when illuminated, raise the excitatory state with respect to these other stimuli (see, e.g., Wolsky, 1933).

(*c*) **Lateral ocelli (stemmata).** The lateral ocelli are, with very few exceptions, the only eyes present in insect larvae. As their name implies, they are located on the sides of the head where they occupy positions corresponding with those of the compound eyes of the imagines. The number of lateral ocelli is variable and not always constant in the same species: in some groups there is a single ocellus present on either side, while in others there may be six, seven or more ocelli. They differ essentially from the dorsal ocelli in the fact that they are innervated from the optic lobes of the brain, and also in that a crystalline refractive body may sometimes be developed beneath the corneal lens and that pigment granules are sometimes absent.

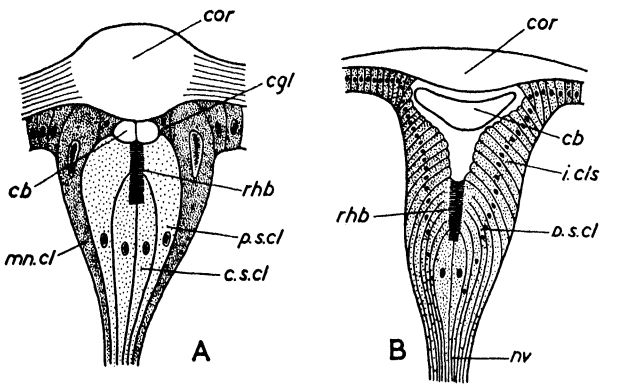


FIG. 86.—Two types of lateral ocelli. A. Lepidopteran larva. B. *Dytiscus* larva (*after* Snodgrass, 1935)

cb, crystalline body; *cgl*, corneagen cell; *cor*, corneal lens; *c.s.cl*, central retinal cells; *i.cls*, pigmented iris cells; *mn.cl*, mantle cell; *nv.*, ocellar nerve; *p.s.cl.*, peripheral retinal cells; *rhb*, rhabdom.

The histological structure is very varied, but four main types may be considered (Fig. 86):

(i) In the Tenthredinidae (Corneli, 1924) the single lateral ocellus is not unlike the typical dorsal ocellus in structure. The cuticle forms a lens-like cornea secreted by a thick underlying layer of corneagen cells (modified hypodermis). Beneath the latter is a retina composed of many retinulae, each made up of four cells whose apposed rhabdomeres form a rhabdom. A broadly similar type of structure is found in *Tipula* (Constantineanu, 1930), *Cicindela* (Friedrichs, 1931) and *Acilius*.

(ii) In *Dytiscus* (Günther, 1912), *Myrmeleon* (Hesse, 1901) and *Sialis*, a lens-like crystalline body is secreted beneath the cornea but the structure otherwise resembles that of the first type.

(iii) In the Lepidoptera and Trichoptera, each larval ocellus has a cornea and crystalline body but only seven retinal cells are present and form a single retinula with their apposed rhabdomeres constituting a single axial rhabdom. The resulting organ is strikingly similar to each ommatidium of a compound eye (see below).

(iv) In the larvae of several Nematoceran Diptera the lateral ocelli may be simplified (Constantineanu, 1930). There are few retinulae and a corneal lens is reduced or absent but the corneagen cells of some species have a vitreous appearance recalling that of a more or less degenerate crystalline body. In the unpigmented ocellus of *Chironomus* even these vitreous cells are absent and a single retinula lies directly beneath unmodified cuticle. The larvae of Cyclorrhaphan Diptera have a pair of very simple photoreceptors which are probably degenerate lateral ocelli. In *Musca* there is a small group of light-sensitive cells on each side of the pharyngeal sclerites and invisible externally (Bolwig, 1946). They are most sensitive to green light and apparently unable to perceive red.

The physiology of the lateral ocelli of Lepidoptera has been studied by Dethier (1942, 1943) who showed that both cornea and crystalline body can form a more or less distinct, inverted image which, irrespective of the distance of the object, falls somewhere on the rhabdom. Acting together, the six pairs of ocelli form twelve visual fields with little or no overlap and so provide a very coarse mosaic of intensities. By moving the head from side to side as it advances, the larva can examine a larger field and is at least capable of orientating itself towards the boundary between light and dark parts of its environment (Hundertmark, 1936). Some appreciation of colour is also probable (Götz, 1936).

Development of ocelli. The dorsal ocelli develop embryonically or post-embryonically, the lateral ones start developing in the embryo but the process may only be completed during post-embryonic life. Few cases have been studied in detail but all parts of the ocellus appear to be derived from the hypodermis or ectoderm. In *Formica* (Caesar, 1913) the dorsal ocelli develop from a fold of epidermis which becomes thickened locally and in which some cells elongate and withdraw basalwards to form the retinulae and become covered by a continuous corneagen layer formed from the remaining cells. In *Acilius* and *Hydrophilus* (Patten, 1888) the lateral ocelli of the larva develop as cup-like ectodermal invaginations which subsequently become closed in different ways. The cells of the floor of the cup differentiate into retinulae while those originally forming the lip secrete the cornea.

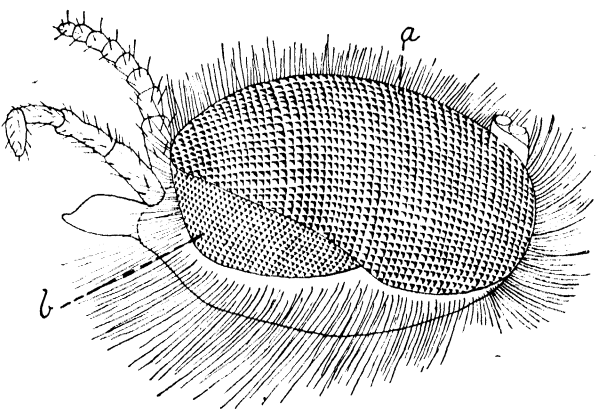


FIG. 87.—Head of *Bibio marci* (male), showing divided eye (left)

a, upper division of eye; *b*, lower division.

(*d*) **Compound eyes.** The principal feature distinguishing compound eyes from ocelli of either type is the fact that, in the former, the cornea is divided into a number of separate facets, whereas there is only a single facet to each ocellus. Compound eyes are formed of aggregations of separate visual elements known as ommatidia, each ommatidium corresponding with a single facet of the cornea.

Certain other features have been regarded as distinctive of compound eyes, but in some cases they are also found in ocelli. Compound eyes, similarly to lateral ocelli, are innervated from the optic lobes of the brain (Fig. 89).

The number and size of the facets of the compound eye vary within wide limits. In extreme cases, as in the worker of the ant *Ponera punctatissima*, each eye is composed of a single facet. According to Forel there are 6–9 facets in the same caste of *Solenopsis fugax*, while among other ants the number varies between about 100 and 600 in the workers, 200 and 830 in the females, and between 400 and 1,200 in the males. In *Musca* the eye consists of about 4,000 facets, in some Lepidoptera from 12,000 to 17,000 (Packard) and in Odonata between 10,000 and 28,000 or more (Tillyard). In most insects the facets are very closely packed together and assume a hexagonal form, but in some instances, where they are fewer in number and less closely compacted, they are circular. The facets are not always of equal dimensions over the whole area of the eye. Thus, in the males of *Tabanus* they are often larger over the anterior and upper parts of the eye, but the two fields are not sharply demarcated. In the males of certain other Diptera, including species of *Bibio* and *Simulium*, the two areas of different sized facets are very distinctly separated, each eye appearing to be double (Fig. 87). The extreme condition is attained among certain Coleoptera (*Gyrinus*, several Cerambycidae, etc.) and Ephemeroptera (*Cloeon*), where the two parts of the eye are so remote from each other that the insect appears to possess two pairs of compound eyes (Fig. 88). In *Cloeon* the anterior division of each eye is elevated upon a pillar-like outgrowth of the head, while the posterior division is normal.

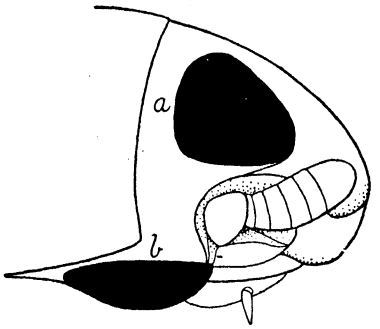


FIG. 88.—Head of *Gyrinus natator*, showing divided eye (right)
a, upper division of eye; *b*, lower division.

The structure of an ommatidium (Fig. 90). The structure of the ommatidia varies in different insects but in all cases the differences are modifications of a common type. The various parts which enter into the composition of an ommatidium, passing from without inwards, are enumerated below.

(i) *The cornea.*—The cornea is the transparent area of cuticle forming the facet or lens of an ommatidium and is often more or less biconvex in form. It is cast off during each act of ecdysis.

(ii) *The corneagen layer.*—The part of the hypodermis which extends beneath the cornea is known as the corneagen layer. It consists of two cells which, in some insects, are only to be detected with difficulty. In other cases they are wanting and in these instances the cornea is secreted by the outer ends of the cells of the crystalline cone.

(iii) *The crystalline cone cells.*—Beneath the corneagen layer or the cornea, as the case may be, there is a group of four cells which in the eucone eyes secrete a transparent body termed the *crystalline cone*. The nuclei of these cells are sometimes known as the nuclei of Semper.

(iv) *The primary iris cells.*—These are densely pigmented cells which are disposed in a circlet surrounding the cells of the crystalline cone and the corneagen layer.

(v) *The retinula.*—The retinula forms the basal portion of an ommatidium and is composed of a group of usually seven pigmented visual cells, each of the latter being continuous with a post-retinal fibre. The visual cells collectively secrete an internal optic rod or *rhabdom* and the portion of the latter contributed by each cell is termed a *rhabdomere.* Each rhabdomere is stated to exhibit an extremely fine fibrillar structure, the individual fibrils passing right through the cell and emerging as the single nerve fibre previously

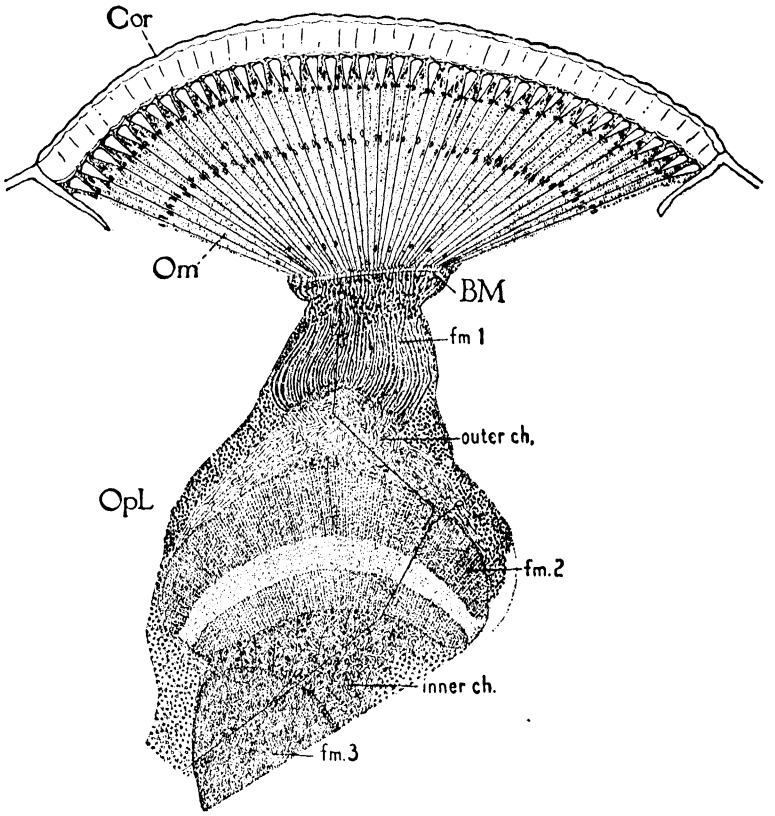


FIG. 89.—Section through the eye and optic lobe of a worker honey bee

BM, basement (or fenestrated) membrane; *Cor*, cornea; fm_1, periopticon; fm_2, epiopticon; fm_3, opticon; *inner ch*, internal chiasma; *Om*, ommatidium; *OpL*, optic lobe; *outer ch*, external chiasma. From Snodgrass, *after* Phillips.

alluded to. The rhabdom forms the central axis of the retinula and is in contact with the extremity of the crystalline cone.

(vi) *The secondary iris cells.*—These are commonly elongated pigment cells which surround the primary iris cells and the retinula, thus serving to isolate an ommatidium from its neighbours.

The proximal extremities of the ommatidia rest upon a fenestrated or *basement membrane* through whose perforations pass the nerve fibres from the retinulae and frequently fine tracheae. The latter, as they enter further into the eye, become arranged parallel with the long axes of the ommatidia. The nerve fibres (post-retinal fibres) collectively unite the ommatidia with the periopticon or outermost tract of the optic lobe of the brain.

The types of compound eyes. Four types of compound eyes are

described among insects. Of these, the first three were recognized by Grenacher (1879) and the fourth type by Kirchhoffer (1909–10).

1. *Eucone eyes.*—In eyes of this type each ommatidium contains a true crystalline cone, which is a hard refractive body formed as an intracellular product of the cone cells: the nuclei of the latter are located in front of the one. Eucone eyes are found in the Thysanura, Orthoptera, Odonata, Ephemeroptera, Trichoptera, Lepidoptera, Hymenoptera, Chrysopidae, certain of the Hemiptera and in the Cicindelidae, Carabidae, Dytiscidae and Scarabaeidae among Coleoptera.

2. *Pseudocone eyes.*—In this type of eye there is no

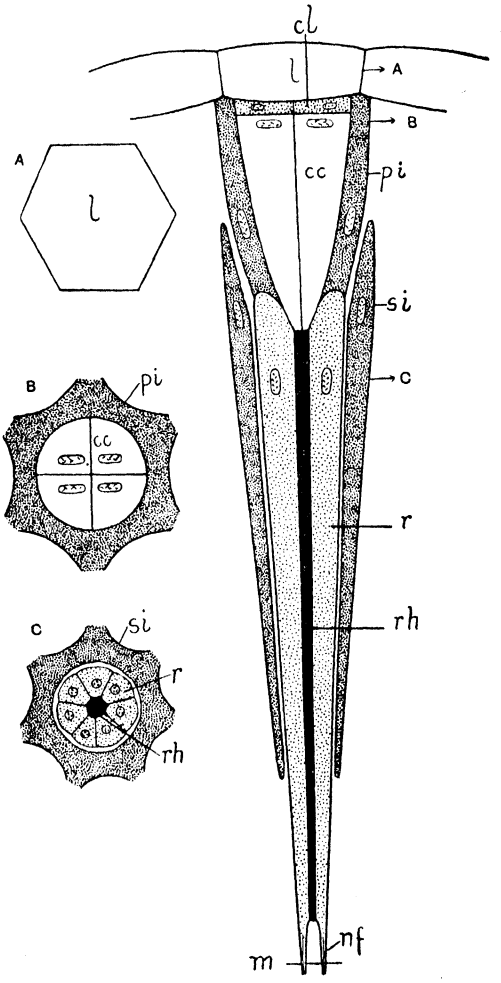


FIG. 90.—Diagram of generalized ommatidium of the eucone type from an eye giving an apposition image

cc, crystalline cone; *cl*, corneagen layer; *l*, corneal lens; *m*, fenestrated membrane; *nf*, nerve fibre; *pi*, primary iris cell; *r*, retinula; *rh*, rhabdom; *si*, secondary iris cells. A, B and C, transverse sections of regions bearing corresponding lettering.

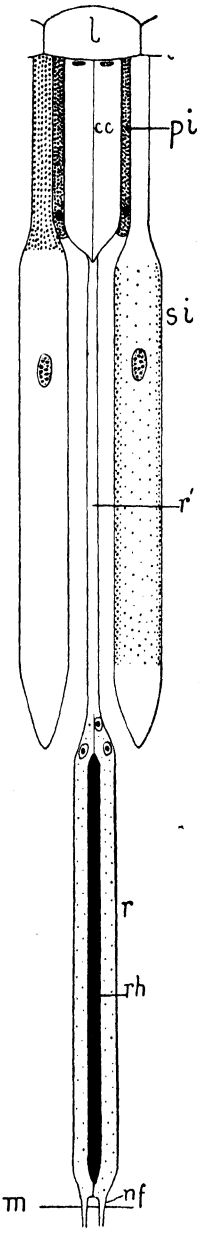


FIG. 91.—Diagram of an ommatidium from an eye giving a superposition image

On the left side the pigment is seen in a condition adapted for night vision and on the right side for day vision. *r'*, filamentous prolongation connecting retinula with crystalline cone. Other lettering as in Fig. 82.

true crystalline cone and the four cone cells are filled with a transparent, semi-liquid material which lies in front of the nuclei. Pseudocone eyes are found in the Brachycera and Cyclorrhapha among Diptera.

3. *Acone eyes.*—In the acone eyes there is a group of elongate, transparent cone cells but the latter do not secrete any kind of cone whether crystalline or liquid. Eyes of this kind are found in the Dermaptera, Hemiptera, certain of the Diptera Nematocera, and in the Staphylinidae, Histeridae, Silphidae, Coccinellidae and Curculionidae among Coleoptera.

4. *Exocone eyes.*—The name exocone is here applied to that type of eye in which the crystalline cone is replaced by a cone of extracellular, cuticular origin which appears as a deep ingrowth from the inner aspect of the corneal facet, in front of the unmodified cone cells. Eyes of this type are found in the Dermestidae, Elateridae, Byrrhidae and Cantharidae (Kirchhoffer, 1909–10).

In night-flying insects there is a structure termed the *tapetum* which reflects the light that has entered the eyes causing the latter to shine in the dark, when they assume the appearance of golden or ruby globes. In eyes of this kind the retinular elements are impregnated with a special colouring substance (erythropsin, xanthopsin) and the spaces between the retinulae are densely packed with fine, longitudinal tracheae filled with air (Fig. 92). It is probable that the effect of the faint nocturnal light is intensified owing to the light passing through the retinulae a second time, when it is reflected from the glistening tracheae of the tapetum (Bugnion & Popoff, 1914).

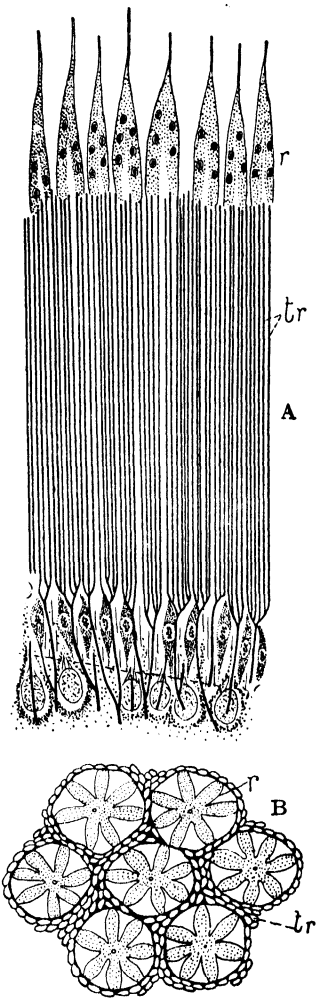


FIG. 92.—A. Retinulae of the eye of *Celerio euphorbiae*, showing groups of fine longitudinal tracheae. B. Transverse section of a group of retinulae of the eye of *Phlogophora meticulosa*, showing the interspaces packed with tracheae

tr, trachea; *r*, retinulae. *After* Bugnion & Popoff.

Development of compound eyes (Bodenstein, 1953). The compound eyes develop embryonically in the Exopterygota though there is a postembryonic increase in the size of individual ommatidia and the differentiation of at least some new ommatidia (Friza, 1928; Przibram, 1930.) In the Endopterygota the adult eyes generally differentiate in the late larval and pupal stages though the process begins earlier in the Diptera (Constantineanu, 1930; Bodenstein, 1949). Detailed accounts of development in Endopterygotes are given by Johansen (1893), Kirchhoffer (1910), Günther (1912), Bott (1928) and Umbach (1934). In general terms, a zone of larval epidermis undergoes cell-division and invagination and the eye develops entirely from this. Certain groups of cells move basalwards and eventually form the retinulae while other conspicuous cells simultaneously become associated with the distal parts of

the developing retinulae and form the crystalline cone cells. The corneagen cells come to surround the crystalline cone and further epidermal cells elongate and form the pigment cells. Though it is usually considered that the post-retinal fibres are the axons of retinular cells, Roonwal (1937) and some earlier workers have claimed that these fibres arise as outgrowths of cells in the developing brain, an observation which conflicts with histological studies of the developed eye, with other ontogenetic data and with the view that the retinulae are composed of primary sense cells.

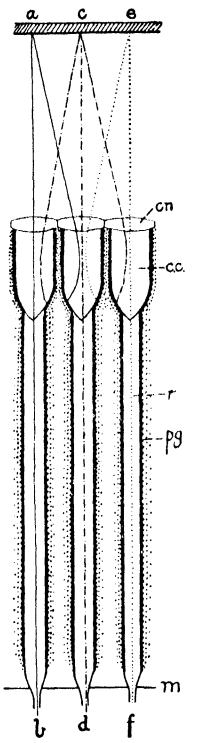


FIG. 93.—Diagram representing vision with an eye giving an apposition image

The only rays of light from an object *a c e* which will reach the retinulae are those parallel to the long axes of the ommatidia (e.g. *ab*, *cd*, *ef*). All oblique rays impinge on the sides of the cones where they are absorbed by the pigment. *cn*, corneal lens; *c.c*, crystalline cone; *r*, retinula; *pg*, pigment; *m*, fenestrated membrane. This Fig. and Fig. 94 are based on Exner.

Atypical eyes. Certain insects possess lateral 'eyes' which have a distinctly ocelliform structure and whose phylogenetic relationship to compound eyes or to ocelli is in doubt. Examples are found in *Pediculus* (Wigglesworth, 1941) where there is a single facet on each side and in male Strepsiptera (Strohm, 1910) where about 50 facets are grouped together. In both cases, each corneal facet surmounts a large number of retinulae. On the other hand, in the Collembola and *Lepisma*, where each facet is associated with a single retinula, the structure is very reminiscent of the ocelli of Lepidopterous larvae. The lateral 'ocelli' of some Aphidoidea and male Coccoidea may also be mentioned here.

Physiology of the compound eye. The exact mechanism whereby light falling on the rhabdoms releases nervous activity in the retinular cells is not known, though it is generally assumed that a photochemical process occurs whereby the breakdown products of light-absorbing substances excite the cells. When fully developed the compound eyes of insects are not merely sensitive to light but are also able to mediate the discrimination of form with various degrees of visual acuity and to perceive the movement and spatial location of distant objects. They are also capable of distinguishing differences in the intensity and wavelength of incident radiation but not all these functions have been investigated to the same extent and the visual capacities of many species remain unknown. Full accounts are given in von Buddenbrock (1935) and later physiological textbooks and only an outline of the visual processes can be attempted here.

(i) **Perception of form and movement.** This depends on the formation of an image by the eye, a process accounted for by the mosaic theory of vision, first proposed by Müller in 1826. According to this, each ommatidium perceives a small luminous zone corresponding to its projection on the visual field and these zones (which will normally differ in intensity) together form an erect image composed of light and dark spots comparable to a newspaper photograph. The focussing of the light by the dioptric part of each ommatidium (cornea and crystalline cone) is a relatively complex process (Exner, 1891) since the system functions as a 'lens-cylinder' with its refractive index decreasing from the central axis to the periphery and in such cases the level at which the rays from an object come to a focus depends on the relation between

the focal length of the system and the length of the cylinder. Connected with this fact and other properties of the ommatidia, it is possible to distinguish two methods of image formation:

(*a*) In the formation of an *apposition image* (Fig. 93), light rays from each external point enter several ommatidia but all are cut off by the pigment separating the ommatidia except for those which one dioptric unit can bring to a focus on the distal end of the underlying rhabdom.

(*b*) In eyes capable of forming a *superposition* image (Fig. 94) the distal end of each rhabdom is well below the apex of the cone and the intervening space is non-refractile and devoid of pigment. Light rays from each external point enter several facets and though some are extinguished by the pigment between adjacent cones the remainder are brought to a focus at the distal end of a single rhabdom, each rhabdom thus receiving light from several cones.

It will be clear from the above account that in the formation of a superposition image a greater proportion of the light from each external point is made available at the distal end of the corresponding rhabdom and it is therefore natural that nocturnal species should have eyes capable of forming superposition images, while the apposition type is formed by the eyes of diurnal insects. In some species, however, the eye can function in both ways through the migration of pigment granules within their cells or the movements of the cells themselves (Fig. 95). Thus, in *Enarmonia pomonella* (Collins, 1934) at low light intensities the pigment separates the cones of adjacent ommatidia but not the region between cone and rhabdom so that a superposition image is formed. If the intensity of the incident light is increased, the pigment migrates proximally so that the region between cone and rhabdom is optically isolated from that of neighbouring ommatidia and the only light reaching a given rhabdom is that refracted by the overlying cone (i.e. an apposition image is formed). The pigment movement is complete in about 30–60 minutes in *Enarmonia*; it can be induced experimentally in individual ommatidia of *Ephestia* and is probably under nervous control (Day, 1941).

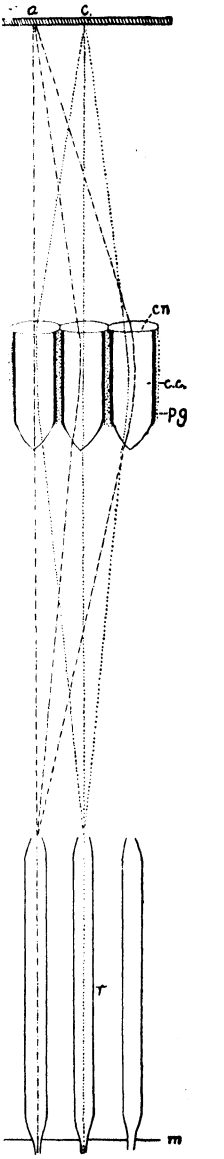


FIG. 94.—Diagram representing vision with an eye giving a superposition image

Each retinula receives not only an image from rays entering its own facet, but also those from peripheral oblique rays from neighbouring facets. Lettering as in Fig. 93.

The visual acuity of the compound eye (i.e. the reciprocal of the subtended angle which must separate two external points before they are recognized as discrete) depends on the fineness of the mosaic image. This, in turn, is controlled by the number of ommatidia (or of ommatidial units, since nervous coupling of ommatidia is probable) and the angular separation of the ommatidia. The latter usually differs in different parts of the eye, which is generally not part of a perfect sphere, and corresponding differences in visual acuity have been demonstrated (e.g. Hecht & Wolf,

1929). Resolving power also varies with the intensity of illumination. In general, the visual acuity of insects is very much lower than that of man; the maximum visual acuity of *Apis mellifera*, for example, is about 1/130 that of man and corresponds exactly to the minimum ommatidial angle (Baumgärtner, 1928). Such low acuity precludes accurate recognition of form, but there are many examples of insects responding visually to particular structures in their environment and in *Apis*, which has been most intensively investigated, it is known (Hertz, 1934–37) that different patterns with subdivided outlines can be recognized though the insects cannot distinguish circles, triangles and squares of about the same size (see also Ilse, 1932). It is likely that patterns with a complex outline are distinguished not by the static properties of the pattern but by the frequent changes in stimulation as the image of the pattern passes over the retina during the movement of the insect (Wolf & Zerrahn-Wolf, 1937). Such a mechanism may well be of considerable importance in form discrimination by flying insects (Autrum, 1949). The perception of distance, particularly important in predacious forms, is accomplished through the overlapping of the visual fields of the two eyes so that an object is located simultaneously by a group of ommatidia from each (Baldus, 1926).

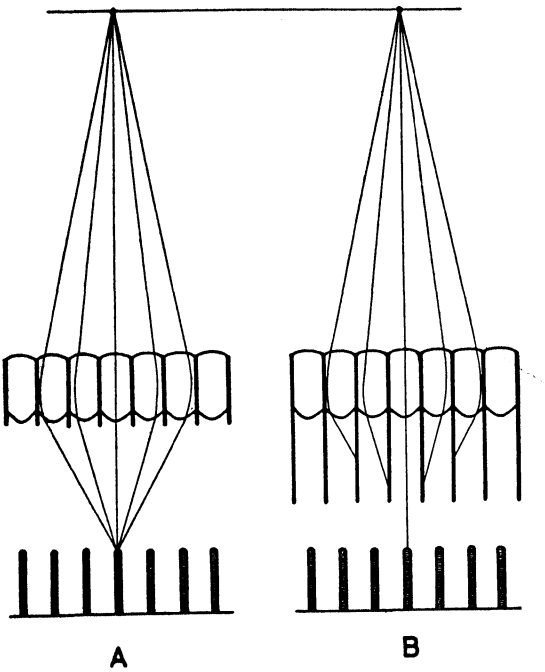


FIG. 95.—A. Compound eye in dark-adapted condition showing formation of superposition image. B. Same, in light-adapted state showing formation of apposition image

(ii) **Perception of colour.** Simple observations such as those of a tendency for an insect to visit certain coloured flowers, do not necessarily demonstrate colour vision since insects are known to discriminate between differences in the intensity of the light reflected from various surfaces. More elaborate experiments have shown that insects may be stimulated by wavelengths between about 2,500 Å and 7,000 Å (i.e. they can often detect ultraviolet radiation invisible to man). They are, however, more sensitive to certain wavelengths than to others and by behavioural studies or the recording of nervous impulses from stimulated eyes (e.g. Autrum & Stumpf, 1953) it is possible to determine a spectral sensitivity curve. Cameron (1938), for example, found *Musca* to be stimulated most by a wavelength of 3,650 Å (ultra-violet), while Weiss *et al.* (1944) found that many species are most sensitive to the ultra-violet and blue-green parts of the spectrum. Surfaces reflecting such wavelengths will therefore appear brighter to an insect than those which do not. Nevertheless, true colour vision has been demonstrated in several species such as *Apis mellifera* (von Frisch, 1914; Kühn, 1927),

various Lepidoptera (Ilse, 1928), Diptera and Coleoptera (Schlegtendal, 1934). It has been found that different species distinguish different parts of the spectrum. For example, *Apis* recognizes four 'colours'—a region from 6,500 Å to 5,000 Å (red, yellow and green) and three others of 5,000–4,800 (blue-green), 4,800–4,000 (blue-violet) and 4,000–3,100 Å (ultra-violet). On the other hand, *Pieris brassicae* can distinguish between yellow and green and apparently does not perceive ultra-violet. A few insects such as *Carausius* and *Troilus* are believed definitely not to possess colour vision and in *Notonecta* only the posterior dorsal ommatidia are fully sensitive to colour (Rokohl, 1942). Finally, *Apis mellifera* and some other insects are able to perceive the plane of vibration of polarized light, the individual retinular cells acting as analysers (von Frisch, 1949, 1950; Autrum & Stumpf, 1950) and this faculty is of importance in direction-finding by foraging bees.

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THE SOUND- AND LIGHT-PRODUCING ORGANS

1. Sound-producing Organs

SOUNDS of different kinds and intensities are produced by a number of species in all the main orders of insects. In some cases, the sound-producing organs are similar in the two sexes (as in many Coleoptera) but frequently they are either confined to, or more strongly developed in, the male (e.g. most Orthoptera and Cicadidae). The biological significance of the sounds which are produced is not clear in many cases but in some species they facilitate mating by attracting the sexes or stimulating the female and in other instances they may express sexual rivalry between males, subserve species-recognition (thus helping to keep members of the same species together), communicate warnings of danger or have a defensive function. A single species may make several sounds, each with its own function.

The methods by which sounds are produced may be classified under the following headings.

(*a*) By the tapping of some part of the body against an external object.
(*b*) By the friction of one part of the body against another part.
(*c*) By the vibration of the wings.
(*d*) By the vibration of a special membrane exerted by muscular action.
(*e*) By miscellaneous vibrations, including those of uncertain origin.

A. SOUNDS PRODUCED BY THE TAPPING OF SOME PART OF THE BODY AGAINST AN EXTERNAL OBJECT

The best-known example of this type of sound-production occurs in the Death-watch Beetle, *Xestobium rufovillosum*, and allied Anobiidae where what is thought to be a sexual call is made by tapping the head against the walls of the burrow (Darwin, 1909). Some male Plecoptera rap the end of the abdomen against the substrate (Macnamara, 1926) and the Psocopteran *Trogium pulsatorium* (the 'Lesser Death-watch') also makes a sound in this way (Solowiew, 1924). Again, the pupae of a few Hesperiidae and Lycaenidae produce what is probably a defensive sound by knocking the body against the walls of their cells or the substrate (Hinton, 1948). Finally, the soldiers of many species of termites (e.g. *Bellicositermes*) respond to slight mechanical disturbances of their nest by hammering their heads against the nest-structure, sometimes in rhythmic unison, though it is uncertain whether this behaviour acts as a danger signal to the colony.

B. SOUNDS PRODUCED BY THE FRICTION OF ONE PART OF THE BODY AGAINST ANOTHER PART

By far the greater number and variety of the sounds emitted by insects are produced by this method, the actual parts concerned with the sound production being known as stridulating organs. Practically every external part of the body which is subjected to friction on an adjoining part has given rise to a stridulating organ in one or other insect.

Stridulating organs are possessed by representatives of several orders of insects, particularly the Orthoptera, Coleoptera and Hemiptera, but it is in the first mentioned order that they are best known (Chopard, 1938). In many species of the families Acrididae, Tettigoniidae and Gryllidae the males are capable of vigorous stridulation: outside these three families fewer other Orthoptera stridulate and the faculty is rarely present in the females (Fulton, 1933). Among the Acrididae the sounds are often produced by a row of pegs on the inner side of each hind femur being worked against the outer surface of each tegmen (Fig. 96). In some others (Oedipodinae) a row of prominences on a secondary tegminal vein is scraped by a ridge on the inner side of each hind femur. In the Tettigoniidae and Gryllidae the sound is produced when a row of teeth on the tegminal vein 1A (the file) is scraped by a sclerotized part of the margin of the opposite tegmen, thus throwing into vibration certain areas of the tegmen. Yet another type of stridulatory apparatus occurs in the Gryllacrididae where ridges on the side of the 2nd or 3rd abdominal segments are rubbed by the posterior femora and several other mechanisms peculiar to individual species of Orthoptera have been described (e.g. by Henry, 1942, and Burtt, 1946). The sounds produced are often very characteristic of the species and each form may produce several types of sound including a normal song and a number of epigamic songs (Faber, 1929–36; Jacobs, 1950). Analysis of Orthopteran stridulation by electrical methods (Pierce, 1948) reveals the complex character of the sound, e.g. in *Gryllus assimilis* the normal song consists of a series of chirps at intervals of about $\frac{1}{3}$ of a second, each chirp comprising 2–6 very short pulses during which sound-waves with a frequency of about 5,000 cycles per second undergo amplitude modulation.

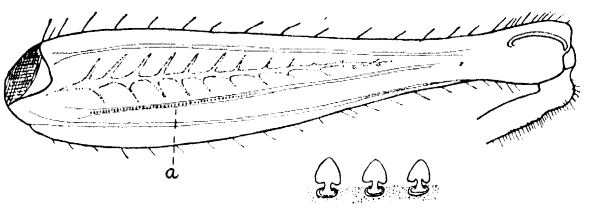


FIG. 96.—Hind femur of an Acridid
a, row of pegs, three of which are shown greatly enlarged.

Among Coleoptera, stridulatory organs have been reported from widely different parts of the body in a variety of species, both from larvae (e.g. *Geotrupes*) and adults (Darwin, 1909; Gahan, 1900; Dudich, 1920–21; Arrow, 1942). One part of the exoskeleton forms a file-like area (*pars stridulans*) which is rubbed by an adjacent region (*plectrum*) when the two undergo relative movement. The organs are generally inconspicuous and equally developed in both sexes; in a few species they are confined to one sex, the female in *Phanopate* but more usually the male (e.g. *Xenoderus*, *Cryptorrhynchus lapathi*). Whether stridulation in beetles has a sexual significance is uncertain; in *Chiasognathus* it is probably defensive while in the sub-social Passalidae—the

loudest stridulators among beetles—it perhaps helps to keep the individuals of a colony together.

Among Hemiptera there is similarly a great diversity of stridulatory organs of this type, especially among Heteroptera (Weber, 1930), where both sexes or the male alone can produce sounds. The peculiar strigil of male Corixidae is apparently used in some unknown way to produce a sound in *Micronecta*, but in those other male Corixids which stridulate the noise is made by the passage of an area of spines on the femur over the angular side-margins of the face (von Mitis, 1935).

Several Lepidoptera are known to be capable of stridulation (Bourgogne, 1951). They usually produce a hissing or rustling sound and four mechanisms may be noted: (*a*) friction between the fore and hind wings, as in *Cidaria dotata* males (Hampson, 1894); (*b*) friction between legs and wings, as in some male Agaristinae (Hampson, 1892) and fertilized females of *Parnassius mnemosyne* (Jobling, 1936); (*c*) friction between adjacent parts of the thoracic wall (e.g. both sexes of the Arctiid *Rhodogastria*, where the sound is accompanied by the emission of froth through reflex bleeding and is probably defensive (Carpenter, 1938)); (*d*) friction between part of the 3rd abdominal sternum and an infolding of the adjacent sternopleural region, as in some male Lymantriids.

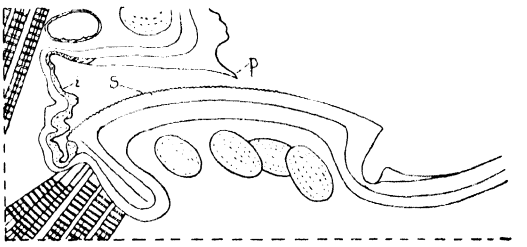


FIG. 97.—Stridulating organ of *Myrmica laevinodis* in median section

p, edge of postpetiole forming a 'scraper'; *s*, stridulatory surface on first gastric segment; *i*, intersegmental membrane. *After* Janet.

In the Hymenoptera stridulating organs are common among certain ants (Janet, 1893) and vary in structure in different species, and in the castes of the same species (Fig. 97). The organ consists of a file and scraper on the mid-dorsal region of the integument, at the base of the first gastric segment where the preceding segment overlaps. In *Mutilla europaea* both sexes have the power of stridulation, and the organ is very similar in its position and structure to that found in ants.

C. SOUNDS PRODUCED BY THE VIBRATION OF THE WINGS

Many insects make a humming or buzzing sound during flight, the frequency of the emitted note appearing to some observers to be the same as that of the wing-beat. Sotavalta (1947) gives numerous examples, but in a more detailed physical analysis of the flight-tone of *Drosophila funebris* Williams & Galambos (1950) found that though each cycle of wing-movement corresponds to one of sound, there are, in addition to the fundamental frequency, prominent harmonics which result in wide departures from a simple sinusoidal type of vibration (see also p. 119).

D. SOUNDS PRODUCED BY THE VIBRATION OF A SPECIAL MEMBRANE EXERTED BY MUSCULAR ACTION

Sound-producing organs of this type are characteristic of the Auchenorrhynchan Homoptera and among the Cicadidae there is found one of the most

complex kinds of sound-producing organs known. These structures are met with in the males, the females being either silent or only possessing rudiments of the apparatus. The great volume of sound emitted by the cicadas marks them out as being the noisiest representatives of the Insecta.

The apparatus, and the sounds produced by it, have been studied by many observers from Réaumur onwards. See especially Carlet (1887) and Myers (1929). The organs in question comprise a pair of shell-like drums or tymbals situated at the base of the abdomen and which vibrate by the action of powerful muscles. In *Magicicada septendecim* the true sound organs are freely exposed, but in many other cicadas the drums are covered by overlapping plates or opercula.

In the more perfect form of the apparatus, which is exhibited for example in *Tibicen plebeia*, the account given by Carlet may be followed (Fig. 98). In this species the *opercula* are a pair of large plates which are backward extensions of the metathoracic epimera, and situated on the ventral side of the body, where they overlap the base of the abdomen. On removing an operculum a pair of cavities containing the external parts of the sound-producing apparatus is disclosed. The larger of these cavities is ventral, and the smaller is lateral in position. Their walls contain three specialized areas of membrane which are known respectively as the *tymbal*, the *folded membrane* and the *mirror*. The *tymbal* is a crisp, plaited membrane surrounded by a sclerotized ring; it forms part of the inner wall of the lateral cavity, and is somewhat shell-like in appearance with its convex surface bulging outwards. The *folded membrane* is in the anterior wall of the ventral cavity, while the *mirror* is a tense, mica-like membrane in the posterior wall of that cavity. In close association with the whole apparatus there is an extensive air-chamber which opens to the exterior by means of the third pair of spiracles. The sound is produced by the rapid in and out movement of the tymbal, which is brought about by a powerful muscle.

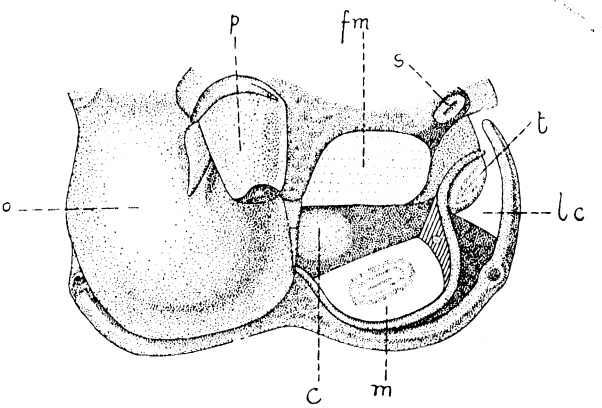


FIG. 98.—Sound-producing apparatus of a cicada with the operculum of one side removed

c, ventral cavity; *fm*, folded membrane; *lc*, lateral cavity; *m*, tympanal organ; *o*, operculum, that of the other side removed; *p*, base of leg; *s*, spiracle; *t*, tymbal. *After* Carlet, *Ann. Sci. nat.* 1887.

The latter arises from the 2nd abdominal sternum and is attached to the inner face of the tymbal. When the muscle contracts the tymbal is pulled inwards: on the relaxation of the muscle the tymbal regains its former position by virtue of the elasticity of its cuticular ring. This method of sound production has been compared to the pushing in and out of the bottom of a tin vessel, which makes a cracking sound. The destruction of the tymbal of both sides of the body renders the insect silent. The sound can also be modified by the operculum which is capable of being slightly elevated, but its main function is protective. The pattern of sound produced by cicadas is seen on electrical investigation to be relatively complex—in *Platypleura capitata* a series of

damped oscillations at 4,500 cycles per second undergoes amplitude modulation to give pulses repeated at the rate of 390 per second (Pringle, 1953). The function of the song is apparently that of bringing individuals together and attracting the females to males (Myers, 1929). The so-called mirror is part of a tympanal auditory organ (see p. 92) which is put out of action by a special muscle when an individual is about to stridulate.

Ossiannilsson (1949) has found that males in many other Auchenorrhynchan families (Delphacidae, Cixiidae, Cercopidae, Membracidae, Jassidae) have small stridulatory organs essentially similar to those of cicadas and more weakly developed organs even occur in some female Cercopids and Jassids. The sounds produced by these insects are always of low intensity and not always audible to the unaided ear, though several types of song (courtship, rivalry, distress, etc.) are said to be distinguishable.

E. SOUNDS PRODUCED BY VIBRATIONS OF UNCERTAIN ORIGIN

In certain insects, particularly Diptera, sounds are produced in a manner different from those already referred to. The actual method of sound production in these cases has given rise to much discussion, and the evidence that is available is of a conflicting nature. Many entomologists are familiar with the highly pitched singing note that is emitted by various flies, particularly in some species of Syrphidae, both when hovering and when at rest. Somewhat similar notes are produced by several Coleoptera and by Hymenoptera. According to Landois (1867) the sound is caused by the vibration either of a series of lamellae, or a tongue-like fold, projecting into the lumen of the trachea close to certain of the spiracles. These structures are membranous infoldings of the tracheal intima which are believed to be set in vibration by the forcible passage of air through the spiracles, thus producing a highly pitched note. Landois states that if the head, wings, legs and abdomen of a *Calliphora* be removed, so that the thorax is left with no vibratory parts other than the halteres, the highly pitched note is maintained. If the thoracic spiracles be closed with gum or wax the sound ceases. Lowne has described peculiar tympanic chambers immediately behind the insertions of the wings in *Calliphora* and in close association with the corresponding spiracles. He concludes that the emission of sounds in this insect is due to the expulsion of air through the thoracic spiracles, and the vibration of a membrane in the tympanic organ. He also mentions that the whole thorax vibrates distinctly when the insect is held between the finger and thumb. Bellesme notes that in Diptera and Hymenoptera the highly pitched sounds continue after removal of the wings and the stoppage of the spiracles. He considers that they are due to very rapid changes in the form of the thorax—in fact a kind of thoracic vibration—due to contractions of the wing muscles. J. Pérez from a study of certain Diptera also finds that the sounds continue when the spiracles are artificially closed, and attributes them to vibrations of the wing bases against certain closely associated sclerites. The fact that different observers have not always used the same species of insect in their experiments may explain some of the discrepancies in the results obtained, but the subject is clearly one in need of renewed investigation.

2. The Light-Producing or Photogenic Organs

Certain insects are self-luminous owing to the possession of special photogenic organs (Buck, 1948): some other insects owe their luminous properties

to the presence of light-producing bacteria, or on account of having ingested luminous food.

True luminous insects are almost confined to the order Coleoptera and more particularly to various genera of Lampyridae and Cantharidae, notably *Lampyris*, *Luciola*, *Phosphaenus*, *Photuris*, *Photinus*, *Phengodes* and others. The Elaterid genera *Pyrophorus* (the 'cucujos') and *Photophorus* are also luminous, and the same remark applies to several species of the Carabid *Physodera* and to *Buprestis ocellata*. Outside the Coleoptera, the larva of the Mycetophilids *Arachnocampa luminosa* and *Ceroplatus testaceus* (Stammer, 1932) has photogenic powers. A small number of other insects are also luminous but are not known to possess special organs for the purpose, and in many cases the light is probably associated with the presence of bacteria, Pfeiffer & Stammer (1930). Examples of this kind include a few Ephemeroptera, together with certain Collembola (Heidt, 1936), larval Diptera and Lepidoptera.

In the Lampyridae, previously mentioned, the luminosity is known in some species to extend to all the developmental stages, and is a character of their plasma. In the egg the luminous substance is diffused, but in the post-embryonic phases it is localized in the photogenic organs. The latter structures vary greatly in size, shape and position in different species and according to the sex and developmental stage. In *Phengodes* and *Phrixothrix*, for example, there are 11 or 12 segmentally arranged pairs of organs while in many species (e.g. *Lampyris noctiluca* females) they are found principally on the 6th and 7th abdominal sterna and in *Pyrophorus* they occur on the pronotum and anterior abdominal sterna. They may be equally developed in both sexes, as in *Luciola* and the Elateridae or the females, which are sometimes apterous and larviform, may be the sole or principal luminous sex.

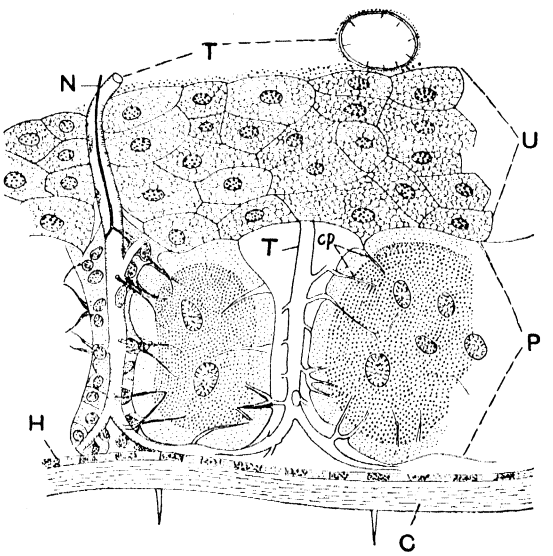


FIG. 99.—Luminous organ of *Photinus*

C, cuticle; *cp*, tracheoles; *H*, hypodermis; *N*, nerve; *P*, photogen layer; *T*, tracheae; *U*, reflector layer. *After* Williams, 1916.

According to the species concerned, the light may be emitted as a continuous glow, an intermittent or pulsating glow of variable intensity or periodic short flashes whose characteristics are influenced by environmental factors. The spectacular synchronous flashing of Lampyrids (Buck, 1938) is not fully explained. The light occupies wavelengths over the range 5,000 to 6,500 Å (Buck, 1941) and is usually yellowish-green though in *Pyrophorus* the abdominal organs emit a reddish light in flight and the thoracic ones a green light when the insect is not flying. The light is usually thought to assist in the attraction of the sexes for mating and in *Photinus pyralis* Buck (1937) found that females

attract males by returning the male flash after an interval of about two seconds.

The organs are located beneath areas of transparent cuticle and their histological structure shows various degrees of complexity from those of *Phengodes*, where the photogenic structures are large independent cells similar to oenocytes, to those where a compact organ (Fig. 99) is composed of masses of photogenic cells arranged in rosette-like fashion around tracheae from which short trunks run into tracheal end-cells. From the latter arise numerous tracheoles which penetrate between the photogenic cells while the inner surface of the organ is covered by a layer of urate-containing cells. These form the so-called reflecting layer, the function of which is uncertain.

As in other luminous plants and animals, the light of insects is emitted when a substance, luciferin, is oxidized by free oxygen in the presence of water and an enzyme, luciferase (Harvey, 1940). The energy for this change is obtained through preliminary reactions involving adenosine triphosphate (McElroy & Harvey, 1951) and very little heat accompanies the emission of light. It is probable that in the luminous organs of complex structure the regulation of flashing depends on a nervously-controlled 'valve-like' action of the tracheal end-cell in admitting oxygen to the photogenic tissue but the method of control in the simpler types of organs without tracheal end-cells is not clear.

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THE ALIMENTARY CANAL; NUTRITION; DIGESTION

1. The Alimentary Canal

THE alimentary canal is a tube of very variable length; in some cases it is about equal to that of the body, while in others its length is greatly increased and it assumes a convoluted course. The shortest and simplest type is found in many larvae, notably those of the Lepidoptera, Hymenoptera and Diptera-Nematocera; in the Apterygota, Dermaptera, certain Orthoptera, etc., this condition is maintained throughout life. In nymphal and adult Homoptera, and in the larval Diptera Cyclorrhapha, it attains its greatest length and number of convolutions and is often several times longer than the whole insect. As a general rule, the greatest length of digestive canal is to be found in those insects which feed upon juices, rather than upon the more solid tissues of animals and plants. Exceptions, however, are found in the larval Hymenoptera, whose aliment is entirely of a fluid nature, and whose digestive canal is a straight, simple tube. Morphologically the alimentary canal is divisible

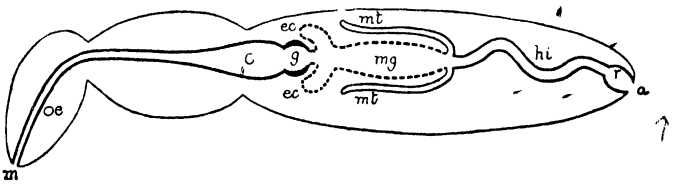


FIG. 100.—Diagram of the digestive system of an insect

The ectodermal parts are represented by heavy lines and the endodermal parts by broken lines.

m, mouth; *oe*, oesophagus; *c*, crop; *g*, gizzard; *ec*, enteric caeca; *mg*, mid intestine; *mt*, Malpighian tubes; *hi*, hind intestine; *r*, rectum; *a*, anus.

into three primary regions according to their method of embryonic origin (Fig. 100). The *fore intestine* arises as an anterior ectodermal invagination (stomodaeum): the *hind intestine* as a similar posterior invagination (proctodaeum); and the *mid intestine*, which ultimately connects the two, develops as what is probably an endodermal sac (mesenteron) (but see p. 213). These differences in embryonic origin result in marked histological differences in the structure of the mid intestine, as compared with either of the other regions. Both the fore and hind intestine, being invaginations of the body-wall, resemble the latter in their essential histology, and are lined with cuticle.

(*a*) **The Fore Intestine.**—The following layers, passing from within outwards, are generally recognizable in the walls of the fore intestine (Fig. 101). 1. The *intima* or innermost lining, which is a cuticular layer directly continuous with the cuticle of the body-wall. 2. The *epithelial layer* continuous

with the hypodermis and secreting the intima: it is often extremely thin and may be syncytial. 3. The *basement membrane* bounding the outer surface of the epithelium. 4. The *longitudinal muscles*. 5. The *circular muscles*. 6. The *peritoneal membrane* which consists of apparently structureless connective tissue and is often difficult to detect. Small amounts of connective tissue may also lie among the muscles. The fore intestine is divisible into the following regions:

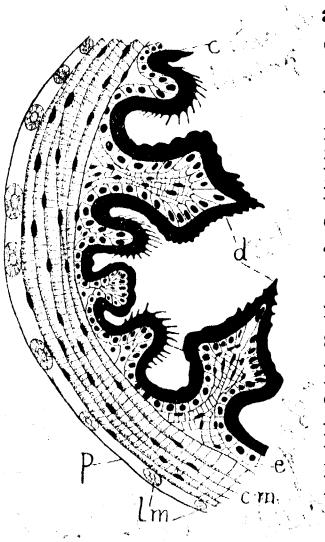


FIG. 101.—Transverse section of the wall of the gizzard of a Tettigoniid (*Decticus albifrons*)

c, cuticular lining; *d*, teeth; *e*, epithelium; *cm*, circular muscles; *lm*, longitudinal muscles; *p*, peritoneal membrane. *After* Bordas.

The *preoral food cavity* is the space lying between the mouthparts and the labrum and is not, strictly speaking, a part of the intestine. In insects with mandibulate mouthparts this space is divided by the hypopharynx into an anterior or dorsal *cibarium* and a posterior or ventral *salivarium*. The cibarium, whose walls are connected to the post-clypeus by the cibarial dilator muscles, may form only a small pouch for the temporary storage of food or be modified into a sucking-pump as in the Thysanoptera, Hemiptera and others. The salivarium may also undergo modification to form the salivary syringe of the Hemiptera and the silk-press of Lepidopterous larvae.

The *pharynx* is the region between the mouth and the oesophagus. It is normally provided with dilator muscles which run from its dorsal surface to the frontal region of the head-capsule and are separated from the cibarial dilator muscles by the frontal ganglion of the stomatogastric nervous system. These muscles are best developed in those forms where the pharynx participates in the formation of a well-developed sucking-pump (Lepidoptera, Hymenoptera, Neuroptera, Dytiscidae).

The *oesophagus* is a simple, straight tube passing from the hinder region of the head into the fore part of the thorax. It is very variable in length and the inner walls are longitudinally folded.

The *crop* is present in many insects and is usually a dilatation of the hinder portion of the oesophagus. It is extremely variable in form, and functions as a food reservoir; its walls are thin and the muscular coat weakly developed. In most Orthoptera and Dictyoptera (Fig. 102), it is very capacious and constitutes the major portion of the fore intestine. In a few insects it is developed as a lateral dilatation of one side of the oesophagus as in *Gryllotalpa*, certain Isoptera and the larvae of *Myrmeleon* and the Curculionidae. Among various sucking insects this dilatation becomes greatly pronounced and connected with the oesophagus by means of a slender tube. Such a food-reservoir is present in most Diptera (Fig. 104) and also in the larvae of some of the Cyclorrhapha and in the higher Lepidoptera (Fig. 105).

The *gizzard* or *proventriculus* is situated behind the crop and is best developed in the Orthopteroid orders and the Coleoptera (Judd, 1948; Thiel, 1936; Balfour-Browne, 1944) (Fig. 102). It is also found in the Mecoptera, Odonata, Isoptera and various Hymenoptera but is reduced to the condition of a valve in the honey bee and most Diptera. The dominant feature in its structure is the great development of the cuticular lining into prominent

denticles, and the increased thickness of its muscles. At the point of junction of the fore and mid intestine, there is present in many insects a *cardiac* or *oesophageal valve*. This structure is formed by the wall of the fore intestine being prolonged into the cavity of the stomach as an inner tube, which then becomes reflected upon itself and passes forwards to unite with the stomach-wall (Fig. 106). It exhibits varying degrees of complexity among different insects and probably prevents or reduces regurgitation of food from the mid gut.

(*b*) **The Mid Intestine.** —This region is also termed the *stomach* or *mid gut* and its shape and capacity vary exceedingly. In some cases it is saclike, in others it is coiled and tubular like an intestine, or it may be divided into two or more well-defined regions as in the Heteroptera and many Cyclorrhapha (Fig. 104). Histologically the wall of the stomach exhibits the following structure (Fig. 103). Internally it is lined by a stratum of *enteric epithelium* the outer ends of whose cells rest upon a *basement membrane*: the latter is followed by an inner layer of *circular muscles* and an outer layer of *longitudinal muscles*. The outermost coat of the stomach is a thin *peritoneal membrane*. Both muscle layers are composed of striated fibres and their positions are the reverse to what obtains in the fore intestine. The structure of the enteric epithelium requires more detailed mention.

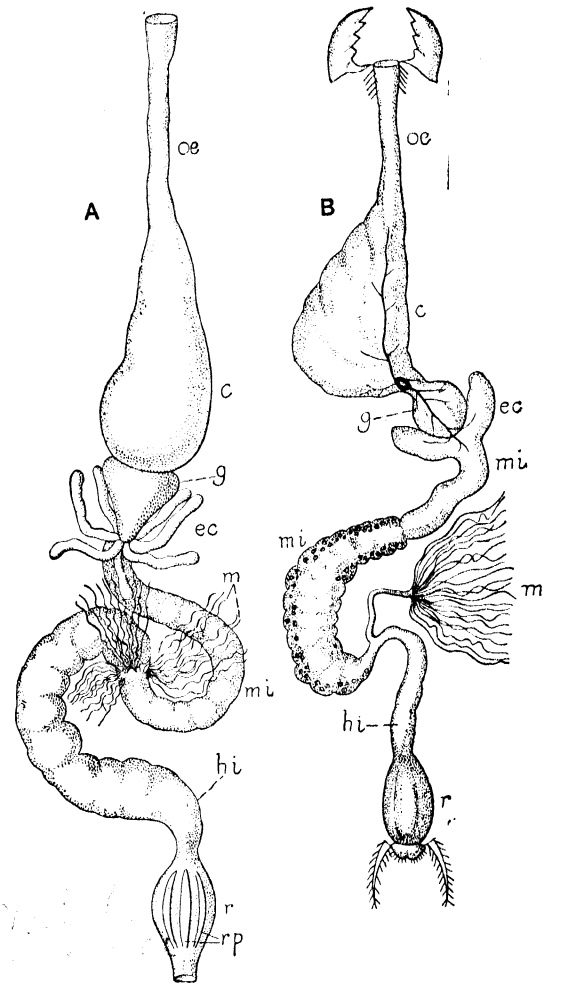


FIG. 102.—A. Alimentary canal of *Periplaneta americana*. B. Alimentary canal of *Nemobius sylvestris* (Gryllidae)

oe, oesophagus; *c*, crop; *g*, gizzard; *ec*, enteric caeca; *m*, Malpighian tubes; *mi*, mid intestine; *hi*, hind intestine; *r*, rectum; *rp*, rectal papillae. *After* Bordas, *Ann. Sci. nat.*, *8th ser.*, 5.

Three main types of cells may be distinguished: (*a*) Columnar (cylinder) cells, (*b*) Regenerative cells and (*c*) Calyciform (goblet) cells. The first-mentioned are those which are at times actively involved in the secretion of enzymes and the absorption of the products of digestion. Their boundaries are generally well-defined, they almost invariably possess a striated border (Newell & Baxter, 1936; Zilch, 1936) and various histological concomitants of secretion have been described in them (see below). The regenerative cells, which are absent in a few groups of adult insects, may be scattered singly beneath the cylinder cells

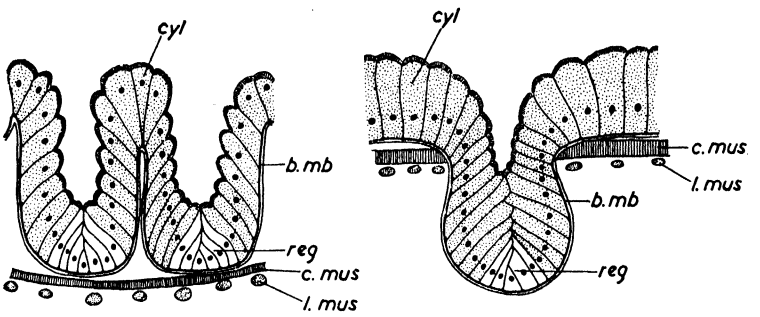


FIG. 103.—Histology of mid gut (*after* Snodgrass, 1935)

b.mb, basement membrane; *c.mus*, circular muscles; *cyl*, cylinder cells; *l.mus*, longitudinal muscles; *reg*, egenerative cells.

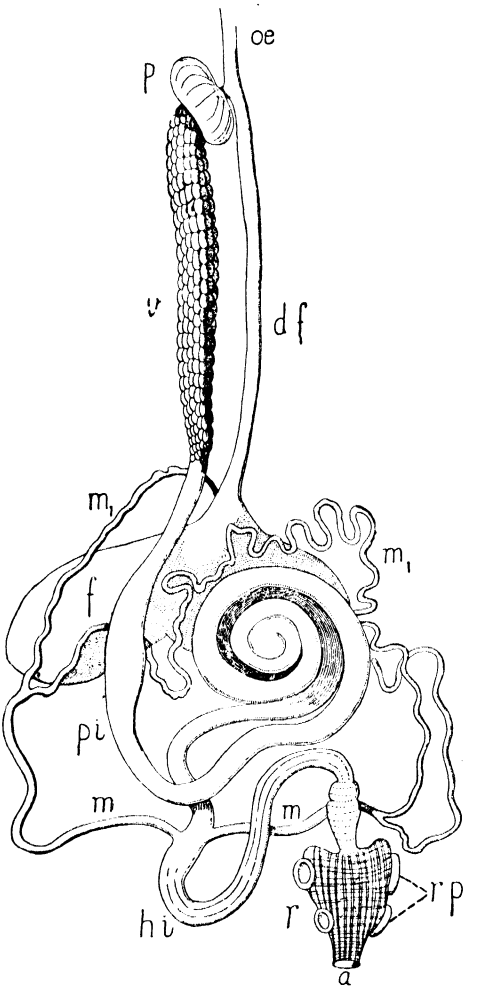


FIG. 104.—Alimentary canal of a fly (*Calliphora*)

oe, oesophagus; *p*, proventriculus; *v*, ventriculus; *df*, duct of food-reservoir *f*; *pi*, proximal intestine; m_1, Malpighian tubes which unite to form a common stem (*m*) on either side; *hi*, hind intestine; *r*, rectum; *rp*, rectal papillae; *a*, anus. Adapted from Lowne.

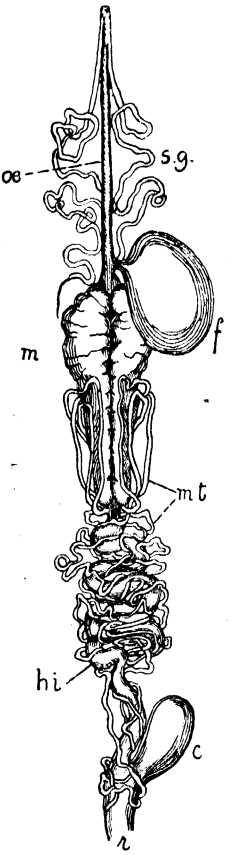


FIG. 105.—Digestive system of *Sphinx ligustri* (imago)

oe, oesophagus; *sg*, salivary gland; *f*, food-reservoir; *m*, mid intestine; *mt*, Malpighian tubes; *hi*, hind intestine; *c*, caecum; *r*, rectum. *After* Newport.

or grouped into clusters (nidi) there or variously arranged in crypt-like outpocketings of the mid gut. Their function is to renew the other epithelial cells when these are destroyed through secretion or in the large-scale processes of degeneration which accompany moulting or pupation in certain species. The goblet cells, of uncertain function, are not found in all insects, being best developed in the Lepidoptera.

In many insects the surface area of the stomach is increased by the development of sac-like diverticula—the *enteric* or *gastric caeca* (Fig. 102). These organs are usually situated at the oesophageal end of the stomach and are very variable in number. In certain Dipterous larvae and in the Gryllidae and Tettigoniidae two large caeca are present; in Dictyoptera and larval Culicidae there are eight, while in the larvae of Scarabaeidae they are more numerous and are disposed in an anterior, a median, and a posterior annular series. Among various predacious Coleoptera they are represented by numerous villiform processes, and in some orders (e.g. Collembola, Lepidoptera) caeca are generally wanting.

In the larvae of certain groups of insects the stomach is a closed sac, the passage being closed between the mid and hind intestine. In these instances the food is always of a fluid nature and there is but little solid residuum. This condition is prevalent in the majority of the larvae of the Hymenoptera Apocrita, and in those of the Neuroptera Planipennia, of *Glossina*, and other viviparous Diptera. The elaborate modifications of the mid gut which occur in the filter-chamber of many Homoptera are discussed on p. 431.

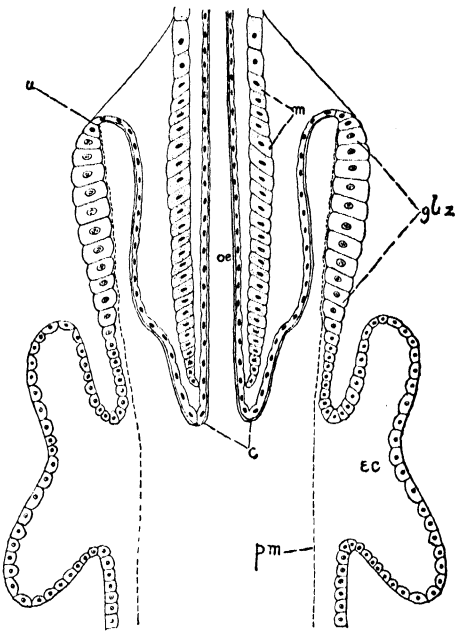


FIG. 106.—Cardiac valve of a Dipterous larva (Nematocera) with the adjacent region of the mid intestine, seen in longitudinal section

oe, oesophagus; *c*, cuticular intima; *m*, muscles; *u*, point of union of fore intestine with mid intestine; *glz*, zone of columnar gland cells which secrete the peritrophic membrane *pm*; *ec*, enteric caecum.

Food particles in the mid gut are generally separated from the epithelium by being enclosed in a tubular sheath, the *peritrophic membrane*. This contains chitin and probably also protein, is usually less than 0·5 μ in thickness and has an ultra-microscopic reticular structure (Mercer & Day, 1952). A peritrophic membrane is said to be absent from most insects feeding on a liquid diet, e.g. all Hemiptera except the Corixidae (Sutton, 1951), many adult Lepidoptera and most blood-sucking species, but it is possible that it has only been overlooked on account of its delicate structure (Waterhouse, 1953). The same may also be true of the few species living on more solid food and in which a peritrophic membrane has not been found (e.g. *Panorpa*, Grell, 1938). The peritrophic membrane has been considered to arise in two ways (Wigglesworth, 1930; Waterhouse, 1953a): (*a*) In some Lepidoptera, Diptera (Fig. 106) and Dermaptera it is secreted by cells near the junction of fore and mid gut and extruded in tubular form by a muscular 'press' in this region; (*b*) in other insects it arises by delamination from part or all of the general surface of the mid gut and a

series of concentric membranes, formed by successive delaminations, is often present. In some cases (e.g. *Apis*, Kusmenko, 1940) a membrane formed predominantly in the anterior part of the mid gut is supplemented by delamination further back.

(*c*) **The Hind Intestine.**—This region consists of the same layers as the fore intestine except that its circular muscles are developed to a varying degree both inside and outside the layer of longitudinal muscles. The commencement of the hind intestine is normally marked by a pyloric valve and the insertion of the Malpighian tubes (vide p. 160). In most insects three regions are recognizable. These are: the *small intestine* or *ileum*, the large intestine or *colon* and the *rectum*. The cuticular lining of the ileum and colon is often thrown into folds and provided with hairlike or spinous projections: among certain Scarabaeid larvae the latter are highly developed and assume an arborescent form. The ileum may be very long as in *Dytiscus* and *Necrophorus*, short as in many other insects, or it may be undifferentiated from the colon, as in many Orthoptera and Hemiptera. Among Lepidoptera, certain Coleoptera, etc., a hollow outgrowth or caecum arises from the colon: it is sac-like in *Sphinx ligustri* (Fig. 105) and many other Lepidoptera, while in *Dytiscus* it takes the form of a tube nearly equal to the abdomen in length. The *rectum* is a more or less globular or pyriform chamber, generally provided with a variable number of inwardly projecting papillae. These (often miscalled 'rectal glands') are composed either of a single layer of tall epithelial cells (Thysanura, Odonata, Orthoptera, Phasmida, etc.) or of two cell-layers, with or without a lumen (Neuroptera, Hymenoptera, Lepidoptera, Diptera). They are generally six in number, occasionally four (most Diptera, Thysanoptera) or very many (some Trichoptera, Lepidoptera). They do not occur in Hemiptera and the larvae of Endopterygotes and are found, among Coleoptera, only in the Silphidae and some Adephagan families (Palm, 1949; Reichenbach-Klinke, 1952). They are often richly tracheated though it seems unlikely that they have a respiratory function. Wigglesworth (1932) considers that they are sites at which water is conserved by resorption from the faeces and inorganic ions may also be resorbed through them.

(*d*) **Literature.**—In addition to the papers cited above and in the sections on the internal anatomy of the various orders of insects, the references on pp. 130–132 may be noted; they include many histological papers.

2. Nutrition

This subject has been reviewed by Trager (1947) and in later physiological textbooks and only an outline of present knowledge is given here. Insects eat a great variety of foods (Brues, 1946) though the normal diets of many species are strictly limited to one or a few materials. The basic nutritional requirements for growth and development are known in biochemical terms for only a few species such as *Blattella*, *Drosophila*, *Aedes* and some insect pests of stored foodstuffs where synthetic experimental diets have been devised. The substances thus shown to be necessary are as follows:

(i) *Water and mineral salts.*—Though normally available in the food, water may also be obtained by an insect in dry surroundings through the oxidation of respiratory substrates (Fraenkel & Blewett, 1944). Certain inorganic ions are known to be necessary for some insects but little is known on the topic.

(ii) *Sources of energy.*—These are normally taken as carbohydrates, the different ones differing appreciably in the extent to which they can be utilized, but fats and proteins can also provide energy on oxidation and in *Aedes* larvae, for instance, stores of fat and carbohydrate can be synthesized from protein (Wigglesworth, 1942).

(iii) *Proteins or amino-acids.*—The amino-acids needed for tissue-replacement and growth are normally obtained by digestion of the proteins in the food. The amino-acid

requirements of a few species have been ascertained in detail and certain acids found to be essential. Thus, *Blattella germanica* reared under aseptic conditions cannot develop normally without valine, arginine, histidine, tryptophane and cystine (House, 1949); other species have different essential needs but glycine and cystine are usually required.

(iv) *Accessory factors* (*vitamins*).—No insect is yet known to require vitamins A, C or D in its diet, though *Blattella* is able to synthesize C (ascorbic acid). Insects do, however, require certain other accessory dietary factors:

(*a*) A sterol. This is normally provided by cholesterol but other chemically similar substances can be equally effective, different species sometimes requiring different substitutes (Fraenkel & Blewett, 1943).

(*b*) B-complex vitamins. These are particularly important, most of the investigated insects requiring thiamin, riboflavin, niacin, pantothenic acid, pyridoxin, biotin and pteroylglutamic acid. Inositol, *p*-aminobenzoic acid and choline are less important or unnecessary, *Tribolium confusum*, for example, being little affected by the omission of choline from its diet.

(*c*) Miscellaneous specific factors. These include linoleic acid, which is necessary for the proper development of *Ephestia* (Fraenkel & Blewett, 1946) and carnitine (Vitamin B_T) which is required by *Tenebrio molitor* (Fraenkel *et al.*, 1950).

It should be noted that many insects depend on micro-organisms for their supply of essential nutrients. In some cases the bacteria, fungi, etc. are found in the material on which the insect feeds; in others a more intimate association occurs, the micro-organisms living in the gut or in special organs (mycetomes) of the insect and sometimes undergoing transmission from parent to progeny (Steinhaus, 1946; Buchner, 1953). As examples of such symbionts may be cited the yeast-like *Actinomyces rhodnii* which occurs in the gut of *Rhodnius prolixus* (Brecher & Wigglesworth, 1944) and the yeasts of *Stegobium paniceum* and *Lasioderma serricorne* which synthesize B-vitamins and a sterol (Pant & Fraenkel, 1950). See also under Digestion, below.

3. Digestion

This includes those processes whereby the food materials are broken down to forms such as monosaccharide sugars and amino-acids which can be absorbed through the wall of the gut. Such changes are catalysed by the digestive enzymes which, apart from those produced in the salivary glands (p 171), are secreted by the cylinder cells of the mid gut. The processes of secretion have often been described histologically and two types distinguished: *merocrine* secretion, in which globules of material are extruded from the inner surface of the cells and *holocrine* secretion in which a cell breaks down completely to discharge its contents. In some cases a secretory cycle in the mid gut cells has been postulated after a somewhat arbitrary serial arrangement of purely cytological data but in a few cases the changes have been related to feeding and where, as in *Dytiscus* (Duspiva, 1939), the cytological changes are also correlated with enzyme determinations, they probably represent an accurate picture of events. In *Blattella*, however, Day & Powning (1949) found that enzymes were produced while the epithelium remained cytologically uniform (the 'resting epithelium' of histologists).

The enzymes produced are, broadly speaking, adapted to the insect's diet, the most abundant enzyme catalysing the breakdown of the predominant dietary component. Three main types of enzymes have been recorded:

(*a*) *Carbohydrases.*—These catalyse the hydrolysis of the more complex carbohydrates and include the polysaccharases—of which the amylases, acting upon starch, are widely distributed in insects—and the glycosidases. The latter control the breakdown of, among other things, the disaccharide and trisaccharide sugars and include α-glucosidases which are responsible for the digestion of maltose, sucrose, melezitose, etc., α-galactosidases, dealing with raffinose and melibiose and, in *Apis* larvae, a β-lactosidase with lactose as its substrate.

(*b*) *Lipases.*—These catalyse the hydrolysis of dietary fats and are of low specificity, though different esters are attacked at different rates.

(*c*) *Proteases* are responsible for the degradation of proteins. The first type are the endopeptidases which catalyse the breakdown of proteins or peptones to polypeptides and which, in insects, are almost invariably of the tryptic type, acting best in alkaline media. The exopeptidases complete protein digestion by facilitating the hydrolysis of peptides to amino-acids. All three types of exopeptidases have been reported from insects—the carboxypeptidases and aminopeptidases catalyse attack on the peptide chains at different points while the dipeptidases are responsible for the breakdown of dipeptides. Endopeptidases appear to occur mainly in the lumen of the gut and exopeptidases in the epithelium, suggesting that absorption may begin before hydrolysis of the protein is complete.

The digestion of a few foods presents some unusual features indicated below:

(*a*) *Keratin.*—Many insects live on wool or fur, but the processes of digestion are best known for the larvae of *Tineola*. Keratin is unusual in that the disulphide linkages which it contains are resistant to attack and even withstand the *in vitro* action of a protease from the gut of *Tineola* larvae. *In vivo*, however, the extremely low redox potential of the gut contents causes a reduction of the disulphide linkages to —SH (sulphydryl) groups and the protease—which differs from trypsin in not being inhibited by —SH groups—catalyses the breakdown (Day, 1951; Powning, Day & Irzykiewicz, 1951).

(*b*) *Wood, etc.*—The woody tissues of plants include the complex polysaccharides lignin, cellulose, the hemicelluloses and starch as well as the simpler carbohydrates, proteins, etc., of the cell-contents. Lignin is apparently never digested and most insects—even phytophagous ones—cannot digest cellulose though they may be able to utilize some of the contents of unbroken cells. A smaller number of species is able to break down cellulose either by secreting a cellulase (e.g. most Cerambycid larvae, *Xestobium rufovillosum*) or through the presence in the gut of symbiotic celluloclastic bacteria (Scarabaeid larvae; Wiedmann, 1930) or Protozoa (*Cryptocercus*, Isoptera—see p. 386). Some other wood-borers, such as *Phymatodes* larvae, cannot deal with cellulose but possess hemi-cellulases while yet further xylophagous species utilize only the cell-contents and polysaccharides below the hemi-celluloses (Parkin, 1940).

(*c*) *Wax.*—A considerable proportion of the wax ingested by *Galleria* larvae is utilized and though the mechanism of digestion is uncertain it is likely that bacteria play a role (Florkin *et al.*, 1949).

(*d*) *Collagen.*—This is normally unaffected by endopeptidases of the tryptic type but *Lucilia* larvae secrete a collagenase (Hobson, 1931).

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THE RESPIRATORY SYSTEM

In the vast majority of insects respiration takes place by means of internal air-tubes known as *tracheae*. The latter ramify through the organs of the body and the appendages, the finest branches being termed *tracheoles*. The air generally enters the tracheae through paired and usually lateral openings termed *spiracles* (or *stigmata*), which are segmentally arranged along the thorax and abdomen. More rarely the spiracles are closed or wanting, respiration in such cases being cutaneous. In the immature stages of many aquatic insects special respiratory organs known as *gills* (or *branchiae*) are present, and these may or may not co-exist with open spiracles. The respiratory organs of insects are always derived from the ectoderm: the tracheae are developed from solid ingrowths or tubular invaginations of that layer and the gills arise as hollow outgrowths. Histologically, both types of organ are composed of a layer of cuticle, the hypodermis and usually a basement membrane, all of which are directly continuous with similar layers forming the general body-wall. All or most of the cuticular lining of the tracheo-spiracular system is shed at ecdysis. A tracheal system is absent in most Collembola, some Protura and some endoparasitic Hymenopteran and Dipteran larvae.

The Spiracles

Number and Position of the Spiracles.—The spiracles are, morphologically, the mouths of the ectodermal invaginations which give rise to the tracheal system. They are normally placed on the pleura of the thoracic and abdominal segments, but their exact position is very variable. In the abdomen of most insects they are seen to lie in the soft membrane between the terga and sterna, sometimes towards the front or back of their segments. In many insects, particularly on the thorax, the spiracles occupy an intersegmental position, being situated just in front of each of the segments to which they are generally referred: or, they may be no longer situated on the pleura but come to lie on the terga, near the side margins of the latter, as is seen in the abdominal spiracles of *Apis* and *Musca*.

An evanescent pair of spiracles is present on the labial segment of the embryo of *Apis* (Nelson, 1915) but, with the possible exception of some Collembola mentioned below, there is no other record of cephalic spiracles in insects. In the developing embryo the spiracles appear as a series of ingrowths lying to the outer side of the rudiments of the appendages. Twelve evident pairs of spiracles are said to be present in the embryo of *Leptinotarsa*, being situated on each of the thoracic and the first nine abdominal segments. In the embryos of most insects, however, the prothoracic pair is wanting and frequently the pair on the 9th abdominal segment is likewise absent. The resulting number—two thoracic and eight abdominal pairs—is the maximum found in the postembryonic stages of any insect apart from some Diplura

and it is probable that their primitive position was intersegmental, the most anterior pair lying between the pro- and mesothorax and the last pair between the 7th and 8th abdominal segments (Keilin, 1944). Deviations from the number and arrangement of spiracles in such a primitive isopneustic system have evolved through the migration of the spiracle to an adjacent segment (usually the posterior one) and the reduction of some or all of the spiracles. These either become closed or remain visible as small scars or are lost completely (see non-functional spiracles, below).

According to the number and arrangement of functional spiracles it is possible to classify respiratory systems as follows (Palmén, 1877; de Gryse, 1926; Keilin, 1944; Hinton, 1947):

1. *The Holopneustic Respiratory System.*—This is the most primitive arrangement found in living insects, 10 pairs of functional spiracles being present, on the first 8 abdominal segments, the metathorax and either the prothorax or the mesothorax. It is characteristic of the nymphs and imagines of many orders and of the larvae of the Bibionidae (Diptera) and some Hymenoptera.

2. *The Hemipneustic Respiratory System.*—This form of respiratory system is the prevalent one among insect larvae and is derived from the holopneustic type through one or more pairs of spiracles becoming non-functional. The following terms are in use to indicate the different distributions of spiracles:

Peripneustic.—Spiracles in a row along each side of the body. In typical examples the prothoracic and abdominal spiracles are open, that of the metathorax being closed. This condition is found in the terrestrial larvae of the orders Neuroptera, Mecoptera, Lepidoptera, of many Hymenoptera Symphyta, and of many Coleoptera; among Diptera it is prevalent in larvae of some Bibionidae and most Mycetophilidae and Cecidomyidae.

Amphipneustic.—Only the prothoracic and the posterior abdominal spiracles are open. This type is a common one among larval Diptera.

Propneustic.—Only the prothoracic spiracles are open. A comparatively rare condition exhibited for example in the pupae of some Dipteran families.

Metapneustic.—Only the last pair of abdominal spiracles are open. The prevalent type in larval Culicidae and Tipulidae and in *Hypoderma* among the Oestridae; also found in the first larval instar of most Cyclorrhapha and in the aquatic larvae of certain Coleoptera (Dytiscidae, Helodidae, etc.).

The last three types may together be denoted as oligopneustic systems and represent an adaptive modification to life in a liquid or semi-liquid medium.

3. *The Apneustic Respiratory System.*—Here none of the spiracles are functional, air entering the closed tracheal system by diffusion through the general body surface or specialized extensions of it known as gills or branchiae (q.v.). Like the oligopneustic types, the apneustic system is an adaptation to life submerged in fluids and is therefore characteristic of aquatic and endoparasitic forms. It occurs, for example, in the nymphs of the Ephemeroptera and Odonata, the larvae of the Trichoptera, of such Dipteran families as the Blepharoceridae, Simuliidae, Chironomidae and Ceratopogonidae and of some Coleoptera (e.g. Elmidae, Haliplidae, Hygrobiidae). It is also found in some larval instars of endoparasitic Hymenoptera and Tachinidae.

In all the above types of respiratory system, the total of functional and non-functional spiracles is equal to 10 pairs. In contrast to them, the term *Hypopneustic* is used to denote systems in which one or more pairs of spiracles have disappeared completely. For example, the Mallophaga and Siphunculata have 1 thoracic and 6 abdominal pairs; the Thysanoptera have 2 pairs of thoracic and 2 pairs of abdominal spiracles; in the Hemiptera Sternorrhyncha their number is very variable and is reduced to 2 pairs in many Coccoidea.

Among Coleoptera, the Scarabaeoidea and Curculionoidea have from 1 to 3 of the hindmost abdominal spiracles wanting. The Diptera usually exhibit a reduction in the number of abdominal spiracles and, among the Cyclorrhapha, a sexual difference is evident in this respect, the females often having 5 pairs and the males 6 or 7 pairs. Among the parasitic Hymenoptera reduction is frequently evident and in the Chalcidoidea, there are commonly only 3 pairs which are situated on the thorax, propodeum and 8th abdominal segment, respectively.

The Diplura and those Collembola with a tracheal system exhibit an atypical arrangement of spiracles (see pp. 267, 280, Fig. 107).

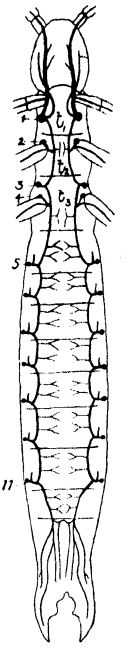


FIG. 107.—Tracheal system of *Japyx*

t_1, t_2, t_3, thoracic segments; 1–4, thoracic spiracles; 5, 11, abdominal spiracles. *After* Grassi, 1887.

Structure of the Spiracles.—In general, the spiracles not only permit gaseous respiratory exchange but are also a major site of water loss and, at ecdysis, are the apertures through which the old tracheal lining is pulled out. They show many adaptations to these diverse functions but a typical functional spiracle includes not only the external opening, and the annular sclerite or *peritreme* which surrounds it, but also the *atrium* or vestibule into which the opening leads, together with the *closing apparatus*. The latter consists of one or more muscles with associated cuticular parts and, by closing the spiracular aperture, prevents excessive loss of water-vapour. The atrium is a specialized region leading from the spiracular opening: it lacks tracheidia and its walls are variously sculptured or are provided with hairs, trabeculae and similar cuticular outgrowths. These help to reduce water-loss and prevent the entry of dust. Closely connected with the spiracles are frequently *peristigmatic glands* which secrete a hydrophobe material preventing the wetting of those organs. The structure of the spiracles presents an enormous range of variety among different groups of insects: it is also usually different in the thoracic and abdominal spiracles of the same insect and may be greatly modified in different instars. It will, therefore, be readily appreciated that their classification is a matter of much difficulty (Krancher, 1881; Mammen, 1912; Steinke, 1919; Bergold, 1935; Hassan, 1944; Keilin, 1944).

The most generalized type of spiracle is devoid of lips and closing apparatus and is little more than a simple crypt as in *Sminthurus*. No special chamber or atrium is developed and the spiracle opens directly into the tracheae.

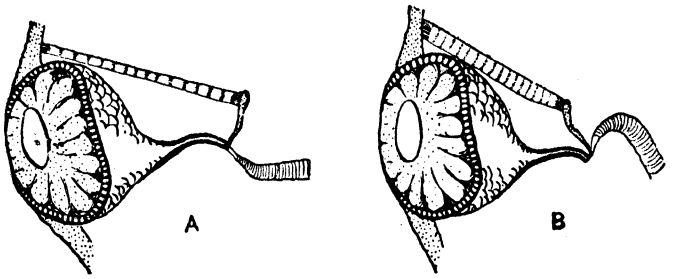


FIG. 108.—Spiracle and occluding apparatus of *Trichodectes*, semi-diagrammatic

A, open; B, closed. *After* Harrison, *Parasitology*, 1915.

In most Hemiptera, more especially in the abdomen, the spiracles are simple apertures surrounded by a peritreme. A well developed atrium is present and between the latter and the trachea is the closing apparatus (absent from the Cryptocerata). This type of spiracle is also found in the Mallophaga and Siphunculata (Webb, 1946), Siphonaptera and in other insects (Fig. 108).

In the Acrididae the thoracic spiracles each have a slit-like opening guarded by two external valves or lips (Figs. 109 and 110, A). The metathoracic spiracles have movable lips (*a*, *p*) united by a ventral lobe (*n*): they open by their own elasticity but are closed by an occlusor muscle (*sm*) arising from a process (*o*) on the margin of the mesocoxal cavity. The abdominal spiracles (Fig. 110, B, C, D) have no projecting lips, the integument being inflected to form two hardened walls of the atrium—one wall (*v*) being movable

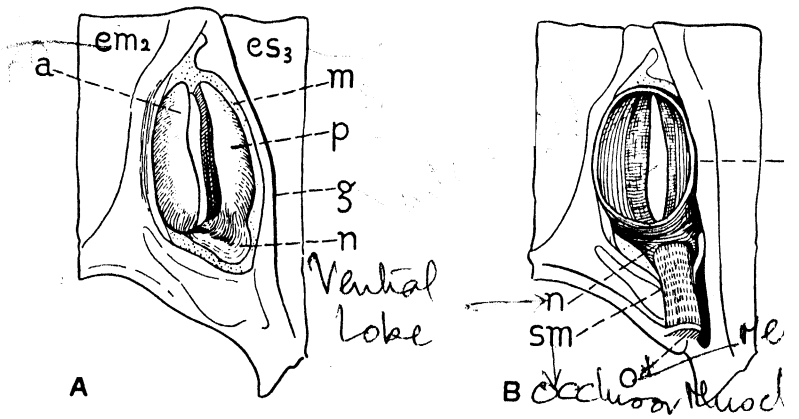


FIG. 109.—Metathoracic spiracle of a grasshopper (*Dissosteira*)

A, outer view. B, inner view. em_2, mesepimeron; es_3, metepisternum; *g*, intersegmental fold; *m*, membrane; *t*, trachea. Further explanation in the text. Adapted from Snodgrass, 1929.

and the other (*d*) fixed. The movable wall is prolonged into a process or manubrium (*q*) to which the occlusor (*sm*1) and opening muscles (*sm*2) are attached.

In the spiracles of Lepidopterous larvae the lips are fringed with repeatedly branched processes, whose finest divisions often require a high magnification for their detection, thus forming a most efficient guarding mechanism to the tracheal system. At the inner end of the atrium is the closing apparatus. The latter consists of a cuticular bow, which partly encircles the trachea, while on the opposite side of the latter is a sclerotized band; a closing lever or rod is closely connected with the band. The occlusor muscle is attached at one end to the bow and at the other to the lever: when the muscle contracts the lever presses the band against the bow, thus closing the entrance into the trachea. The latter is opened partly by means of the elasticity of the cuticular parts which regain their former position, and partly by the aid of an antagonist muscle or an elastic fibre (Fig. 111).

In the larvae of *Melolontha* and other Scarabaeidae (Boas, 1893; Meinert, 1895) the spiracles are circular: each consists of a crescentic sieve-plate and a projecting tegumentary fold or bulla which is almost completely surrounded by it (Fig. 112). The true opening is a curved slit situated near the margin of the bulla and running concentrically with it. The sieve-plate consists of an outer pore membrane supported beneath by a layer of trabeculae (Fig. 113).

In larvae of the Elateridae, Cleridae, Nitidulidae and other Coleoptera are *biforous spiracles*. Each has two contiguous openings which are more or

less slit-like and separated by a partition wall. Each opening communicates either by means of a tubular passage with a common atrium, or opens directly into the trachea (Fig. 112).

In Dipterous larvae the spiracles are without closing apparatus (Keilin, 1944). In the third stage larvae of the higher Cyclorrhapha the posterior spiracles consist of a pair of cuticular plates. Each plate is surrounded by a peritreme and bears as a rule three openings which may be pyriform (*Muscina*) or in the form of straight slits (*Calliphora*) or sinuous slits (*Musca*). Each opening is traversed by a number of fine cuticular rods presenting the appearance of a grating, and all three openings communicate with a common atrium. Just internal to the openings there is a system of branched cuticular trabeculae which form, along with the grating previously alluded to, an efficient barrier to the entrance of foreign particles. The walls of the atrium are also lined with fibrous processes and form the so-called *felt chamber* which probably reduces water-loss in the absence of a closing mechanism. The anterior spiracles each consist of a variable number of digitate processes whose apices are perforated by openings. Each opening communicates with a small atrium and the atria of each spiracle all join with the main tracheal trunk of their side (Fig. 115). In the larvae of *Oestrus*, *Hypoderma* and other of the Oestridae instead of three openings to each spiracle there are multiple pores. In *Glossina* there are about 500 of these pores to a side which form the sculpturing on the lobe-like posterior abdominal spiracles (Newstead, 1918). The pores are connected by means of tubular continuations with a tripartite felt chamber. A similar arrangement obtains in the larva of *Hippobosca* except that the pores are much less numerous, while in *Melophagus* there are only three to each lobe.

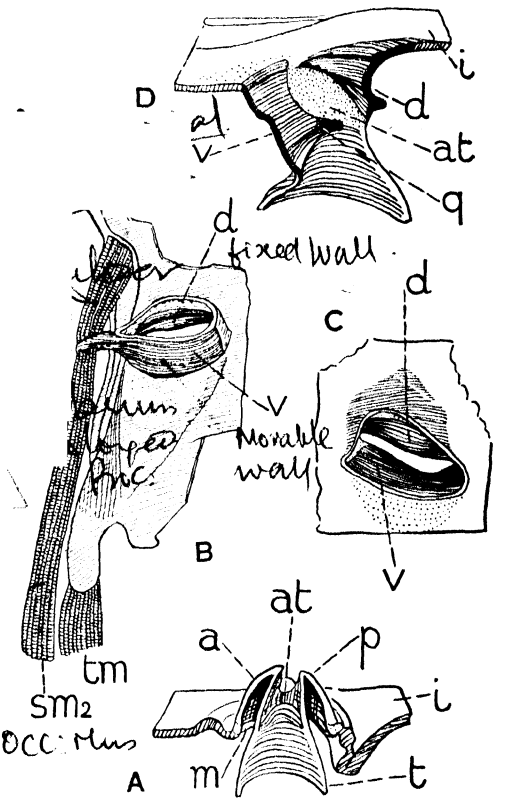


FIG. 110.—Spiracles of an Acridid (*Dissosteira*)

A, D, sections through metathoracic and 1st abdominal spiracles respectively. B, inner view, and C, outer view of 1st abdominal spiracle. *at*, atrium; *i*, integument; *tm*, tympanal muscles. Further explanation in the text. Adapted from Snodgrass, 1929.

The shedding of the old spiracles at ecdysis and the formation of new ones takes place in three different ways (Keilin, 1944; Hinton, 1947). In the most primitive type, where the new spiracular aperture is sufficiently wide to allow withdrawal of the old tracheae and atrial apparatus, the new structures are formed around the old ones after the latter have separated from the hypodermis. The remains of the old spiracle and tracheal lining are then pulled out through what becomes the new aperture. This method of moulting is the most common one, but where the aperture or atrium of the new spiracle is so obstructed by cuticular processes that withdrawal is mechanically

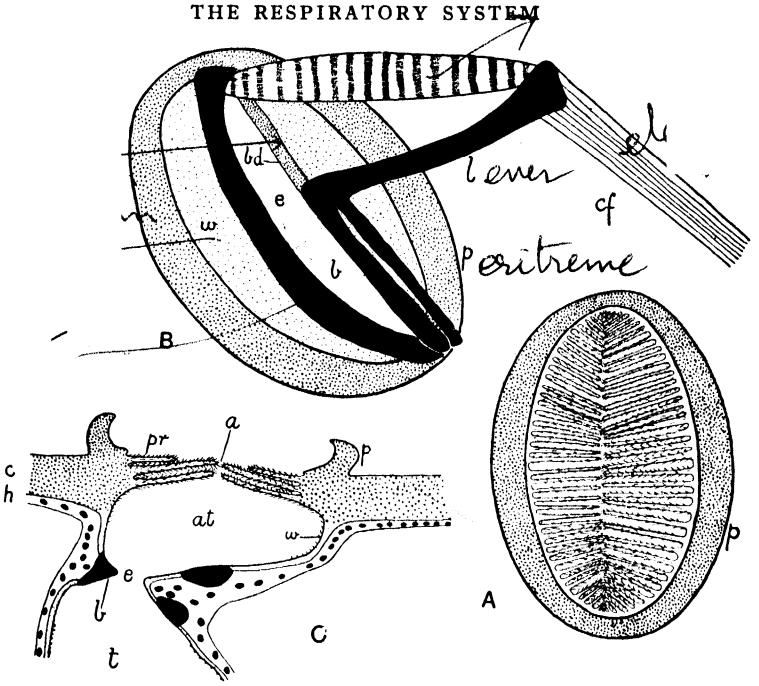


FIG. 111.—Spiracle of a Lepidopterous larva (*Sphingidae*)

A, seen from the outside showing fringed processes of the lips; B, seen from the inside, lips omitted; C, sectional view. *a*, spiracular aperture; *at*, atrium; *b*, bow; *bd*, band; *c*, cuticle; *cf*, elastic fibre which opens spiracle; *e*, entrance into trachea; *h*, hypodermis; *l*, lever; *p*, peritreme; *pr*, fringed processes of lips; *w*, wall of atrium; *t*, trachea.

impossible, one or other of the following methods is adopted. In the Mecoptera and some Diptera the spiracle opens by numerous small apertures arranged around a central solid area. Before moulting occurs a new spiracle forms around the old one so

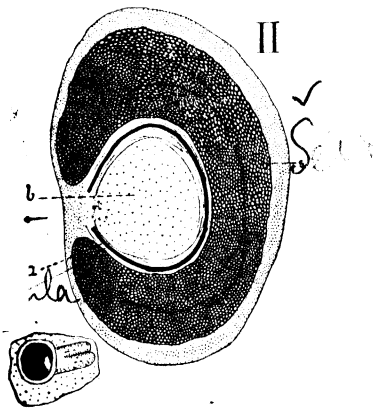


FIG. 112.—I. Biforous spiracle of a Clerid larva. *After* Böving and Champlain. II. Abdominal spiracle of the larva of *Melolontha melolontha*

a, spiracular opening; *b*, bulla; *s*, sieve-plate. The arrow is directed anteriorly.

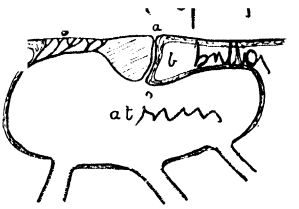


FIG. 113.—Longitudinal section of a spiracle of the larva of *Melolontha*

at, atrium: other lettering as in Fig. 112.

that the former possesses a central ecdysial aperture through which the old structures are drawn out and which then closes by hardening and contraction of the cuticle to form the solid central part. In other Diptera and many Coleoptera there develops

around the old spiracle a simple cuticular tube (the ecdysial tube) connected with which and situated to one side of the old structures, is the new spiracle. The old spiracle and tracheae are then pulled out through the unobstructed ecdysial tube at moulting and the tube later shrivels, its former opening giving rise to the stigmatic scar (Fig. 116).

In the apneustic and hemipneustic systems of immature forms all or some of the spiracles are non-functional. They consist of a surface scar from the inside of which a more or less solid, cuticular stigmatic cord (Palmén, 1877) runs to an adjacent part of the tracheal system. Before moulting, an ecdysial tube, continuous with the new tracheal system, forms around the stigmatic cord and the appropriate part of the old tracheal lining is later pulled out through the ecdysial tube by means of the stigmatic

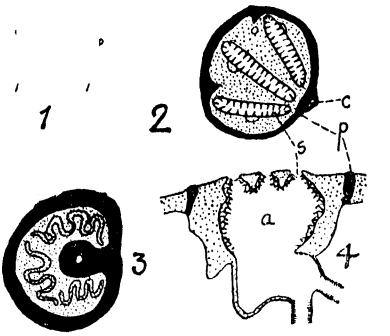


FIG. 115.—Spiracles of larval Diptera

1, anterior spiracle of *Musca domestica*; 2, posterior spiracle of *Calliphora erythrocephala*; 3, posterior spiracle of *Musca domestica*; 4, vertical section through spiracle of *Calliphora*; sclerotized parts only shown; *a*, atrium; *c*, stigmatic scar; *p*, peritreme; *s*, spiracular slit.

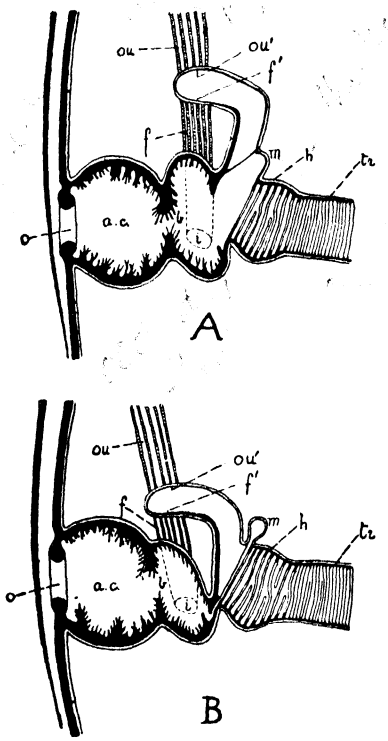


FIG. 114.—Longitudinal sections of the last abdominal spiracle of an ant

A, open; B, closed; *o*, spiracular opening; *a.c*, anterior chamber; *b*, occluding chamber; *f*, closing muscle and *f'* mobile insertion of same; *h*, thickened portion of trachea; *i*, fixed insertion of closing muscle; *m*, flexible membrane; *o*, spiracular opening; *ou*, opening muscle; *ou'*, fixed insertion of same; *tr*, trachea. *After* Janet, 1902.

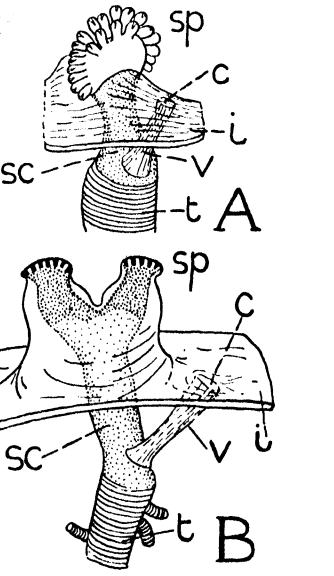


FIG. 116.—Spiracles of *Rhagoletis* (Trypetidae)

A, anterior spiracle of 3rd instar larva. B, right pronotal spiracle of pupa. *c*, cicatrix or closed end of remains of passage *v* through which spiracle of 2nd instar was cast off during ecdysis; *i*, integument; *sc*, spiracular chamber; *sp*, spiracle; *t*, trachea. Adapted from Snodgrass, *J. agric. Res.*, 1924.

cord. The tube then shrivels to form the stigmatic cord and scar of the new instar. If, however, this new instar is to have a functional spiracle in that position, the necessary structures form around the old stigmatic cord and remain functional after moulting. The functions of the stigmatic cords are therefore: (*a*) to anchor the tracheal system to the cuticle, (*b*) to draw out the old tracheal lining at ecdysis and (*c*) to form a structure around which an ecdysial tube or new functional spiracle can develop.

The Tracheae and Tracheoles

The *tracheae* are elastic tubes and when filled with air present a silvery appearance. The innermost lining of a trachea is a layer of cuticle known as the *intima* (endotrachea) which is directly continuous with the cuticle of the body-wall though chitin is not present in the finer tracheal branches of all species or in the large trunks of some insects. Most of the tracheal system is shed at ecdysis but the finer branches are sometimes completely dissolved before moulting while in *Sciara* larvae there is no casting off of the cuticle in small and remote branches (Keister, 1948). When examined microscopically a trachea presents a very characteristic striated appearance which is due to the fact that the intima is specially thickened at regular intervals to form closely arranged thread-like ridges which project into the lumen (Fig. 117). These bands or thickenings are known as *taenidia* and, as a general rule, they pass round the trachea in a helical manner although their continuity is frequently interrupted: in other cases they form independent rings. The function of the taenidia is to keep the tracheae distended, and thereby allow of the free passage of air. If a trachea be teased out the intima will tear between the taenidia and the latter will uncoil after the fashion of an unwound wire. In some insects several taenidia exist side by side and in teased preparations a ribbon-like band uncoils which is formed of several parallel thickenings. Taenidia are absent, as a rule, from the large tracheae close to the spiracles, the intima in such positions presenting a tesselated or other type of thickening. In some insects (*Zaitha*, *Lampyris*, *Luciola*, etc.) cuticular piliform processes arise from the taenidia and project into the cavity of the trachea (Stokes, 1893).

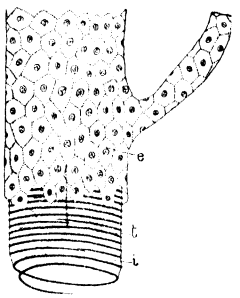


FIG. 117.—Portion of a trachea stained with iron-alum haematoxylin. (Highly magnified)

e, epithelial layer (ectotrachea); *i*, chitinous intima (endotrachea) with taenidium *t*.

An epithelial layer (ectotrachea) lies outside the intima and is composed of pavement cells with relatively large nuclei. The larger tracheae of some insects are faintly coloured with reddish-brown or violet pigment which is lodged in the cells of the epithelial layer. A delicate basement membrane forms the outermost coat of the tracheae.

The ultimate branches of the tracheal system are termed *tracheoles* and are canals with a diameter of 0·2–0·3 μ whose thin walls bear helical or circular taenidia visible only under the electron microscope (Richards & Korda, 1950). They may contain liquid or air, end blindly or in anastomosis with each other and their walls are freely permeable to water. The tracheoles are intracellular structures, developing in almost all cases from large, stellate end-cells (tracheoblasts) (Fig. 118) and later becoming joined to a developing trachea. The tracheoblasts, though ectodermal, develop independently of the tracheal epithelium and their processes commonly anastomose to form a fenestrated membrane over the surface of various viscera—the tracheated 'peritoneal layer'. Tracheoles also ramify between the cells of the insect tissues and even penetrate the cells of muscle, and perhaps other tissues, to end intracellularly. In the fat-body of the larvae of *Gastrophilus*, the tracheoles lie wholly within the cytoplasm of large tracheal cells of a special type (Fig. 119) which contain haemoglobin and act as an oxygen store (Dinulescu, 1932).

The general arrangement and distribution of tracheae present important

differences among the various groups of insects (Lehmann, 1926). In many Apterygotes, such as *Machilis*, *Campodea* (Fig. 120) and the Sminthuridae, the tracheae arising from each spiracle remain unconnected with those from

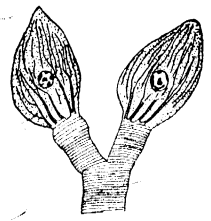


FIG. 119.—Tracheal cells from the fat-body of a *Gastrophilus* larva

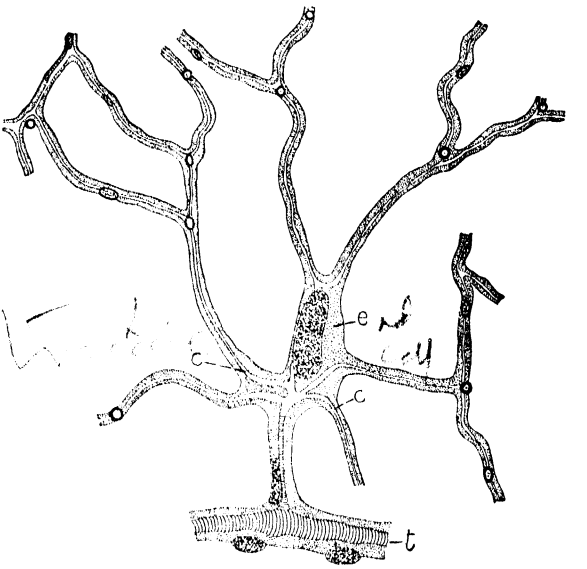


FIG. 118.—Tracheal end-cell and tracheoles from the silk gland of the larva of *Phalera bucephala* (Lepidoptera)

e, end-cell; *c*, tracheoles; *t*, trachea. *After* Holmgren, *Festschr. Liljeborg*, 1896.

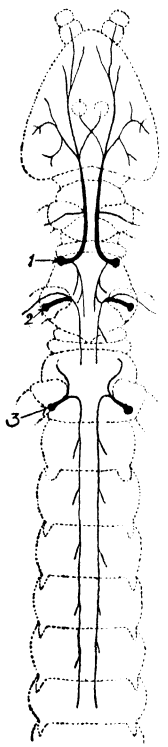


FIG. 120.—Tracheal system of *Campodea*

1, 2 and 3, Spiracles. *After* Grassi, 1887.

the others, but the Lepismatidae and Japygidae resemble the majority of Pterygotes in having a system developed from the union of a series of tracheospiracular metameres by transverse and longitudinal trunks (Fig. 121). Clear indications of such a metameric arrangement are present from the earliest postembryonic stages, though growth is accompanied by an increase in the complexity of the branches present (Fuller, 1919; Keister, 1948). A metameric basis is evident not only in holopneustic forms but also in the hemipneustic and apneustic systems owing to their retention of non-functional spiracles. The most constant features of well-developed tracheal systems are the presence of lateral longitudinal (spiracular) trunks (rarely absent, as in *Cimex*), of dorsal longitudinal trunks connected with the lateral trunks by palisade tracheae, and, less frequently, of ventral longitudinal trunks. Transverse dorsal or ventral commissures connect the systems of each side.

The dorsal longitudinal trunks give off segmental branches which pass to the heart and dorsal musculature. Visceral branches, which supply the digestive canal and reproductive organs, take their origin from the palisade tracheae or directly from the spiracular tracheae. The nerve cord and ventral musculature are supplied by branches derived from the ventral transverse commissures. The tracheae supplying the legs arise from the spiracular (or,

in Odonata, the dorsal) longitudinal trunks in the thoracic region, and the basal tracheae of the developing wings usually take their origin in close association with those of the leg tracheae of the meso- and metathorax (Comstock, 1918). The head and mouthparts are principally supplied by branches derived from the anteriormost spiracle and the dorsal longitudinal trunk.

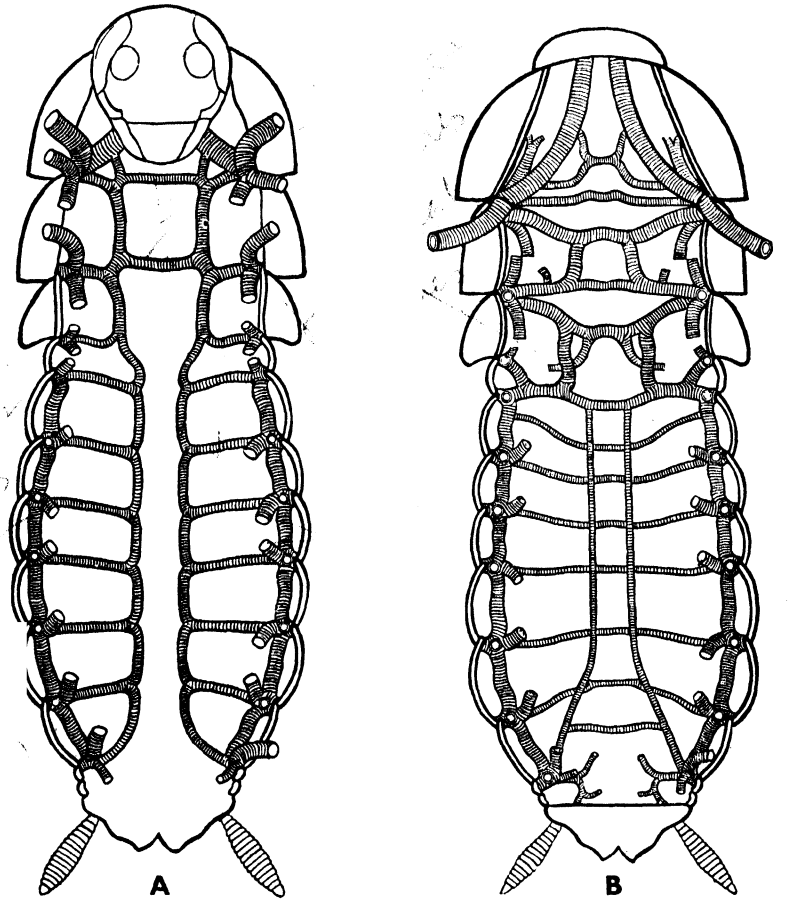


FIG. 121.—Tracheal system of *Periplaneta*

A, with the ventral integument and viscera removed showing dorsal trachea; B, with dorsal integument and viscera removed showing ventral tracheae. *After* Miall and Denny.

Hypopneustic tracheal systems deviate to varying degrees from the segmental arrangement, longitudinal trunks and transverse commissures tend to be reduced or disappear and each of the few spiracles gives rise directly to a greater or lesser number of branches which supply different parts of the body. The hypopneustic system may be markedly reduced, as in some Coccoidea.

The Air-Sacs

In many winged insects the tracheae are dilated in various parts of the body to form thin-walled vesicles or *air-sacs*. For the most part they are extremely delicate in structure and usually lack the taenidia which ordinarily

keep a tracheal tube open. The air-sacs are consequently distensible and, when inflated, are easily seen as glistening white vesicles. When collapsed and empty they are generally exceedingly difficult to detect. In *Melolontha*, for example, the air-sacs are dilatations of the secondary tracheae and are relatively small in size but exceedingly numerous. In *Melanoplus* there is a pair of large thoracic air-sacs and five pairs in the abdomen which are likewise dilatations of the secondary tracheae: there are also many smaller vesicles among the muscles. The air-sacs attain their greatest development in *Volucella, Musca* and other Cyclorrhapha and in *Apis* and *Bombus* among Hymenoptera (Fig. 122). In these instances the abdominal air-sacs attain very large dimensions and are dilatations of the main longitudinal tracheal trunks. Air-sacs are also met with among Lepidoptera and Odonata.

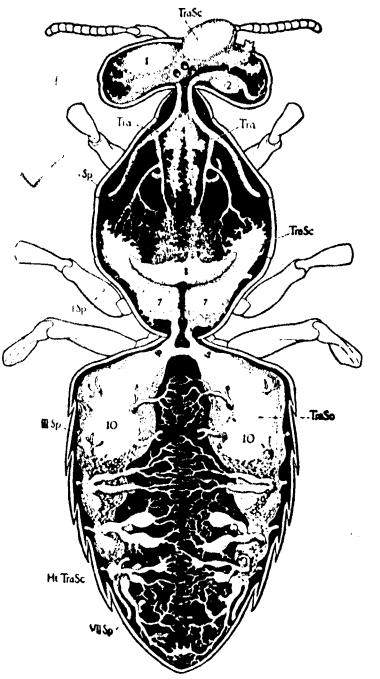


FIG. 122.—Tracheal system of worker honey bee seen from above

(One pair of abdominal air-sacs removed and transverse ventral commissures of abdomen not shown.) The air-sacs (*TraSc*) are indicated in arabic numerals: *sp*, spiracles. *After* Snodgrass, *U.S. Bur. Entom. Tech. Ser.* No. 18.

The principal function of the air-sacs is a respiratory one as they serve to increase the volume of 'tidal air' which is changed when respiratory movements are made (p. 144), but other functions are also known. An insect with air-sacs has a lower specific gravity than a similarly sized one without them and they may therefore make easier the flight of large species. In some higher Cyclorrhapha the sacs occupy a space in the abdomen of the newly emerged fly which is available for the later expansion of the ovaries while their occurrence beneath tympanal organs permits the membrane to vibrate more freely than would otherwise be possible. The air-sacs of the larvae of *Chaoborus* and *Mochlonyx* act as hydrostatic organs, enabling the insect to float at any level in the water it inhabits (Damant, 1924) while it has been suggested (Miall, 1903) that the pair in the abdomen of the littoral Carabids *Aepus* and *Aepopsis* acts as an air storage organ when its possessor is submerged.

Physiology of Respiration

Atracheate insects and those stages of the life-cycle during which the tracheal system is filled with liquid obtain their oxygen by direct diffusion from the environment into the body fluids. When a functional tracheal system is present, however, the carriage of oxygen to the tissues requires that the gas (*a*) enters the tracheal system, (*b*) is transported to its finest branches and (*c*) passes from them into the cells concerned.

The entry of oxygen into the tracheal system of terrestrial forms occurs for the greater part through the spiracles in all except a few apneustic insects like the larvae of *Forcipomyia*. In this, as in the apneustic aquatic and endoparasitic forms mentioned later, there is, over part or most of the body, a rich

subcutaneous plexus of fine tracheae which provides a large surface across which diffusion can occur. The transport of oxygen to the internal tracheal endings of insects was long thought to depend simply on diffusion of oxygen along a gradient of partial pressure, but only with the work of Krogh (1920) was an accurate study of this undertaken. The relation between the oxygen consumption of an insect and its tracheal dimensions is given by the formula:

$$S = \frac{k(p - p')A}{L}$$

where S = ml. of oxygen used per second; p = partial pressure of oxygen in the atmosphere (*c.* 0·2 of an atmosphere); p' = partial pressure of oxygen at the ends of the tracheae; A = mean cross-sectional area of the tracheae in sq. cm., L = mean tracheal length in cm. and k = the diffusion constant for oxygen (i.e. 0·18). From this formula it may be shown that diffusion is alone quite sufficient to account for transport of oxygen through the entire tracheal system of small or inactive insects—the observed oxygen uptake of *Cossus* larvae, for instance, could result from a difference of only 11 mm. Hg in oxygen tension between the atmosphere and the beginning of the tracheoles. Diffusion is the only factor involved in oxygen transport in all pupae, almost all terrestrial larvae and a large number of small imagines. In larger adults it is probably the mode of transfer in the terminal parts of the tracheal system but in other parts is supplemented by mechanical ventilation. Active compression of the abdomen and, more rarely, of the thorax, results in the expulsion through the spiracles of air from the air-sacs and those tracheae whose walls are less resistant to collapse. The ensuing passive expansion of these parts causes a fresh supply of air to be drawn in, as much as two-thirds of the tracheal volume being changed in some cases. The ventilatory movements may take the form of dorsoventral compression—in which the terga or sterna or both are moved—or, in the Aculeate Hymenoptera, may be the result of alternate telescoping and protrusion of the abdominal segments. Reference to the diffusion formula cited above will show that in non-ventilating insects the maximum possible body size is limited, since the oxygen consumption is affected more by a linear increase in size than is the rate of diffusion. The same effect also operates, though to a lesser extent, in ventilating forms since oxygen passes along the finer branches only by diffusion.

The control of respiratory activity results from 'diffusion control', due to the opening and closing of the spiracles and 'ventilation control' caused by variations in the frequency and intensity of the respiratory movements. Spiracular movements are regulated in *Xenopsylla cheopis* (Wigglesworth, 1935) by the oxygen concentration of the tracheal air and the accumulation of carbon dioxide in the tissues, the spiracles being open for a greater length of time when the oxygen is depleted and the concentration of carbon dioxide is high. The effective stimulus is probably the greater acidity of the tissue fluids induced by oxygen lack or excess of carbon dioxide. The nervous basis of these reactions is not fully understood but they are under the control of ganglia in the ventral nerve-cord, those of the abdomen being made more sensitive by the activity of the so-called secondary thoracic centres. The ventilating movements are likewise influenced by oxygen and carbon dioxide concentrations and subject to nervous co-ordination (Stahn, 1928). By combining ventilation movements with controlled opening and closing of the spiracles a directed flow of air through the tracheal system is made possible (Fraenkel, 1932; McCutcheon, 1940). In some Acridids air enters at times

through the two thoracic and two anterior abdominal spiracles and leaves by the more posterior abdominal pairs while in *Melophagus* there is an anteriorly directed flow (Webb, 1945).

Gaseous respiratory exchange between the tracheoles and the tissues depends on diffusion. The tracheoles may be entirely filled with gas or contain liquid in their terminal parts, the amount of liquid in the tracheole being affected by the osmotic pressure of the surrounding fluid. Thus, in active muscle with an inadequate oxygen supply the accumulation of metabolites raises the osmotic pressure of the tissue fluids, liquid is withdrawn from the tracheoles through colloid imbibition and is replaced by air, so improving the supply of oxygen to these tissues (Wigglesworth, 1930–31; 1953).

The diffusion processes which account for the inward transport of oxygen also permit the outward movement of carbon dioxide, but the tissues and cuticle are far more permeable to carbon dioxide than to oxygen so that an appreciable proportion of the former can escape through the tracheal walls and the general surface of the body. The blood plays a relatively minor role in respiration (p. 155).

Water loss from the general body surface is restricted by the epicuticular wax layer (p. 10) but the permeability of the tracheoles makes loss of water through the spiracles a serious matter in terrestrial species. Excessive loss is prevented by the use of the spiracular closing mechanism whenever possible or the development of a felt-chamber which reduces the diffusion of water-vapour across the spiracular opening. Xerophilous species may show strongly developed mechanisms of this sort (Bergold, 1935) while, on the other hand, for example, aquatic Heteroptera lack a closing mechanism (Mammen, 1912).

Respiration of Aquatic and Endoparasitic Insects

These modes of life are similar in that the insects are surrounded by a liquid or semi-liquid medium and must either extract dissolved oxygen from it by diffusion or retain a connexion with an atmospheric supply (Wesenberg-Lund, 1943; Keilin, 1944; Clausen, 1950; Hinton, 1953).

(*a*) **Aquatic Insects.**—The least highly modified to an aquatic habit are those with an open respiratory system, air entering the tracheae through one or more pairs of spiracles. These include several different types:

(i) There are first the oligopneustic forms without external air-stores (e.g. larvae of many Diptera and Dytiscidae). They are commonly metapneustic and possess a hydrofuge spiracular area with which they penetrate the surface film and so secure atmospheric oxygen. In many cases the spiracles are situated on the end of a siphon which may be short (e.g. some Stratiomyid and Culicid larvae) or long and retractile as in the 'rat-tailed' larvae of Ptychopteridae and most Eristaline Syrphidae. Comparable open prothoracic 'respiratory horns' occur in the pupae of many aquatic Nematoceran Diptera.

(ii) An essentially similar respiratory adaptation occurs in those forms where the spiracles are situated on sharply pointed processes which penetrate the air-containing cavities of the submerged parts of aquatic plants. Such a method of obtaining oxygen has been evolved in the larvae and pupae of several widely distinct genera of Diptera and Coleoptera (Varley, 1937): *Donacia, Lissorhapterus, Noterus, Taeniorhynchus, Notiphila,* etc.

(iii) Many aquatic Coleoptera and Cryptocerate Heteroptera are provided with renewable external air-bubbles which lie beneath the elytra (e.g. *Dytiscus*) or are trapped in a hydrofuge hair-pile on other parts of the body. Such bubbles are in contact with the spiracles and act not only as hydrostatic organs and stores of oxygen but also as 'physical gills' (Ege, 1915). As oxygen is removed from the bubble by the insect, equilibrium is restored by the diffusion of oxygen into the bubble from the

water more rapidly than the nitrogen of the bubble diffuses out. The insect can thus use the bubble to extract from the water far more oxygen than was originally present, though the bubble gradually decreases in size as the nitrogen diffuses away and requires periodic replacement from the atmosphere. This may be brought about by the insect pushing the hind end of the body through the surface film or by the use of a more specialized respiratory siphon (Nepidae, Belostomatidae) or, in the Hydrophilidae (Hrbáček, 1950), by hydrofuge antennal hairs forming an air-channel along part of the antennae to the ventral surface of the insect.

(iv) A few forms, such as the Heteropteran *Aphelocheirus* and some aquatic beetles (*Haemonia*, *Phytobius*, some Elmidae), have adopted 'plastron respiration' (Thorpe, 1950). The plastron is a special type of air-store in the form of a thin film communicating with the spiracles and so held by a system of hydrofuge hairs or scales that its volume remains constant. Provided there is adequate oxygen dissolved in the water, the plastron can act as a *permanent* physical gill which needs no renewal and insects so equipped can remain submerged continually.

Other aquatic insects are provided with a closed (apneustic) tracheal system into which oxygen passes from the surrounding medium (Koch, 1938). Such an arrangement is found in the immature stages of the Ephemeroptera, Odonata, Plecoptera, Trichoptera, Sialidae and larvae of many Dipteran families. Respiratory exchange occurs over the general body surface and across the thin cuticle of special respiratory organs—the gills or *branchiae*. The latter name was given in the past to almost any thin-walled integumentary outgrowth with a relatively large surface area and it was usual to distinguish between tracheal gills and blood-gills. Physiological studies (Thorpe, 1933, etc.) have shown that the blood-gills have little or no respiratory function while in some cases the tracheal gills may be of less importance than the remainder of the body surface. Nevertheless the anatomical and taxonomic interest of these structures is sufficient to demand a short account of them (Fig. 123).

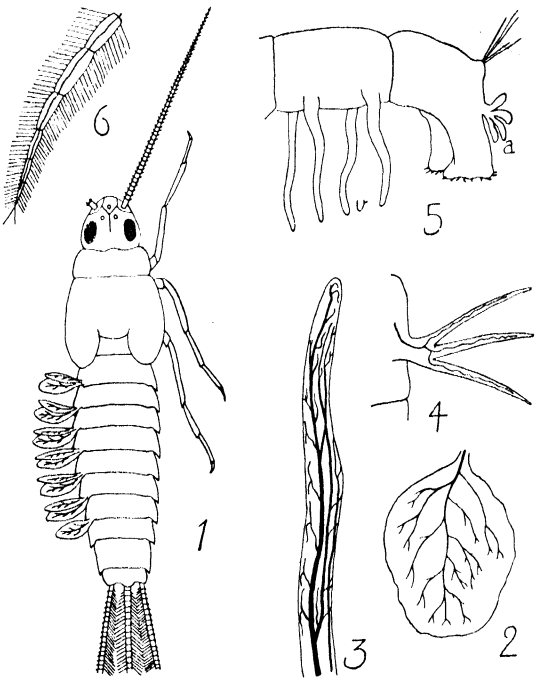


FIG. 123.—Gills of Aquatic Insects

1, Nymph of *Cloeon* showing tracheal gills of left side; 2, 7th tracheal gill of *Cloeon* more highly magnified; 3, tracheal gill of a *Phryganea* larva; 4, tracheal gill of a larva of *Nymphula stratiotata*; 5, hind extremity of a larva of *Chironomus* showing anal blood-gills (*a*) and ventral blood-gills (*v*); 6, jointed tracheal gill of a larva of *Sialis*.

Tracheal gills are filiform or more or less lamellate organs which are well supplied with tracheae and tracheoles. They are present in the majority of aquatic larvae and in some aquatic pupae. In many cases they are the only organs of respiration but in others (larval Culicidae for example) they are accessory in function and co-exist with open spiracles. Tracheal gills are usually borne on the abdomen: they are less frequently present on the thorax, and are only

very rarely found on the head (*Jolia* and *Oligoneuria* among Ephemeroptera). In a few instances the gills of the larvae persist throughout life in the imago: they are best exhibited in *Pteronarcys* whose imagines possess thirteen pairs of gill-tufts on the ventral surface of the thoracic and first two abdominal segments. Tracheal gills similarly persist in other Plecoptera and in *Hydropsyche* among Trichoptera but, as a rule, they are retained in a more or less shrivelled condition.

In the Ephemeroptera tracheal gills are usually borne on the first seven abdominal segments and may be either lamellate or filamentous in character. When lamellate each gill may consist of a simple leaf-like expansion (*Cloeon*) or the lamella may form a cover which protects a tuft of filamentous gills beneath (*Heptagenia*). In *Caenis* the upper lamellae of the 2nd pair of gills form opercula which conceal and protect the gills behind. In *Prosopistoma* the gills are entirely hidden within a special branchial chamber.

In the Plecoptera primitive abdominal gills occur in the Eustheniidae, but in the nymphs of other forms they are replaced by secondary tufts of filaments which are variable in position.

Tracheal gills are universally present in the nymphs of *Odonata*. In the Anisoptera they are in the form of an elaborate system of folds of the wall of the rectum, the latter chamber being modified to form what is termed the branchial basket. In most of the Zygoptera there are three external caudal gills and no rectal gills; in a few rare cases lateral filamentous abdominal gills are also present.

Among Neuroptera gills are present in the larvae of the Sialoidea and in *Sisyra* among the Plannipennia. They consist of seven or eight pairs of filaments, usually jointed, borne segmentally on the abdomen.

Filamentous abdominal gills are present in the majority of larval Trichoptera and frequently persist in the pupae of those insects. In some genera although the larvae are gill-less the pupae are provided with well-developed branchial organs.

Among Lepidoptera tracheal gills have long been known in the larva of *Nymphula stratiotata*; they consist of a series of delicate filaments arising from the sides of the trunk segments.

Among Coleopterous larvae tracheal gills are filamentous in character and are only present in a few of the families. In *Hygrobia* they are ventral and are located near the bases of each of the pairs of legs and on the first three abdominal segments. In the Gyrinidae there are 10 pairs of hair-fringed lateral abdominal gills; somewhat similar organs are also found in *Hydrocharis* and *Berosus* among the Hydrophilidae. In *Peltodytes* they take the form of numerous elongate jointed filaments which arise from the dorsal surface of the thorax and abdomen.

Among Dipterous larvae there are four lamellate anal gills in the Culicidae; in *Phalacrocera* the tracheal gills are in the form of numerous elongate filamentous processes which arise from almost all parts of the body segments; in *Simulium* and *Eristalis* rectal gills are present.

Spiracular gills. In some aquatic pupae, the peritreme and atrial region of one or more pairs of spiracles is drawn out to form long processes which Hinton (1953) terms spiracular gills. They occur in the beetle *Psephenoides* and in representatives of the Dipteran families Tipulidae, Blepharoceridae, Deuterophlebiidae, Simuliidae and Empididae, all from swiftly flowing streams liable to rapid fluctuations in water level. Such pupae as have been tested are able to live in damp air and to complete their development out of water, so that the spiracular gills are regarded by Hinton as structures adapted both for aquatic and aerial respiration.

The so-called **blood-gills** are commonly tubular or digitiform and are sometimes eversible. They derive their name from the fact that they contain blood but not as a rule tracheae, although occasional tracheoles may be present. In some instances there is little real distinction between these organs and tracheal gills. Blood-gills are of infrequent occurrence and are not exclusively confined to aquatic insects. They are found among many larval

Trichoptera which have 4 to 6 finger-like tubes at the anal extremity. Among Diptera they are well developed in the larvae of *Chironomus*, some species of which bear two pairs of ventral blood-gills on the penultimate segment, and a group of four shorter anal gills. Small anal blood-gills are also met with among aquatic Tipulid larvae. In Culicids and Chironomids, at least, the function of these structures is the absorption of water and inorganic ions (Wigglesworth, 1933; Koch, 1938) rather than respiration.

(*b*) **Endoparasitic Insects.**—In most endoparasitic Dipterous larvae and a few parasitic Hymenoptera, a connexion is established between the atmosphere and the open tracheal system of the parasite. In 1st-instar larvae of the Encyrtidae (Maple, 1947) this is brought about by the larva retaining a close association with the egg-shell which is connected with the surface of the host by a stalk-like prolongation and bears the so-called aeroscopic plate—a strip of modified chorion acting as an air-channel. Larvae of the Conopidae become attached to a tracheal trunk of their host though they appear not to penetrate it. Others perforate the body-wall or trachea so as to put their spiracles in contact with the atmosphere (e.g. old 3rd instar larvae of *Cryptochaetum*, Thorpe, 1934) and the host is sometimes stimulated to surround the parasite, except for the spiracular region, with a cuticular sheath (Pantel, 1898; 1910). In the remaining endoparasitic forms with a closed tracheal system, respiratory exchange occurs through the thin cuticle, beneath which lies a rich tracheal supply. Other early instars of parasitic species are either atracheate or have a system filled with liquid and in them the oxygen must diffuse directly into the haemolymph. The larvae of many Ichneumonidae, Braconidae and Chalcidoidea possess tail-like appendages which are probably not respiratory structures, but the paired, richly tracheated tail filaments of *Cryptochaetum* larvae and the blood-filled caudal vesicle of Braconid larvae are responsible for some oxygen uptake (Thorpe, 1932–41).

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THE CIRCULATORY SYSTEM

AMONG insects the circulatory system is largely an open one, there being only a single closed organ or dorsal vessel. The greater part of the circulation of the blood takes place in the cavities of the body and its appendages, the blood occupying the spaces not appropriated by the internal organs. The larger of these spaces may be enclosed by special membranes and form definite sinuses. With the exception of the aorta-like anterior prolongation of the dorsal vessel, which usually divides into terminal branches, and the segmental blood-vessels of the Dictyoptera, there are as a rule no definite veins or arteries such as are found in many Arthropoda. In the appendages and wing-veins, however, the blood flows in ingoing and outgoing streams along defined channels analogous to blood-vessels. In the larva of *Cloeon* the hindmost chamber of the heart gives off three caudal arteries which enter the respective tail appendages.

The organs and tissues belonging to the circulatory system are separately dealt with below.

The Diaphragms and Sinuses.—When the diaphragms are completely developed the general body-cavity or haemocoele is divided into three sinuses by means of two fibro-muscular septa (Fig. 124). The *dorsal diaphragm*—which is partly double in *Grylloblatta* and some Tettigonioidea—is the principal septum and the one most generally prevalent. It extends across the abdominal cavity above the alimentary canal and the blood-space thus enclosed is known as the *dorsal* or *pericardial sinus*. The latter is situated beneath the abdominal terga and within it is located the heart. The *ventral diaphragm*, when present, stretches across the abdominal cavity just above the ganglia of the ventral nerve-cord, and the space limited by it is the *ventral* or *perineural sinus*. Between the dorsal and ventral sinuses is the large central cavity or *visceral sinus* containing the principal internal organs.

Pairs of *alary muscles*, composed of striated fibres and a tissue resembling elastic connective fibres, arise from the terga and spread out fanwise over the surface of the dorsal diaphragm. The fibres of one alary muscle meet, beneath the heart, those of the corresponding muscle of the opposite side of the body. In some insects, including the Collembola, Dipterous larvae, and Anoplura, the alary muscles are attached to the walls of the heart (Fig. 126). These muscles vary in number; in *Periplaneta*, for example, there are 12 pairs of alary muscles (Fig. 125), in the hive bee 4 pairs, in *Haematopinus* 3 pairs and in the larva of *Chironomus* 2 pairs (see also Nutting, 1951).

The Dorsal Vessel.—The dorsal vessel extends from near the caudal extremity of the body, through the thorax, and terminates in the head. It is situated along the median dorsal line just beneath the integument and is protected by the dorsal diaphragm below. Morphologically it is a continuous tube, usually closed posteriorly, and always open at its cephalic extremity. It is divisible in two regions, viz. the *heart* or pumping organ and a conducting vessel or *aorta*.

The *heart* (Gerould, 1938; Nutting, 1951) is maintained in position within the pericardial sinus by means of suspensory filaments attached to the abdominal terga and frequently to the dorsal diaphragm also. It may be divided by successive constrictions into a series of chambers but is otherwise an unconstricted tube, and its segmentation is only evidenced by the presence of paired incurrent ostia (described below) and the alary muscles. In the most primitive condition there are thus indications that the heart occupies the three thoracic segments and the first nine abdominal ones. Among most insects, however, the heart is restricted to the abdomen and is variously shortened

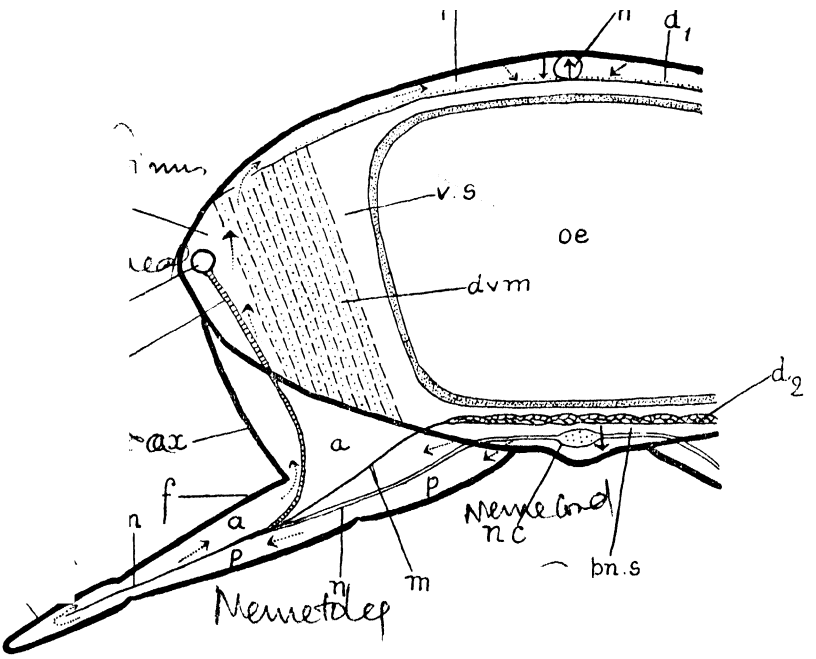


FIG. 124.—Schematic transverse section of the thorax of *Periplaneta* showing the diaphragms and sinuses

The plain arrows indicate the course of the circulation towards the head and the dotted arrows signify transverse currents more or less parallel with the plane of the paper. *h*, dorsal vessel; *d*, pericardial diaphragm; *p.s*, pericardial sinus; *oe*, oesophagus; *v.s*, visceral sinus; *dvm*, dorsoventral muscles; *t*, lateral tracheal trunk; t_1, leg trachea; d_2, ventral diaphragm; *pn.s*, perineural sinus; *nc*, nerve-cord; *n*, nerve to leg. The cavity of the leg is divided into an anterior sinus *a* and a posterior sinus *p* either by muscles or by a membrane *m*; in the femur the trachea and nerve are attached to the membrane; *cx*, coxa; *tb*, tibia and tarsus. Adapted from Brocher, *Ann. Soc. ent. Fr.*, 1922.

from both extremities so that fewer segments are indicated. Thus, in the Dictyoptera, *Grylloblatta* and some primitive Tettigonioidea the primitive number of 12 segments is involved; in *Japyx* there are 10, in *Lucanus cervus* 7, among aculeate Hymenoptera there are 5 divisions and in *Musca* 3; in a few insects the heart is reduced to only one chamber. Histologically the heart is composed of a single layer of cells with large nuclei, and striated muscle fibrillae are differentiated within the cytoplasm. The cellular layer is bounded both externally and internally by a delicate membranous tunic. The blood enters the heart through lateral inlets or *incurrent ostia*, a pair of which is situated at each constriction. The wall of the heart is reflected inwards and forwards at each ostium to form an *auricular valve*, which precludes the return flow of the blood into the dorsal sinus. In many insects each pair of auricular

valves also functions as a ventricular valve, which prevents the backward flow of the blood in the heart itself (Fig. 129). In the larva of *Aeshna* the ventricular valves are separately developed and situated some distance in front of each pair of ostia.

In many Orthopteroid insects Nutting (1951) has described various types of excurrent apertures through which blood may leave the heart. These include (i) the *lateral segmental blood-vessels*, of which 2 thoracic and 4 abdominal pairs occur in the cockroaches and the latter 4 pairs also in some Mantids; (ii) the valved *excurrent ostia* of which *Grylloblatta* has as many as 2 thoracic and 8 abdominal pairs and which, in different insects, may open above or below the dorsal diaphragm or between its two layers in a few cases or which, in the Grylloidea and some Tettigonioidea, lead into blind diverticula through whose phagocytic walls the blood plasma is thought to diffuse; (iii) 1 to 6 *unpaired ventral excurrent ostia* opening into the undivided haemocoele of a few species (*Pteronarcys*, *Oligotoma* and *Thermobia*).

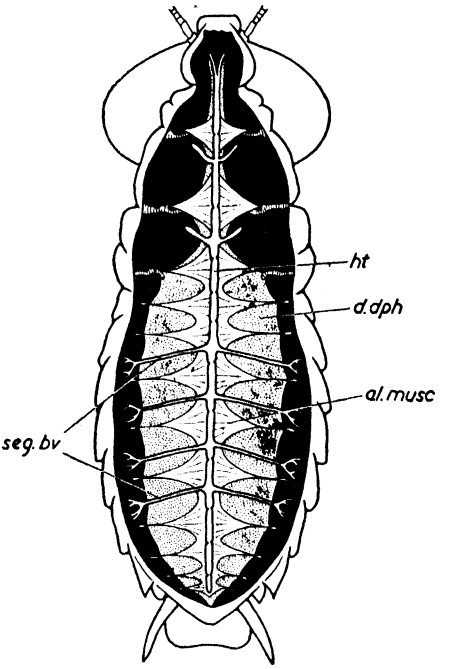


FIG. 125.—Heart and blood vessels of *Blaberus* (Blattidae) Ventral view

al.musc, alary muscles; *d.dph*, dorsal diaphragm; *ht.*, heart; *seg.bv*, segmental blood vessels. (From original of Plate 1, William N. Nutting, *J. Morph.*, **89**: 557.)

The *aorta* is the anterior prolongation of the dorsal vessel and it functions as the principal artery of the body. Its junction with the heart is frequently marked by the presence of *aortic valves*. The aorta extends forwards through the thorax to terminate in the head near the brain. In some insects its anterior extremity is an open funnel-like mouth but, more usually, it divides into two or more *cephalic arteries*, each of which may subdivide into smaller vessels

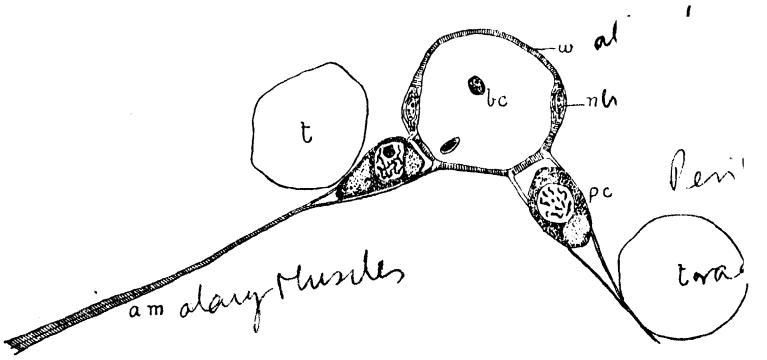


FIG. 126.—Transverse section of the heart of a Tachinid larva

bc, blood corpuscles; *w*, wall of heart; *n*, nucleus; *am*, alary muscle; *pc*, pericardial nephrocyte; *l*, trachea. *After* Pantel, *La Cellule*, 1898.

Accessory Pulsatory Organs.—In addition to the heart, accessory pulsatory organs have been described in many insects. They are sac-like structures situated in various regions of the body and pulsate independently of the heart, ensuring an

adequate circulation of blood through the appendages. Brocher (1919) has observed thoracic pulsatile organs in *Herse* and *Dytiscus* where they are present just beneath the meso- and metathoracic terga. In *Herse* the mesotergal pulsatile organ is well developed and is directly connected with a special diverticulum from the loop of the aorta (Fig. 127): the metathoracic organ, on the other hand, is very small. In *Dytiscus* the

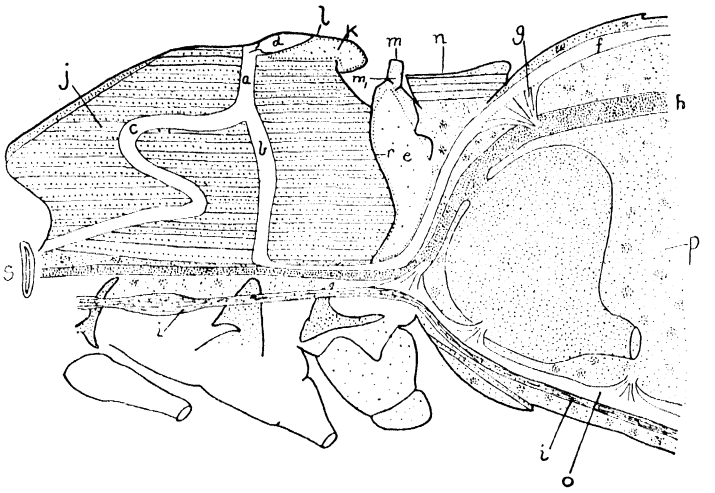


FIG. 127.—Section through the thorax and base of the abdomen of *Herse convolvuli* showing the circulatory system (Diagrammatic)

a, branch of aorta to mesothoracic pulsatile organ *d*; *b*,*c*, loop of aorta; *e* and *k*, air-sacs; *f*, heart; *g*, alary muscle; *h*, gut; *i*, ventral nerve-cord; *j*, mesotergal muscles; *l*, scutellum; *m*, metatergum and its pulsatile organ m_1; *n*, 1st abdominal tergum; *o*, ventral diaphragm; *p*, blood space; *r*, mesophragma; *s*, spiracle. Adapted from Brocher, *Arch. Zool. Exp.*, 1919.

reverse obtains, the metathoracic organ being the best developed. Comparable pterothoracic pulsatile organs also occur in the Odonata (Whedon, 1938) and other orders. Among Hemiptera special pulsatile organs are present in the legs (Weber, 1930); in *Periplaneta* and other insects, including Lepidoptera, there is a pulsatile vesicle at the base of each antenna (see Brocher (1932)). Thomsen (1938) describes a pair of accessory hearts in the scutellum of several Cyclorrhaphan Diptera and four pulsating areas in the veins at the base of the wings.

The Blood.—The blood (or haemolymph) of insects is contained in the general body-cavity, where it freely bathes the various internal organs and also enters the appendages and the tubular cavities of the wing-veins. General reviews of the composition and functions of insect blood are given by Mellanby (1939), Maloeuf (1939) and Buck (1953) while a selection of other papers is listed at the end of this chapter. Blood is the only extracellular fluid in the insect body and makes up 15–75 per cent. of the volume of the insect, the amount and composition varying with the species and its physiological condition. It consists of the liquid *plasma* and numerous blood-cells or *haemocytes*.

The plasma, which contains about 85 per cent. water, is usually slightly acid and includes inorganic ions, amino-acids, proteins, fats, sugars, organic acids and other substances in variable amounts. Potassium, sodium and chloride ions are the major inorganic constituents, the ratio of the first two varying greatly with sodium tending to predominate in carnivorous species and potassium in phytophagous ones. Magnesium, calcium and phosphorus are also present, the magnesium content often being unusually high. The organic constituents account for a considerable proportion of the total osmotic pressure and particularly striking is the high concentration of amino-acids

(e.g. Levenbook, 1950). Other organic acids such as succinic and citric also help to balance the cations present. It is of interest that in some aquatic larvae the concentration of organic substances (probably amino-acids) can vary in such a way as to compensate osmotically for large changes in the chloride concentration (Wigglesworth, 1938; Beadle & Shaw, 1950). The carbohydrates, fats and proteins of insect blood have been less fully studied. Glucose is the usual fermentable sugar, though fructose replaces it in *Gastrophilus* larvae. In the blood of *Platysamia* pupae, nine proteins have been distinguished immunologically (Telfer & Williams, 1951). The plasma is often pigmented, though little is known of the chemical nature of the coloured materials; haemoglobins have long been known from the plasma of some Chironomid larvae (see below) and Chefurka & Williams (1951) have identified α-carotene, chlorophylls a and b, riboflavin and taraxanthin from the blood of *Platysamia* pupae. The plasma has numerous functions. It provides a store of water on which the tissues can draw during desiccation and in some cases acts as an appreciable organ of food-storage (e.g. the blood-sugar of *Apis*, Beutler, 1936). It also transports food materials and hormones and exerts a mechanical function in the eversion of protrusible structures such as the ptilinum of Cyclorrhaphan Diptera or the penis of many male insects and in the dilation of the wings at the emergence of the adult. Because of the well-developed tracheal system of most insects, the blood has a relatively small respiratory role and is less concerned with oxygen transfer than with the carriage of carbon dioxide, from 30–80 per cent. of the total carbon dioxide of the blood being bound as bicarbonate (Levenbook, 1950a). In the Chironomid larvae with haemoglobin, the latter is of some respiratory significance at low oxygen tensions (e.g. Walshe, 1947, 1950). Reflex bleeding—i.e. the emission of blood through pores or slits in the cuticle—occurs when some insects are disturbed and presumably has a protective function though it has not always been distinguished from a similar secretion by hypodermal glands (q.v.).

The blood-cells or haemocytes arise in the embryo from the median walls of the coelomic sacs and are thought to increase during postembryonic development solely by the division of existing haemocytes. The number of cells present in the circulating blood of various adult species varies from about 1,000 per cubic mm. to about 100 times this number (Tauber & Yeager, 1935–36). Females tend to have higher counts than males and Endopterygote larvae have relatively more cells than the corresponding adults, though the reverse is true of Exopterygote nymphs. Particularly high counts are recorded from insects which are infected with bacteria or other parasites and at the time of ecdysis and oviposition. Such blood-cell counts do not record all the haemocytes present since large numbers are found attached to the surfaces of the viscera. Very many attempts have been made to classify the haemocytes histologically (Rooseboom, 1937) but they are not entirely satisfactory since, apart from differences between species, the cells vary greatly in shape according to whether they are free or attached and according to the techniques used for observing them. It is also probable that many so-called cell-types are merely stages in the development of a single type and that others are arbitrary selections from a continuous range of variation. Most authors agree, however, in distinguishing the *proleucocytes* which are small, rounded, basophil cells whose nucleus occupies most of their volume. They often show mitosis, are more abundant in the younger instars and probably represent a stage from which all or most of the other types develop. Another widely recognized

group are the *oenocytoids* which make up a small proportion of the total, are ovoidal, with a diameter of 8–12 μ, have a large nucleus and acidophil cytoplasm. They occur in the Coleoptera, Lepidoptera, Hemiptera and Diptera but not in the Orthoptera. The remaining cells which, with the proleucocytes, make up the bulk of the haemocytes, have been divided into classes on such characters as their general shape (ovoidal, amoeboid, fusiform or vermiform), the relative size and structure of the nucleus, the staining reactions of the cytoplasm and the occurrence and characteristics of the cytoplasmic inclusions. In this way Yeager (1945), for example, has recognized in all 10 main categories and 32 types of cells in the larva of the Noctuid *Prodenia eridania* and his elaborate classification has been applied to *Tenebrio molitor* by Jones (1950). On the other hand, Millara (1947), Arvy, Gabe & Lhoste (1948–49), Arnold (1952) and others have proposed simpler classifications of the haemocytes of various species while Ermin (1939) considered that in *Blatta* the

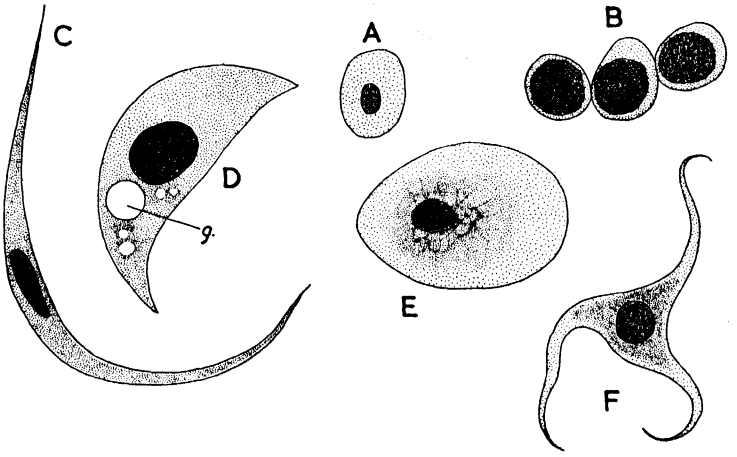


FIG. 128.—Representative blood-cells of *Prodenia eridania* (based on photographs of Yeager, 1945)

A. Oenocytoid. B. Proleucocytes. C. Nematocytoid. D. Macroplasmatocyte; *g*, glycogen inclusion. E. Palaeocystocyte. F. Multiramous plasmatocyte.

proleucocytes and the large blood-cells are merely connected by various transitional forms. In addition, there occur peculiar types of haemocytes restricted to a few species, such as the fat-laden blood-cells of *Pyrrhocoris apterus* or the wax-filled haemocytes of some Coccids and Aphids.

The principal function of the haemocytes is *phagocytosis*, i.e. the ingestion of small solid particles. This is demonstrated by the fact that most of the blood-cells other than the proleucocytes and the oenocytoids readily take up injected particles of Indian ink, but they also ingest bacteria and the tissue fragments which result from histolysis during pupation (see p. 236). Accumulations of phagocytic blood-cells may form discrete phagocytic organs near the excurrent ostia of some insect hearts (Nutting, 1951) while fully laden phagocytes may agglomerate and become encapsulated by other blood-cells in various tissues or in the haemocoele (Ermin, 1939). In the larvae of some species of *Chironomus* there are no free haemocytes, but a network of fixed phagocytes occurs in the posterior part of the abdomen, while in other Chironomid larvae there are free haemocytes with or without fixed cells (Lange, 1932). Haemocytes also form a sheath around the bodies of parasites

while the non-nucleate connective tissue membrane around such viscera as the ovaries, the basement membrane of the hypodermis and the fibrous non-cellular capsule which surrounds experimentally introduced foreign bodies may all be derived from haemocytes which degenerate after forming a fibrillar, argentophil membrane (Lazarenko, 1925; Ochsé, 1946). Blood-cells collect at the site of wounds, ingesting debris and forming a plug. Finally, some haemocytes fulfil the function of food storage since they contain inclusions of glycogen and fat which decrease on starvation of the insect (Yeager & Munson, 1941; Munson & Yeager, 1944).

Insect blood does not clot readily and in some cases clotting has not been observed. When it does develop, a clot forms either primarily by coagulation of the plasma, or by agglutination of haemocytes or both (Yeager & Knight, 1933; Beard, 1950). Grégoire & Florkin (1950) have claimed that clotting occurs through the formation of a reticulate coagulum around a special type of haemocyte in *Carausius* and *Acheta*.

The Circulation of the Blood (Brocher, 1932; Beard, 1953).—The heart is the principal pulsatory organ and undergoes rhythmical contractions which are brought about by the muscle fibrillae of its walls. Whether the rhythm is purely myogenic or, as Krijgsman (1952) believes, is controlled by a neurogenic pacemaker, is not certain. Contraction of the heart takes the form of a wave of peristalsis which runs forward from the posterior end. In some species this wave travels so quickly that the whole heart seems to contract at once; in other cases it is so slow that two or three waves can be seen travelling forwards at the same time. Diastole results from the relaxation of the heart muscle aided, in some insects, by contraction of the alary muscles or the elastic tension of their fibres (Dubuisson, 1929; De Wilde, 1948). During diastole the blood enters the heart by the incurrent ostia, which may exclude some or all of the haemocytes. On contraction the expanded lips of these ostia act as valves so that the blood is prevented from returning through them to the pericardial sinus and is propelled forwards (Fig. 129). In its forward passage, some blood leaves the heart by the excurrent ostia and lateral segmental vessels when these are present. The remainder enters the cephalic haemocoele, from which a part is pumped into the antennae by accessory pulsatile organs. The circulation of blood through the wings of many insects occurs in definite channels between the inner walls of the veins and the enclosed trachea and takes the form of a distally directed flow in the front half of the wing and a return flow along the posterior margin (Clare & Tauber, 1940–42). It is brought about by the thoracic pulsatile organs which aspirate blood from the posterior part of the wing-base. Circulation through the legs may also be achieved through accessory hearts at their bases, helped by movements of the legs and the presence of diaphragms within them. From the head and thorax the blood flows backwards in the haemocoele and is probably assisted in this direction by undulatory movements of the ventral diaphragm.

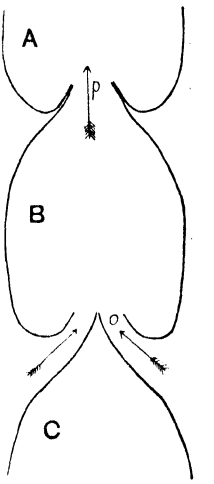


FIG. 129.—Valves of the heart

A, B, C, chambers of the heart; AB, at the moment of systole; BC, at the moment of diastole. *p*, interventricular passage; *o*, ostium.

The rate at which the heart beats is greatly affected by temperature and the activity and physiological state of the insect and also varies in different species,

there being 14 beats per minute in *Lucanus* larvae at 18° C., and over 150 in *Campodea* at 20° C. In *Sphinx ligustri* and *Bombyx mori* the rate declines steadily throughout larval and pupal development and slower rates are recorded from some parasitized Lepidopterous larvae. Reversal of the direction in which peristalsis is propagated may occur as a temporary phenomenon in many insects and in *Bombyx mori* it occurs regularly in the late larva and pupa and intermittently in the adult (Gerould, 1938).

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THE EXCRETORY ORGANS, FAT-BODY AND OTHER HAEMOCOELIC STRUCTURES

(*a*) Excretory Organs

THE function of an excretory system is the maintenance of a relatively constant internal environment for the tissues of the body; among the regulatory processes involved are the elimination of the nitrogenous waste-products of protein breakdown and the control of the ionic composition of the haemolymph. The principal excretory organs of insects are the Malpighian tubes, and an accessory excretory function is performed by the fat-body, while the nephrocytes, gut and, in some Apterygota, certain cephalic glands have also been regarded as excretory to some extent.

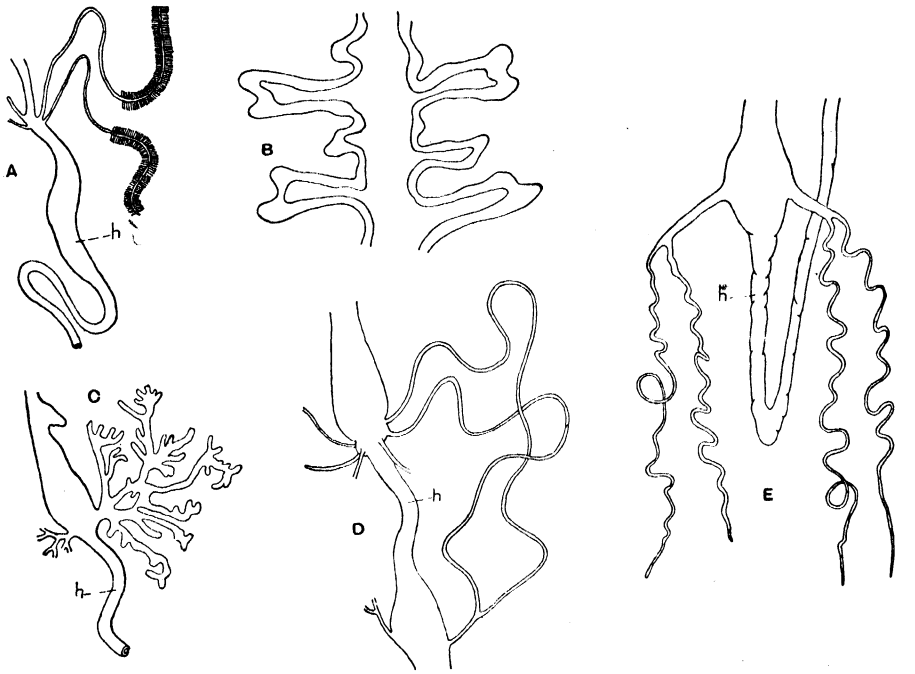


FIG. 130.—Malpighian tubes

A, *Melolontha melolontha*. B, portion with diverticula more highly magnified. C, *Galleria mellonella*. D, *Timarcha tenebricosa*. E, *Calliphora* (larva). *h*, hind intestine. A–D *after* Veneziani, *Redia*, 1904.

The **Malpighian Tubes** (Fig. 130).—First discovered by the Italian anatomist Malpighi, these organs are almost universally present among insects. They are long, slender, blind tubes lying in the haemocoele where they are freely bathed by the blood. They open at their proximal extremities into

the intestine, near the junction of the hind gut with the mid gut. They have generally been regarded as derivatives of the ectodermal proctodaeum, but Henson (1937–46) and others believe them to originate from an undifferentiated zone of cells between mid and hind gut and Henson considers them outgrowths of the mesenteron. Distally they are usually free but in some insects the distal ends of the tubules are closely applied to the hind gut. This 'cryptonephridial' condition occurs in the larvae and adults of many Coleoptera (Marcus, 1930; Poll, 1932; Stammer, 1934; Lison, 1937a; 1938), in some Symphytan larvae (Poll, 1937), in Myrmeleontid larvae (Poll, 1936) and in almost all Lepidopteran larvae (Poll, 1939). The tubules may be held against the rectum by a thin cylindrical sheath or lateral sac of peritoneal cells (Coleoptera and Symphytan larvae) or lie below the muscle layer of the hind gut, as in Lepidopteran larvae (Poll, 1939). Cryptonephry probably enables the insect to conserve water by withdrawing it from the faeces. The exterior of the Malpighian tubes is richly supplied with a reticulum of fine tracheae whose larger branches serve to maintain these organs in position. The number of Malpighian tubes is very variable but tolerably constant within the limits of most of the orders (Veneziani, 1905). These vessels usually occur in twos, or multiples of two, and their primitive number according to Wheeler (1893) is six. It is only very exceptionally that more than six are present in the embryo and they are often reduced to four. Specialization either by addition or reduction is frequent: their number is often less than 6 and may exceed 100 through postembryonic differentiation of so-called secondary tubules (Henson, 1937–46).

The typical number of these vessels present in the various orders is given below.

Anoplura, Thysanoptera, Hemiptera, Diptera and Siphonaptera 4.
Psocoptera, Coleoptera 4–6. Isoptera 2–8. Thysanura 4–16.
Mecoptera, Trichoptera and Lepidoptera 6. Neuroptera 6–8. Dermaptera 8–20.
Ephemeroptera 8–100. Plecoptera 50–60. Odonata 50–200. Orthoptera 30–200.
Hymenoptera, 6–20 in ants and over 100 in many Aculeata.

The Coccoidea and larval parasitic Hymenoptera are exceptional in having only two Malpighian tubes and the Culicidae have the unusual number of five. In certain Diplura, the Protura, and Stepsiptera these vessels are doubtfully represented by papillae: in the Collembola, *Japyx*, and the Aphidoidea they are wanting altogether. Although the Malpighian vessels are usually simple tubes they are sometimes arborescent, as in *Galleria mellonella*, or they may give off short closely-packed diverticula as in *Melolontha* (Fig. 130). Very frequently the tubes unite in groups of two or three and they may open into a common ampulla or bladder, which discharges into the intestine. When very numerous the Malpighian tubes may be grouped in bunches, each bunch discharging by a separate duct or ureter: in the Gryllidae all the tubes converge to open into a common ureter of considerable length. Not infrequently the Malpighian tubes exhibit morphological and physiological differences. Thus, in *Haltica* and *Donacia* four of the tubes discharge into a common ampulla while the remaining two shorter vessels have isolated insertions. In many species some or all of the tubes show a division into two or three zones (Fig. 131) which differ in structure and function.

When viewed in transverse section a Malpighian tube is seen to be composed of about three to eight large and variably-shaped epithelial cells with prominent nuclei. The latter increase in size during development and may become palmate (Henson, 1937) or form giant endopolyploid nuclei. Where

each cell borders the lumen of the tubule it possesses a brush or honeycomb border, the appearance of which may vary over different parts of the tubule. The epithelial cells also show an outer striated zone in many insects and rest externally on a basement membrane (tunica propria) which is covered by a peritoneal coat often containing muscle fibres. The muscles, in which striations are sometimes difficult to detect, may run in bands or as a reticulum over the whole tube or be restricted to the proximal region; they appear not to be innervated but are responsible for peristaltic movements of the tubules. In the Thysanura, Dermaptera and Thysanoptera there are no muscles and peristalsis does not occur (Palm, 1946). In some of the species with a cryptonephridial arrangement, the distal parts of the tubules have small thin areas (leptophragmata) adjoining the haemocoele and giving a strong reaction for chlorides (Conet, 1934; Lison, 1938; 1939).

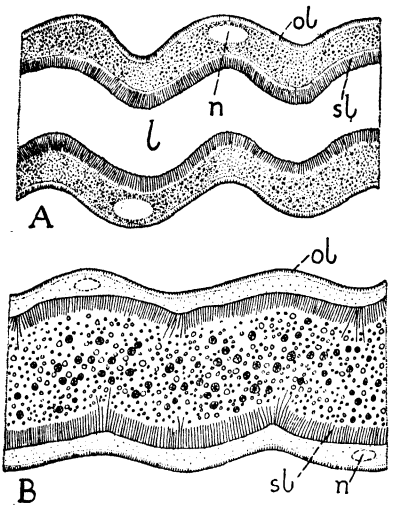


FIG. 131.—Malpighian tubes of *Rhodnius* (Reduviidae) seen in optical sections of living material. A, upper region of tube with excretory granules in the cells. B, lower region of tube with excretory spheres in the lumen

l, lumen; *n*, nucleus of excretory cell; *ol*, outer striated zone; *sl*, inner striated margin (filamentous in B). Adapted from Wigglesworth, *J. exp. Biol.*, 1931.

There are great variations in the chemical composition of the urine secreted by the Malpighian tubules, depending on the nature and amount of food taken and, in aquatic forms, on the ionic composition of the external medium (Wigglesworth, 1931; Boné & Koch, 1942; Ramsay, 1952). The principal nitrogenous excretory material is uric acid, which may be present in solution or crystallize in the lumen of the tubules as sphaeroids of the free acid or its salts. Small amounts of urea, free amino-acids and other substances are present while blowfly larvae excrete allantoin, together with large amounts of ammonia which is formed mainly in the mid gut from adenosine-containing components of the food and reaches the tubules through the blood (Brown, 1938; Lennox, 1941). Inorganic ions are also found in the tubules, there being an active secretion of potassium and a passive diffusion of sodium into the lumen in many insects (Ramsay, 1953). Inorganic concretions may also accumulate in part of the lumen (Keilin, 1921), those of *Lucilia* having a diameter of 16–20 μ and consisting mainly of the phosphates and carbonates of magnesium and calcium (Waterhouse, 1950). In *Rhodnius* it is likely that water and the acid urates of sodium and potassium are secreted in the distal part of the tube, followed in the proximal section, through interaction with carbon dioxide, by the precipitation of uric acid and the resorption of water and bicarbonates (Wigglesworth, 1931; Ramsay, 1952). Injection of certain water-soluble dyestuffs into the haemocoele of insects is followed by their elimination through the lumen of the tube or their accumulation in its cells through resorption (Lison, 1937; 1942). Although different tubules or parts of a tubule differ in their behaviour in these respects, the significance of the results in terms of normal function is not entirely clear.

The Malpighian tubules of some insects also have accessory secretory functions. Those of Cercopid nymphs, for example, produce a foam-stabilizing substance (Licent, 1912) and in several Neuropteran and Coleopteran larvae they secrete the silk from which the pupal cocoon is constructed.

The **Fat-body.**—The fat-body (Pardi, 1939) is composed of irregular masses or lobes of rounded or polyhedral cells (trophocytes) which are usually vacuolated and contain inclusions of various kinds. In many insects the fat-

body is built up of tightly compacted cells: in others it is a more or less laminate tissue with numerous lacunae, or it may take the form of loose strands. In colour it may be either white, yellow, orange or greenish. This tissue is derived from the mesoderm by a differentiation of the walls of the coelomic cavities and it consequently has a primitive metameric disposition. With the breaking down of the embryonic coelom, and the development of a haemocoele, the fat-body forms the irregular boundaries of the permanent body-cavity. In many insects it is possible to distinguish an outer or *parietal layer*, beneath the body-wall, and an inner or *visceral layer*, which surrounds and enters between the various organs (Fig. 132). In some larvae the parietal layer is interrupted at each segment and thus retains a segmental arrangement: the visceral layer, on the other hand, forms a continuous sheet passing from one segment to another. The fat-body alters very much in its histological structure during the life of an insect (e.g. Lartchenko, 1937). In the earlier instars its nuclei are rounded or oval (Fig. 133, 3) but they often later alter in character, becoming stellate or ribbon-like (Fig. 133, 2 and 4). In many cases the cellular structure is no longer evident and the fat-body has the appearance of a syncytium (Fig. 133, 1) though cell-boundaries may reappear on starvation. The cells of the fat-body seem to be closely related to the haemocytes. They may be indistinguishable in young stages, or haemocytes may become laden with fat and incorporated into the fat-body and fat-body cells are said in some species to be capable of phagocytosis.

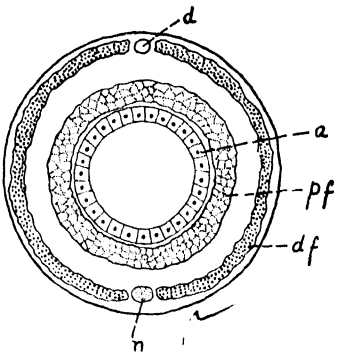


FIG. 132.—Schematic transverse section of an insect larva showing distribution of the fat-body

a, alimentary canal; *d*, dorsal vessel; *n*, ventral nerve-cord; *pf*, *df*, visceral and parietal layers of fat-body.

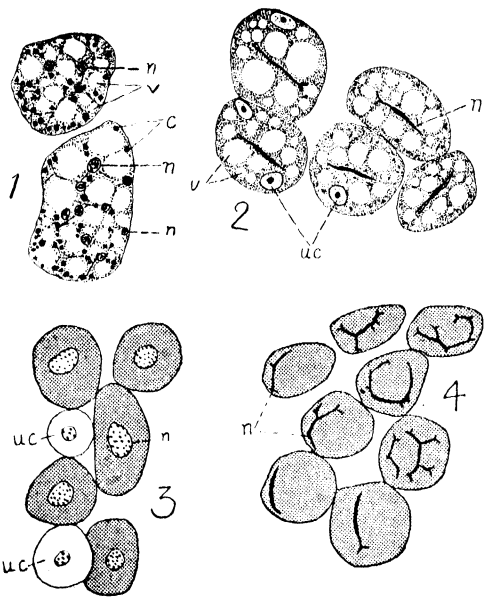


FIG. 133.—Fat-body of various insects

1, Adult Termite (soldier); 2, Adult larva of *Caliroa limacina*. 3. Young larva of *Formica rufa*. 4, Adult larva of same. *c*, urate concretions; *n*, nucleus; *uc*, urate cells; *v*, vacuoles filled with fat globules. Nos. 3 and 4 adapted from Pérez, *Bull. Sci. Fr. et Belg.*, 37.

In some insects deposits of uric acid or urates appear in the fat-body during life. In the Collembola, *Blatta*, and Hymenopteran larvae (Apocrita), these excretory granules are formed in specialized urate cells of the fat-body, the Malpighian tubules being either absent or non-functional or not secreting urates. In other cases, even though the tubules secrete urates, some may also be deposited in the trophocytes. In the larvae of the Apocrita, Lepidoptera

and Cyclorrhaphan Diptera, the urates of the fat-body are transferred to the Malpighian tubules at pupation. Calcium salts, in the form of calcospherites, accumulate in the fat-body of phytophagous Dipteran larvae (Keilin, 1921).

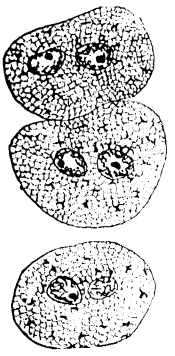


FIG. 134. — Three ventral nephrocytes from the larva of *Limnophora riparia*, highly magnified

After Keilin, *Parasitology*, 1917.

Although the fat-body carries out these functions of storage excretion, its principal role is the elaboration and storage of food reserves consisting of fat, glycogen and protein. Larvae of *Aedes aegypti* (Wigglesworth, 1942) accumulate glycogen in the fat-body when fed on starch and some sugars, while fat is deposited when fed on olive oil. Feeding on casein causes an accumulation of protein together with glycogen and some fat. The reserves of the insect fat-body are depleted during starvation and are also mobilized during periods of great activity, such as prolonged flight (p. 49), in moulting (Wigglesworth, 1947) or during hibernation, maturation of eggs and at pupation; during the last-mentioned phase the larval fat-body disintegrates in some species.

The **labial glands** of the Collembola, Diplura and Thysanura discharge by means of an excretory duct which opens at the base of the labium (Fahlander, 1940). According to Bruntz (1908) these organs consist of a saccule which eliminates ammonia-carmine and a labyrinth which similarly deals with indigo-carmine when these substances are injected into the body-cavity but their normal functions are unknown.

The **Nephrocytes** (Fig. 135).—The nephrocytes consist of scattered or localized groups of cells or syncytial aggregates often with more than one nucleus per cell. When localized they occur in two principal groups: (1) the dorsal or pericardial nephrocytes and (2) the ventral nephrocytes. The dorsal nephrocytes are commonly termed the pericardial cells, and consist of two chains or segmental groups of cells arranged in a linear series one on either side of the heart in the pericardial sinus; such cells are present in the immature stages and adults of most insects. The ventral nephrocytes occur in Dipterous larvae where they constitute the 'garland-like cell-chain' of Weismann. In these insects they usually form a chain of cells which is suspended in the body-cavity below the fore intestine and attached by its two extremities to the salivary glands. The nephrocytes are able to absorb colloidal particles, chiefly of 16–20 Å. radius, from the blood; proteins, chlorophyll and such dyestuffs as trypan-blue and ammonia

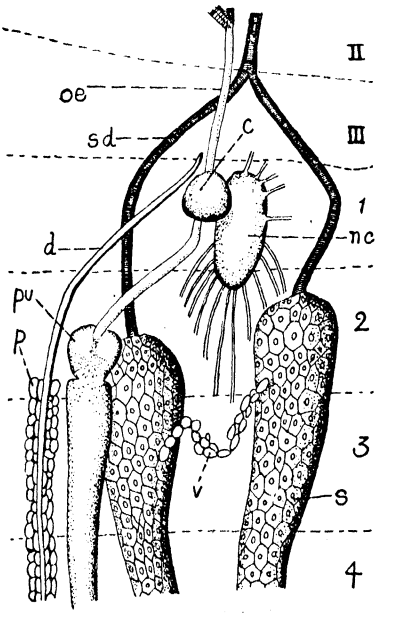


FIG. 135.—Dissection of the anterior region of the larva of *Phaonia cincta* (Anthomyidae), showing the pericardial nephrocytes *p*, and the ventral nephrocytes *v*

II, III, 2nd and 3rd thoracic segments; 1–4, abdominal segments; *c*, cerebral ganglion; *d*, dorsal vessel; *nc*, ventral ganglionic centre; *oe*, oesophagus; *pv*, proventriculus; *s*, salivary gland; *sd*, salivary duct. Adapted from Keilin, *Parasitology*, 1917.

carmine appear in them after haemocoelic injection. For this reason they were regarded as organs of storage excretion but except in a few cases where pigments or other materials accumulate in them, their contents do not seem to increase with age. They are now considered to be analogous to the reticulo-endothelial system of vertebrates, and take up particles of colloidal dimensions from the blood (athrocytosis) rather as the haemocytes take up larger bodies (phagocytosis). Whether they have further metabolic functions is not known. For further information, see Cuénot (1895), Keilin (1917; 1924), Keilin & Nuttall (1921), Hollande (1922), Lesperon (1937), Lison (1942) and Palm (1952).

The **Gut** perhaps plays some part in excretion since certain injected dyestuffs are secreted by its walls or accumulate in their cells while the periodic 'renovation' of the mid gut in some Collembola (p. 279) suggests an excretory function and the biliverdin resulting from haemoglobin breakdown in the tissues of *Rhodnius* is discharged into its lumen (Wigglesworth, 1943).

(*b*) The **Oenocytes**

These large cells (15–150 μ or more across) have been recorded from most orders of insects (Richards, 1951). They arise from the ectoderm or hypodermis, usually near the abdominal spiracles (Figs. 136 and 137) and sometimes remain closely associated with the bases of the hypodermal cells. In other cases they project into the haemocoele or become separated from the hypodermis to form segmentally arranged clusters or are even dispersed among the fat-body. They are usually amber-coloured but may be brown, red, green or colourless and either arise repeatedly during postembryonic development or, in some Endopterygotes, are composed of a larval and an imaginal generation (e.g. *Pieris*, Kaiser, 1950). In the so-called resting stage there is a homogeneous,

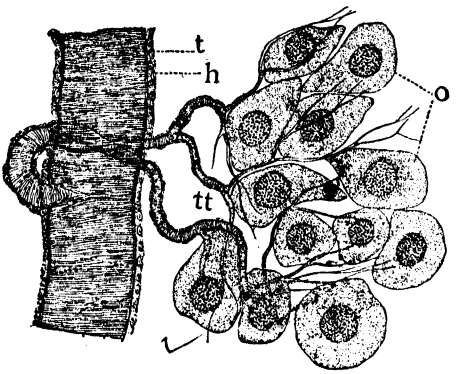


FIG. 136.—Cluster of oenocytes from a nearly mature Phryganeid larva

o, oenocytes; *t*, trachea; *tt*, small tracheal branches; *h* tracheal hypodermis.

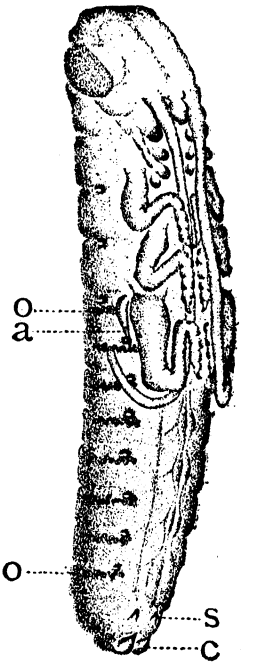


FIG. 137.—A nearly mature embryo of *Xiphidium*

o, oenocyte cluster; *a*, appendage of 1st abdominal segment; *s*, style; *c*, cercus. This and Fig. 136 after Wheeler, *Psyche*, 1892.

eosinophil cytoplasm with a sparse distribution of lipoprotein granules, fats, glycogen, etc. (Lhoste, 1950) but cycles of activity with pseudopodial

development, branching of the nucleus and cytoplasmic vacuolation also occur and are known in some cases to be associated with the deposition of new cuticle at a moult (Wigglesworth, 1948; Kaiser, 1950; Kramer & Wigglesworth, 1950). They are thought to secrete the cuticulin layer of the epicuticle and, in cockroaches, the surface grease which covers the integument but whether they have other functions is not known. In Culicid larvae, where small (15–25 μ) oenocytes are generally distributed and large ones (55–60 μ) are segmentally arranged, only the latter show cyclical changes correlated with moulting (Hosselet, 1925).

Literature on Excretory Organs, Fat-Body, etc.

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THE GLANDS OR ORGANS OF SECRETION

THE glands of insects are composed of one or more cells which secrete substances used in or eliminated from the body. Two main types of secretory structures occur. The *exocrine glands* are provided with a more or less well-defined aperture or duct and discharge their secretions outside the body or into the lumen of one or other of the viscera, while the *endocrine* (incretory) *glands* have no specialized ducts, their products (hormones) diffusing into the blood which transports them to all parts of the body.

Exocrine Glands

The normal hypodermal cells, the secretory cells of the mid gut and those of the Malpighian tubules all form glandular epithelia but, for convenience, are dealt with on pp. 11, 129 and 161 respectively. The numerous other exocrine glands considered here are almost all derived from ectoderm and may retain a thin or perforated cuticular layer. They are sometimes unicellular or simple aggregations of single cells (Figs. 138 and 139) or form more highly organized multicellular structures. The latter may be tubular, in the form of a simple alveolus (Fig. 138) or, when the central cavity or duct is branched or divided the gland is said to be compound. There are consequently compound tubular and compound alveolar (or racemose) glands. The secretory cells line the subdivisions of a tubular gland and the ultimate alveoli, or acini, of the other type. Such elaborate glands are usually provided with a non-secretory duct, opening by a specialized aperture, and may also possess a reservoir for temporary storage of the secretion (Fig. 143).

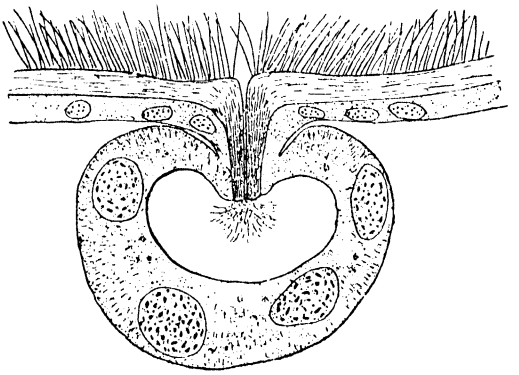


FIG. 138.—Section of the integument of the larva of *Gnophomyia tripudians*, showing simple gland
After Keilin, 1913.

Histologically, a gland is composed mainly of the secretory epithelial cells which are often very

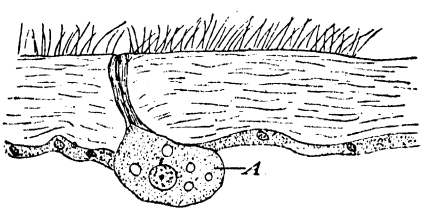


FIG. 139.—Section of the integument of the larva of *Ula macroptera* (Tipulidae) showing unicellular hypodermal gland (A)
After Keilin, *Arch. Zool. exp.*, 1913

large and elaborate in structure. Their nuclei may be ovoidal or much branched (Fig. 144) and may contain polytene chromosomes as in the salivary glands of Dipteran larvae (Metz, 1939; Painter, 1939). The cytoplasm usually contains mitochondria, a Golgi apparatus and various granules or vacuoles, while the surface through which the secretion discharges is often marked by a brush-border. Externally these cells are bounded by a tunica propria of connective tissue and internally they often secrete a cuticular lining. In some cases the secretion of each cell is discharged by a minute simple or branched intracellular ducteole which communicates with the lumen of the gland (Fig. 140). Works describing the very varied histology of glands are listed by Day (1948). Little is known of the biochemical processes whereby the secretory products are synthesized, but the composition of some insect secretions (silk, wax, lac, etc.) has been studied more fully and Maloeuf (1938) gives a general review.

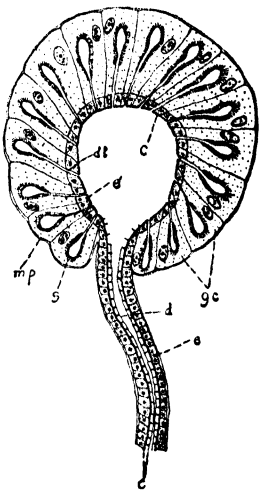


FIG. 140. — Semi-diagrammatic section of an acinus of the pygidial gland of a Carabid, *Feronia* (*Pterostichus*)

c, cuticular lining; *d*, lumen of duct; *dt*, ducteole; *e*, epithelial lining of duct and *e'* of acinus; *gc*, gland cells; *mp*, membrana propria; *s*, striated zone. Based on Dierckx, *La Cellule*, 16.

The principal types of exocrine glands are dealt with under the following headings.

Wax Glands (Fig. 141).—Glands which secrete wax are more especially characteristic of Homoptera where they are uni- or multicellular structures distributed in various parts of the integument. They are particularly evident in the Coccoidea (Rogojanu, 1935; Pollister, 1937). The wax is secreted in the form of a powdery covering, as a clothing of threads, or as thin lamellae. Chinese white wax, which was formerly a commercial product, is secreted by the Coccid *Ericerus pe-la*. Wax glands are also frequent among Aphidoidea and in *Eriosoma lanigerum* the secretion (which is, strictly speaking, a fat rather than a wax) is exuded both in a powdery and a filamentous condition. In the latter case it is discharged through plates composed of a ring or an aggregation of several large cells, each cell containing a central excavation, or wax chamber, within which the secretion accumulates (Fig. 141c). In the Flatid *Phromnia marginella*

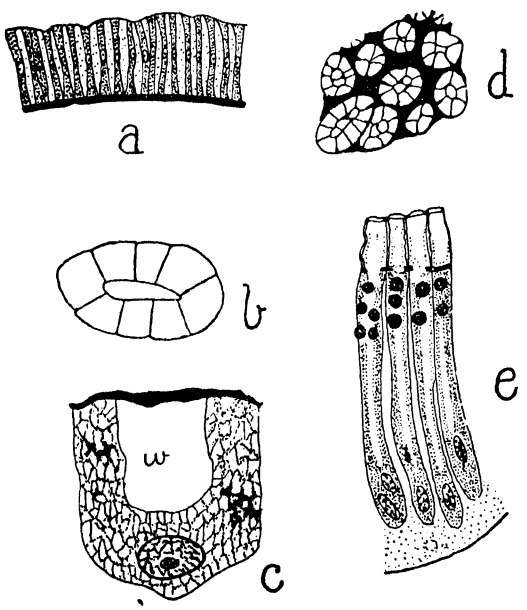


FIG. 141.—Wax glands

a, Section of a portion of a wax plate of a worker hive bee with gland cells (*after* Dreyling). *b*, Surface view of a wax plate of *Eriosoma lanigera* (apterous vivip. female). *c*, Section of a wax cell of the same showing wax chamber *w* (*after* Baker). *d*, Surface view of a portion of a wax plate of *Phromnia marginella*. *e*, Wax cells of the latter seen in section. *After* Bugnion & Popoff.

Sŭlc (1929) has shown that the dense clothing of waxy filaments which covers the nymphs is secreted by groups of unicellular glands composed of greatly elongated hypodermal cells (Fig. 141e). Overlying each group of cells is a cuticular plate studded with small pores which are the openings of the separate gland cells. The larvae of some Coccinellidae and of a species of *Selandria* (Tenthredinidae) are invested with a mass of flocculent material believed to be of wax. The wax glands of the hive bee are alluded to under Hymenoptera (vide Reimann, 1952).

Lac Glands.—Lac is secreted by certain Coccoidea (Lacciferidae) and, in particular, by *Laccifer lacca* which yields the lac of commerce, a resinous substance produced in large quantities by the female insect as a protective covering (Glover, 1937). The lac is a product of gland cells distributed in the integument (see also Mahdihassan, 1938). Chemically it consists very largely of resin together with colouring matter, wax, proteins and small amounts of other substances. It is noteworthy that *Laccifer lacca* flourishes best on trees containing gums or resins, or which are rich in certain kinds of latex, and the food-plant influences the colour and quantity of the lac produced (Imms & Chatterjee, 1915).

Cephalic Glands.—In addition to the peculiar frontal gland of the Isoptera (p. 379) and the small antennal glands of unknown function in *Myrmica* and *Periplaneta*, the head of insects contains several paired glands associated with the mouthparts. These may be, at least in part, homologous with the segmentally arranged coelomoducts of Annelids and lower Arthropods (Fahlander, 1940) and appear generally to be of ectodermal origin, though Pflugfelder (1934) claims that the labial glands of *Pontania* larvae are largely derived from the mesodermal coelom-sac walls. Three types of cephalic glands occur widely:

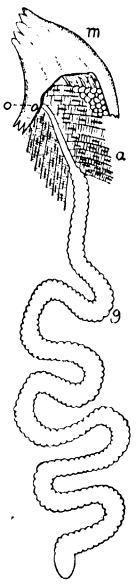


FIG. 142. — Right mandibular gland (*g*) of the larva of *Acherontia atropos*

m, mandible and its adductor muscle *a*; *o*, external aperture of gland. *After* Bordas, *Ann. Sci. nat., Zool.*, 1910.

(1) *Mandibular Glands.*—Small glands open near the base of the mandibles in Apterygota, Isoptera, Dictyoptera, Coleoptera, Trichoptera and Hymenoptera (Bruntz, 1908; Suslov, 1912). In the larvae of the Lepidoptera they attain a considerable size (Fig. 142) and secrete saliva, the normal salivary (labial) glands having become specialized for silk-production in this group.

(2) *Maxillary Glands.*—Glands belonging to the maxillary segment are sometimes present. They are found for example in Collembola, Protura, in the larvae of Neuroptera Planipennia and of certain Trichoptera. Part of the salivary gland complex of *Icerya* is possibly a maxillary gland (Pesson, 1944).

(3) *Labial Glands.*—These organs are commonly known as salivary glands and are paired structures, generally situated in the thorax, on either side of the fore intestine. Their ducts combine to form a median salivary duct which opens on the labium, usually near the base of the hypopharynx. In many insects the ducts of the labial glands possess taenidia in their cuticular lining, and bear a close resemblance to tracheae. Although these glands have been detected in only some Coleoptera (Pradhan, 1939), they are present in the majority of other insects and assume a great variety of form and structure. Among Orthoptera and Dictyoptera they are commonly very large and composed of a number of lobes, each lobe consisting of groups of glandular acini: a salivary reservoir is also present in many species in relation with each gland (Fig. 143). In Hemiptera the salivary glands are differentiated into 1–4 lobes and a reservoir ('accessory gland') is also present (Baptist, 1941). In adult Lepidoptera the labial glands form filamentous tubes. Among the majority of

Diptera they are likewise tubular organs which, in the Muscidae, may considerably exceed the total length of the body. Among Hymenoptera labial glands are extremely well developed and assume great complexity. In the hive bee they consist of two pairs of racemose organs, one pair being cephalic and the other thoracic in position, and their four ducts unite to form a common canal (see p. 687).

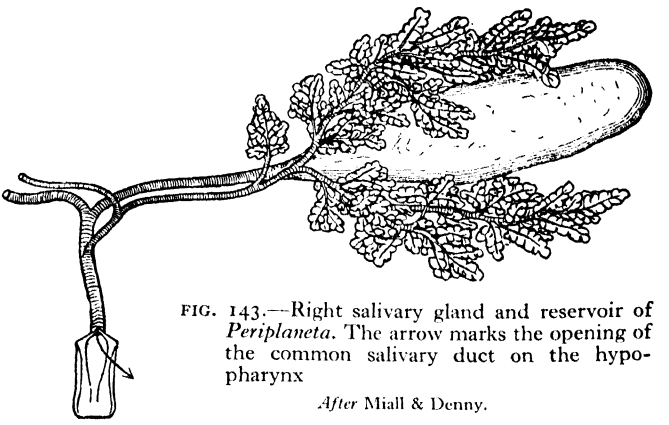


FIG. 143.—Right salivary gland and reservoir of *Periplaneta*. The arrow marks the opening of the common salivary duct on the hypopharynx

After Miall & Denny.

In the Psocoptera there are also two pairs of labial glands which differ in structure and function (Weber, 1938) and very similar glands occur in the few investigated Mallophaga (e.g. Risler, 1951). In *Panorpa*, the labial glands are greatly enlarged in the male and their secretion is eaten by the female in copulation (Grell, 1938).

The labial glands secrete silk in Lepidopteran larvae and mature Symphytan larvae but elsewhere their main function is to produce saliva. This watery secretion, with an approximately neutral pH, acts as a lubricant in feeding and contains enzymes which initiate digestion of the food, either outside the body or in the fore gut. Amylases and invertases are most often present but proteases and lipases also occur, the enzymes corresponding to the major dietary constituents of the insect concerned. In *Periplaneta* the enzyme-secreting cells are histologically distinct from other acinar cells (Day, 1951). In some, but not all, blood-sucking insects the saliva contains substances which are injected into the host while feeding and inhibit the coagulation of its blood (e.g. Yorke & Macfie, 1924). The reaction to the 'bite' of *Pediculus humanus* is also due to a secretion from one of the two pairs of salivary glands, and in the Miridae the saliva has a toxic action on plant tissues (Smith, 1920).

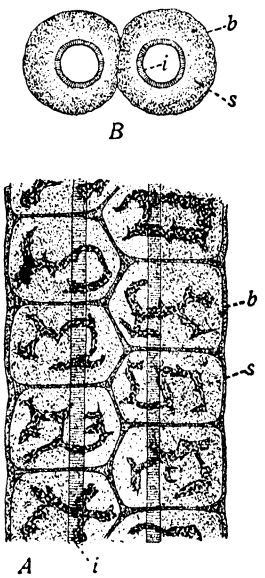


FIG. 144.—Sections of silk gland of the larva of *Bombyx mori*

A, longitudinal; B, radial. *b*, basement membrane; *i*, cuticular intima; *s*, gland cell with branched nucleus. From Folsom *after* Helm.

Silk Glands.—In Lepidopterous and Trichopterous larvae the labial glands are transformed into organs for producing the silk utilized in the formation of the larval shelters and cocoons. The silk glands are cylindrical tubular organs of exceedingly variable length with characteristically branched nuclei (Fig. 144). The formation of silk has attracted the attention of a number of workers whose conclusions are summarized by Lesperon (1937); see also Bradfield (1951). Silk is secreted by the gland in the form of fibroinogen which undergoes denaturation on extrusion to form a tough, elastic protein, fibroin, and is surrounded by an outer layer of a water-soluble, gelatinous protein known as sericin. In the larvae of the Carabid *Lebia scapularis*, and of the Neuroptera Planipennia, silk is produced as a secretion of the Malpighian tubes: among Embioptera and male *Hilara* spp. (Empididae) it is secreted by

dermal glands situated in the anterior tarsi, while the egg-cocoon of *Hydrophilus* is formed from secretions of the female accessory reproductive glands (Laabs, 1939).

Repugnatorial Glands.—Many dermal glands, in different parts of the body of various insects, produce secretions which are probably defensive as they have a nauseous smell or other repellent properties. The dorsal stink-glands of many nymphal Heteroptera, which open between some of the abdominal tergites, are of this type (Henrici, 1938) and so are the metepisternal stink-glands of adult Heteroptera (Henrici, 1940; Betten, 1943). Among Coleoptera, pygidial glands which open near the anus are frequent, particularly in the Adephaga (Fig. 140). They are often of complex structure and their secretion has pungent or corrosive properties (Dierckx, 1899–1901; Palm, 1946). Among Lepidopterous larvae eversible repugnatorial glands are present on the 6th and 7th segments in the Lymantriidae. See also poison glands (below).

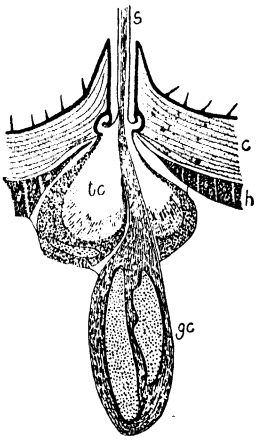


FIG. 145.—Section of the integument and a glandular seta of the larva of *Arctia caia*

c, cuticle; *gc*, gland cell; *h*, hypodermis; *s*, seta; *tc*, trichogenous cell. *After* Holmgren, *Ent. Tidsk.*, 1896.

Attractant Glands.—Many Lepidoptera possess scent glands which are responsible for the attraction of the sexes or stimulation of the female to complete mating; they differ widely in position and structure according to the species and sex (e.g. Illig, 1902; Dickens, 1936; Barth, 1937–52). On the wings of many male Lepidoptera there are peculiarly shaped scales known as *androconia* which are either distributed among the ordinary scales, or located in restricted patches. The characteristic odours of certain male butterflies appear to be produced by gland cells situated at the bases of the androconia, the latter functioning as organs for the outlet and dissemination of the secretion. Groups of odoriferous gland cells are often present in various other situations where they are associated with tufts of setae or scales. Thus, in the males of *Hepialus hectus* (Fig. 146) the hind tibiae are curiously swollen and bear patches of long clavate or cylindrical scales whose bases are connected with large gland cells (Deegener, 1902). In other male Lepidoptera they are present on the legs or at the base of the abdomen (*Acherontia atropos*, *Sphinx ligustri*, etc.) or at the apex of that region (Danainae). Freiling (1909) has described odoriferous scales on the wings of both sexes of *Adopoea lineola* and *Pterophorus pentadactylus*: eversible sacs or tufts of specialized scales or hairs in association with the terminal abdominal segments of several female Lepidoptera produce a secretion which may attract males from a considerable distance (see p. 96; also Götz, 1951).

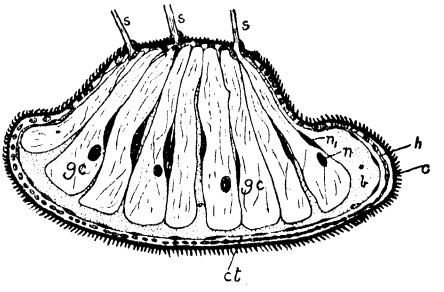


FIG. 146.—Transverse section of the distal part of the hind tibia of *Hepialus hectus* (male)

b, blood space; *c*, cuticle; *ct*, connective-tissue sheath; *gc*, gland cells; *h*, hypodermis; *n*, central, n_1, peripheral nuclei of gland cell; *s*, scent-scale. *After* Deegener, 1902.

The dorsal abdominal glands of some male Blattids (p. 360) and the metanotal gland of *Oecanthus* males secrete a substance licked by the females at copulation. The aromatic secretions of various symphiline Coleoptera, living in the nests of ants or termites, are produced by dermal glands situated at the bases of tufts of hairs located in various regions of the integument (Mou, 1938) while some Lycaenid larvae have eversible spinose tubercles at the end of the abdomen which are similarly licked by the ants with which they are associated (p. 558).

Poison Glands.—These organs are best developed in Apocritan Hymenoptera where they are associated with the ovipositor or sting (p. 685). Several Lepidopteran larvae, including representatives of the Megalopygidae, Eucleidae, Saturniidae, Arctiidae and Lymantriidae, are provided with hypodermal poison glands associated with setae or spines which, when broken, allow the discharge of a secretion causing urticaria in man (Gilmer, 1925; see Fig. 145).

Accessory Reproductive Glands.—See pp. 182 and 187.

Endocrine Glands

The anterior part of the insect body contains a number of endocrine glands, many of which, from their position in the head, are known as the retrocerebral glands. Functionally they form a co-ordinated and balanced system which controls postembryonic development and metamorphosis though other effects have also been described. General accounts of their structure and function are given by Hanström (1940), Cazal (1948) and Pflugfelder (1952) and the following endocrine organs have been recognized.

Neurosecretory Cells of the Brain.—Relatively large cells, often fuchsinophil and showing histological signs of secretory activity, occur in various parts of the brain (especially the pars intercerebralis) of several insects (e.g. Weyer, 1935; Scharrer & Scharrer, 1945; Rehm, 1951). In immature stages of *Rhodnius* (Wigglesworth, 1952), *Platysamia* (Williams, 1946–53), *Tenebrio* (Stellwaag-Kittler, 1954) and some other species it is known experimentally that the brain produces a hormone which leads indirectly to moulting or metamorphosis. In *Carausius*, however, where clearly defined neurosecretory cells are absent, the pars intercerebralis can be removed without affecting development, provided that the nerves to the corpora cardiaca (q.v.) are left intact (Pflugfelder, 1952). In diapausing pupae of *Platysamia*, exposure to low temperatures causes the brain to secrete a hormone which leads to renewed development (Williams, *op. cit.*, see also p. 245) and in adult female *Calliphora* Thomsen (1952) has shown that the median neurosecretory cells of the protocerebrum are necessary for the deposition of yolk in the maturing eggs, apparently by hormonal action on the corpora allata and corpora cardiaca (q.v.). A brain hormone also causes expansion of the dark chromatophore system in *Carausius* (Dupont-Raabe, 1949).

Prothoracic Glands.—These paired thoracic structures, which apparently arise as epithelial invaginations of the labial segment of the head, are present in the immature stages of several orders of insects, including the Dictyoptera (Scharrer, 1948), Hemiptera (Wigglesworth, 1952), Lepidoptera (Lee, 1948; Kaiser, 1949), Coleoptera (Stellwaag-Kittler, 1954) and Mecoptera (Schwink, 1950). They are somewhat variable in form and innervation (Fig. 147), their cells show cyclical secretory activity which is greatest between moults and the gland atrophies in the adult insect. In *Platysamia*

Williams (*op. cit.*) showed that the prothoracic glands are stimulated by a hormone from the brain to secrete their own hormone which induces

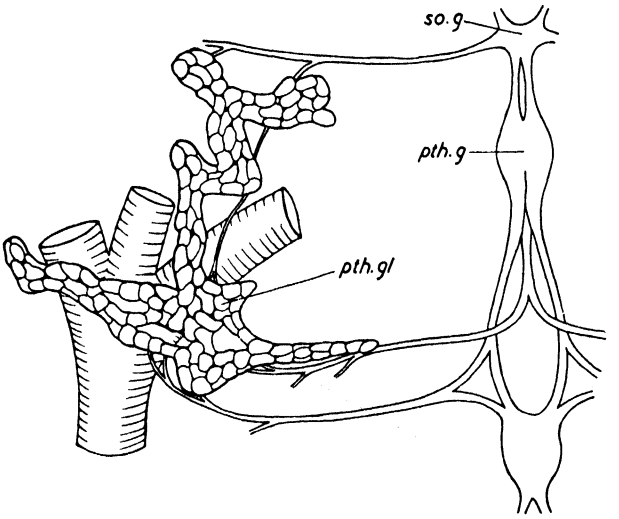


FIG. 147.—Prothoracic gland and its nerve supply in *Saturnia* larva (*after* Lee, 1948)
pth.g, prothoracic ganglion; *pth.gl*, prothoracic gland; *so.g*, suboesophageal ganglion.

moulting of the larva and, in the absence of another hormone from the corpora allata, results in metamorphosis. A similar endocrine mechanism controls postembryonic development in other insects (e.g. Wigglesworth, 1952; Sellier, 1951). It is possible that certain other endocrine glands mentioned below are homologous with the prothoracic glands.

Corpora Cardiaca (Fig. 148).—Situated in close association with the aorta behind the brain, in all Pterygotes, the Thysanura and Japygidae, is a pair of small bodies, the corpora cardiaca (corpora paracardiaca, postcerebral or pharyngeal 'ganglia'). Each is connected to the protocerebrum by a pair of nerves and to the hypocerebral ganglion of the stomatogastric system by a single nerve and the two glands often show some degree of median fusion. Histologically, the corpora cardiaca contain nervous and other more or less chromophil cells which are apparently neurosecretory in nature since they possess inclusions with various characteristic staining reactions. Extirpation of these structures has no effect on the development of Odonate nymphs (Pflugfelder, 1952) but in *Periplaneta* the

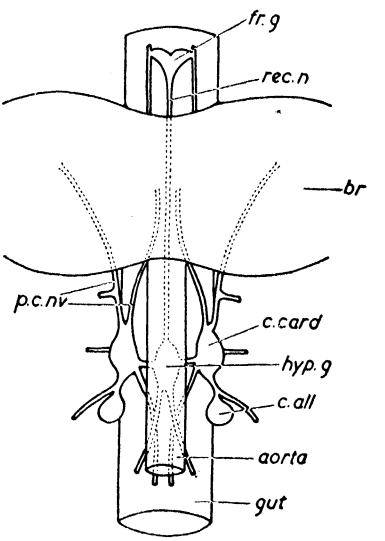


FIG. 148.—Stomatogastric nervous system and associated endocrine glands. Diagram of typical condition (*after* Cazal, 1948)
br, brain; *c.all*, corpus allatum; *c.card*, corpus cardiacum; *fr.g*, frontal ganglion; *hyp.g*, hypocerebral ganglion; *p.c.nv*, external and internal paracardiac nerves; *rec.n*, recurrent nerve

corpora cardiaca appear to control the secretory activity of the prothoracic glands (Bodenstein, 1953). In females of *Calliphora*, the corpora cardiaca are caused by the brain to secrete a hormone which promotes egg-development (Thomsen, 1952) and extracts of the glands of other insects are known to cause the contraction of Crustacean chromatophores and to increase the frequency of contraction in heart and gut muscles of insects (Cameron, 1953).

Corpora Allata.—These are closely associated with the corpora cardiaca and occur in the Japygidae and the Pterygota. Though usually paired, globular bodies, they are fused into a median mass beneath the aorta in some Hemiptera, Dermaptera, etc. They arise from ectoderm in most cases (though derivation from the other germ-layers has been reported) and are generally innervated by fibres from the protocerebrum which first traverse the corpora cardiaca. The corpora allata increase in size throughout development but may decline somewhat in older adults (e.g. Pflugfelder, 1948). Two main histological types are found: the vesicular type is composed of an epithelial wall enclosing a central vacuolar region which sometimes contains further cells while the other type is a solid mass of cells which may be differentiated into cortex and medulla. The cells show histological signs of periodic secretory activity, those of *Pieris*, for example, being very active in young last-instar larvae after which they become quiescent, with renewed activity developing during the pupal stage (Kaiser, 1949). The corpora allata are known experimentally to produce a 'juvenile hormone' which tends to inhibit the realization of imaginal characters during development. In the immature stages this hormone is actively liberated and opposes the action of the hormone produced by the prothoracic gland so that the normal sequence of nymphs or larvae is produced. During the last larval or nymphal instar the corpora allata become inactive and the resulting change in hormonal balance induces metamorphosis (Wigglesworth, Williams, *op. cit.*). In some adult insects the hormone of the corpora allata is necessary for normal maturation of the eggs (e.g. Scharrer, 1946; Joly, 1948; Thomsen, 1952) but in *Carausius* normal eggs can be produced after the extirpation of the glands (Pflugfelder, 1952). The corpora allata also have an effect on the general metabolism of the adult as indicated by changes in the composition of the fat-body (Pfeiffer, 1945) and in *Calliphora* they are necessary for the full development of the accessory reproductive glands of both sexes (Thomsen, 1948).

Pericardial Glands and **Ventral Cephalic Glands.**—Pflugfelder (1939) has described the mesodermal pericardial glands in the posterior part of the head of *Carausius* and *Phyllium* and has also (1947; 1949) found ventral head-glands which arise by ectodermal proliferation in many Orthopteroid insects but are absent from the Hemipteroid orders and the Holometabola. Both types of glands degenerate in the adult and the few available experimental studies suggest that they function in the same way as the prothoracic glands of other insects with which, in fact, they may be homologous (Scharrer, 1948).

Weismann's Ring (Ring Gland).—The

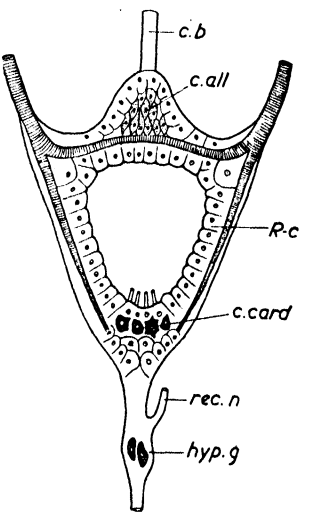


FIG. 149.—Diagram of Weismann's ring from *Calliphora* larva (*after* Thomsen, 1951)

c.b, cephalo-pharyngeal band; *R-c*, R-cells (probably homologous with pericardial glands of other insects). Other lettering as in Fig. 148.

larvae of Cyclorrhaphan Diptera do not display the usual arrangement of retrocerebral endocrine glands. Instead, there is present behind the brain and around the aorta a small ring-like structure supported by tracheae (Fig. 149). In addition to the tracheal matrix cells and the hypocerebral ganglion, Weismann's ring contains three types of glandular cells which are respectively homologous with the corpora allata, corpora cardiaca and pericardial (or prothoracic) glands (Thomsen, 1951, and earlier workers). Conditions in some Brachyceran larvae are intermediate between the above and those in the more normal Nematocera. Physiological studies involving the extirpation and implantation of all or parts of the ring (Possompès, 1949; 1950) show that its various portions control metamorphosis in a manner similar to the corresponding glands of other insects.

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THE REPRODUCTIVE SYSTEM

THE form and structure of the reproductive organs present a very wide range of variation in different insects. In their embryonic condition they are at first essentially similar in the male and female, becoming differentiated later in development. Among the more primitive orders (Fig. 150) much of this similarity is still evident but an increasing divergence in structure becomes noticeable in the higher groups. The gonads are a pair of mesodermal structures which probably evolved from coelomic sacs whose paired coelomoducts go to form all or most of the lateral gonoducts (lateral oviducts or vasa deferentia according to sex) of the adult insect. Primitively, this pair of ducts opened separately and it is not improbable that the paired reproductive openings of the Ephemeroptera represent a retention of the generalized condition. Among the vast majority of insects, however, the mesodermal gonoducts do not open directly to the exterior but join a median passage (the common oviduct and vagina or the ejaculatory duct) which develops from one or more invaginations of the ventral body-wall and is lined by cuticle. The extent of this unpaired portion and its precise mode of development vary in the sexes and in different groups but the result is that the definitive system of adult efferent ducts includes both mesodermal and ectodermal parts. The situation is complicated by the development of accessory glands as outpocketings of either part of the genital tract and the occurrence in the female of one or more spermathecae and a pouch-like bursa copulatrix.

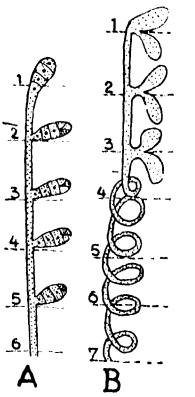


FIG. 150.—Gonads of a young *Lepisma* (mesodermal portions only)

A, female; B, male. The numerals refer to the abdominal segments. Adapted from Grassi, 1887.

In males, the genital opening usually lies behind the 9th abdominal sternum at the end of the penis and in females it is on or behind the 8th or 9th sternum with, in the Ditrysian Lepidoptera and some others, separate openings leading respectively into the vagina and bursa copulatrix. Fuller details of the less common arrangements are given in the sections dealing with the orders concerned (see especially Protura, Collembola, Ephemeroptera, Dermaptera, Raphidioidea and Lepidoptera) and note also the reviews of Heberdey (1931), Snodgrass (1935) and Weber (1939–43, 1952).

The sexual organs, and their counterparts in the male and female, may be tabulated as below.

MALE REPRODUCTIVE ORGANS	FEMALE REPRODUCTIVE ORGANS
1. Paired testes composed of follicles (testicular tubes)	Paired ovaries composed of ovarioles (ovarian tubes)
2. Paired vasa deferentia	Paired oviducts
3. Vesiculae seminales	Egg-calyces

MALE REPRODUCTIVE ORGANS	FEMALE REPRODUCTIVE ORGANS
4. Median ejaculatory duct	Common oviduct and vagina
5. Accessory glands:	Accessory glands:
(*a*) Mesadenia	(*a*) ——
(*b*) Ectadenia	(*b*) Colleterial glands
6. ——	Spermatheca
	Bursa copulatrix
7. Genitalia	Ovipositor

The sexes of insects are almost always separate but mention must be made of the abnormal individuals known as gynandromorphs and intersexes as well as the two established cases of functional hermaphroditism referred to on p. 193. *Gynandromorphs* or sex-mosaics are teratological forms in which some parts of the body show female characteristics while the remaining parts are male. They therefore have a striking appearance when secondary sexual differences in colour-pattern or structure occur, as in the many cases recorded from the Lepidoptera. Frequently one side of the insect is male and the other is female (Fig. 151) but antero-posterior gynandromorphs and forms with an irregular mosaic-like distribution of sexual characters are also known. In *Drosophila* (Morgan & Bridges, 1919), gynandromorphs can arise through loss of a sex-chromosome in one of the early cleavage nuclei of the embryo so that the deficient cells form male tissues while those with the full complement of two sex-chromosomes form female tissues. In many Lepidoptera they are formed from abnormal eggs with two nuclei, one of which has an X-chromosome and the other a Y-chromosome (Cockayne, 1935). *Intersexes* are forms in which, owing to a disturbance of the normal balance between male- and female-determining genes during development, an adult is produced which is more or less intermediate in structure between the two (Goldschmidt, 1938: Nüesch, 1947). They often result from the crossing of closely related species or geographical races or after exposure to extreme temperatures.



FIG. 151.—Gynandromorph of *Bupalus piniarius*: right side male, left side female

After Dziurzynski, *Berlin Ent. Zeits.*, 1912.

1. The Male Reproductive Organs (Figs. 152–154)

The Testes.—The testes in most Apterygota closely resemble the ovaries in form and size but in the majority of insects they are much smaller than the organs of the female of the same species. They are variably situated in relation to the alimentary canal and in some cases they lie above the latter, in others they are placed at the sides of the gut or wholly ventral to it. The testes are maintained in position by the surrounding fat-body and tracheae and, unlike the ovaries, the suspensory filaments are absent or only very slightly developed. As a general rule, each testis is a more or less ovoid body partly or completely divided into a variable number of follicles or lobes which also present almost innumerable variations in form and arrangement among different insects. In *Lepisma* there are three or four bilobed follicles which exhibit a segmental disposition but in most Apterygota each testis is a simple sac or greatly enlarged follicle. Among Neuroptera, Adephagan Coleoptera and Diptera the testes are small and unifollicular: in *Pediculus* and *Pthirus* they are bifollicular, and in the Orthoptera the follicles are exceedingly numerous. They may be short and globular as in *Periplaneta* and *Tetrix*, or elongate and tubular as in *Oedipoda*. In the Mallophaga, Siphunculata and certain Coleoptera, each follicle is connected with the vas deferens by a relatively well developed slender tube or *vas efferens*. In many insects the peritoneal investment of the follicles is developed to the extent of enveloping the testis as a whole in a common coat or *scrotum* which is frequently pig-

mented. Among the majority of Lepidoptera, and in *Gryllotalpa* and certain Hymenoptera, the testes are in close contact along the median line and are enclosed in a single scrotum.

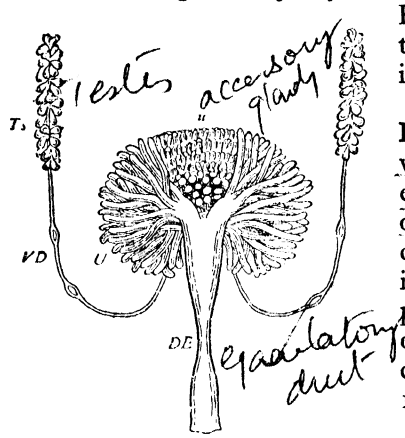


FIG. 152.—Male reproductive organs of *Periplaneta*, ventral view

Ts, testis; *VD*, vas deferens; *u*, *U*, accessory glands; *DE*, ejaculatory duct. *After* Miall and Denny.

The Structure of a Testicular Follicle.—The testicular follicles are lined with a layer of epithelium, whose cells rest externally upon a basement membrane, outside which there is a peritoneal coat of connective tissue. Each follicle is divided into a series of zones characterized by the presence of the sex cells in different stages of development, corresponding to the successive generations of these cells (Depdolla, 1928). These zones are as follows—

(1) The *germarium* is the region containing the primordial germ cells or spermatogonia which undergo multiplication.

(2) The *zone of growth* is where the spermatogonia increase in size, undergo repeated mitosis and develop into spermatocytes.

(3) The *zone of division and reduction* where the spermatocytes undergo meiosis and give rise to spermatids.

(4) The *zone of transformation* where the spermatids become transformed into spermatozoa.

Masses of developing spermatozoa from the spermatocyte stage onwards are enclosed in, and perhaps nourished by, the *testicular cyst-cells* from which they are released in the vas deferens, the abandoned cyst-cells finally degenerating after transfer of the seminal liquid to the female (Anderson, 1950a). In addition, the testis of the Orthoptera, Dictyoptera and some Lepidoptera, Diptera and Homoptera contains large elements known as *Verson's cells* or apical cells whose abundant mitochondria are transferred to the spermatogonial cytoplasm during spermatogenesis (Carson, 1945).

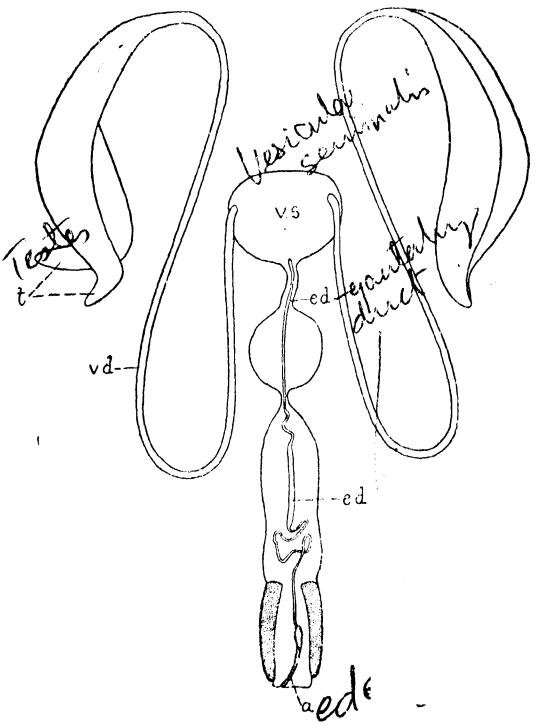


FIG. 153.—Male reproductive organs of *Forficula auricularia*

t, testis; *vd*, vas deferens; *vs*, vesicula seminalis; *ed*, ejaculatory duct; *a*, aedeagus.

The Genital Ducts.—The *vasa deferentia* are the paired canals

leading from the testes and are partly or wholly mesodermal in origin. They vary greatly in length and, in the majority of insects, each vas deferens becomes enlarged along its course to form a sac or *vesicula seminalis* in which the spermatozoa congregate and which is sometimes a large, complex structure: in some of the Diptera the vasa deferentia open into a common vesicula seminalis. Histologically the vas deferens consists of an outer peritoneal coat, a middle coat of muscle fibres, and an inner coat of epithelial cells. Posteriorly, the vasa deferentia unite to form a short common canal which is continuous with a median ectodermal tube or ejaculatory duct. The latter is provided with a powerful muscular coat consisting of an outer layer of circular fibres and an inner layer of longitudinal fibres. Within the muscle layers is a stratum of epithelial cells which secrete a cuticular lining to the lumen of the ejaculatory duct.

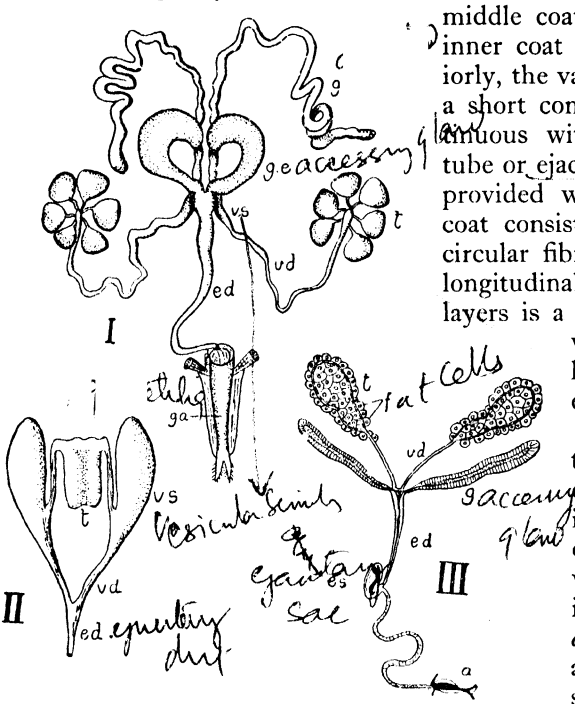


FIG. 154.—Male reproductive organs. I, *Tenebrio obscurus*, *after* Bordas, 1900. II, *Sphecodes fuscipennis*, *after* Bordas, 1895. III, *Calliphora*, *after* Lowne

a, aedeagus; *ed*, ejaculatory duct; *es*, ejaculatory sac; f_1 fat cells; *ga*, external genitalia; *g*, accessory gland; *ge*, do., ectadenes; *gm*, do., mesadenes; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis.

The Aedeagus.—The terminal section of the ejaculatory duct is enclosed in a finger-like evagination of the ventral body-wall which forms the male intromittent organ or *aedeagus* which, with its associated structures, assumes a wide variety of forms and is dealt with on p. 57 and in the sections dealing with the separate orders of insects.

The Accessory Glands.—From one to three pairs of accessory glands are usually present in relation with the genital ducts (Escherich, 1894; Blatter, 1897). They are tubular or sac-like in form, but very little information exists with regard to their functions. In most cases their secretions mix with the spermatozoa (e.g. Anderson, 1950) and in some insects they are directly concerned with the formation of the spermatophores. According to Beauregard the secretion of the 3rd pair of accessory glands in *Lytta vesicatoria* is extremely rich in cantharidin. Escherich divides the accessory glands into two categories: (1) *mesadenia*, or those derived from the mesoderm, and formed as evaginations of the vasa deferentia: and (2) *ectadenia*, or those of ectodermal origin, and formed as evaginations of the ejaculatory duct (Fig. 154). This classification may be adopted as a convenient one, but due reservation needs to be made on account of the paucity of knowledge concerning the development of these organs. Escherich's observations relate to Coleoptera and among these insects ectadenia are generally present. In the Adephaga they constitute the only pair of accessory glands while among the Polyphaga one or more pairs of mesadenia are also present. Among Orthoptera and

Dictyoptera the accessory glands are very greatly developed, forming dense bunches of tubuli which, in *Periplaneta*, form the 'mushroom-shaped gland' of Huxley. The accessory glands are wanting in some insects, including the Apterygota, and *Musca*, *Tabanus*, etc., among Diptera.

2. The Female Reproductive Organs (Figs. 155–157)

The Ovaries.—The ovaries are typically more or less compact bodies lying in the body-cavity of the abdomen on either side of the alimentary canal. Each organ is composed of a variable number of separate egg-tubes or *ovarioles* which open into the oviduct. The primitive number of ovarioles composing an ovary is uncertain and probably does not exceed eight, the latter number being retained in *Periplaneta* for example. In some Thysanura and Diplura (*Japyx*, *Campodea* and *Lepisma*) there are 5–7 ovarioles on each side which open one behind the other in metameric succession into an elongate oviduct. A comparable longitudinal repetition of ovarioles also occurs in the Ephemeroptera, Acrididae and some Dermaptera but elsewhere it has become lost owing to the shortening of the oviducts. Specialization either by the reduction or the multiplication of the ovarioles is extremely frequent. In insects which produce a small number of relatively large eggs such as the viviparous Dipteran *Glossina* and in *Termitoxenia* there is a single ovariole to each ovary. In certain of the Aphididae, in the sexual female there is a single ovary with one ovariole, the other ovary having atrophied. Two ovarioles are present in each ovary of *Melophagus*, *Hippobosca*, and certain Coleoptera and Hymenoptera: among Lepidoptera there are commonly four. Examples of specialization by multiplication are much more frequent. Thus in *Calliphora* and *Hypoderma* there are 100 or more ovarioles to an ovary; in some ants there are over 200; in *Melöe* they are even more numerous while the maximum number is attained in the Isoptera where among species of *Eutermes* it exceeds 2,400. In a few apparently anomalous instances ovarioles are wanting and the ovaries are more or less sac-like without any serial arrangement of the developing eggs. Such ovaries are well exhibited among Collembola. In *Chironomus*, *Anopheles* and some Braconidae (*Aphidius*) although there is an evident differentiation into follicles ovarioles are wanting: this is a secondary and highly modified condition.

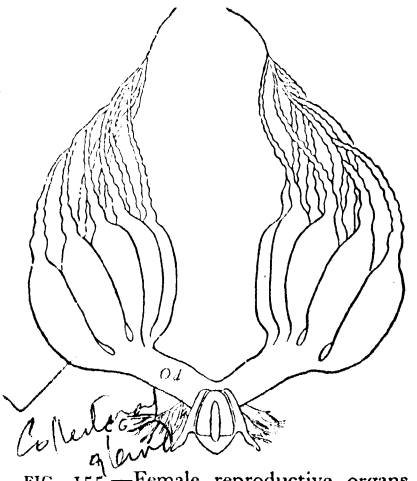


FIG. 155.—Female reproductive organs of *Periplaneta*

Od, oviduct; *CG*, colleterial gland. *After* Miall & Denny.

The Ovarioles.—A typical ovariole is an elongate tube in which the developing eggs are disposed one behind the other in a single chain, the oldest oocytes being situated nearest the union with the oviduct (Gross, 1903). The wall of an ovariole is a delicate transparent membrane: its inner coat is a layer of epithelium whose cells rest upon a basement membrane or tunica propria: outside the latter is a peritoneal coat of connective tissue which, in many insects, contains muscle fibres and is covered by a reticulate layer of tracheal end-cells (e.g. Bier & Meyer, 1952).

Three zones or regions are recognizable in an ovariole (Fig. 158)—(1) The *terminal filament.* This is the slender thread-like apical prolongation of the peritoneal layer. The filaments of the ovarioles of one ovary combine to form a common thread which unites with that from the ovary of the opposite side to form a median ligament. The latter aids in maintaining the ovaries in position and is attached either to the body-wall, the fat-body or to the pericardial diaphragm. In some insects the ovarian ligament is wanting and the filaments end free in the body-

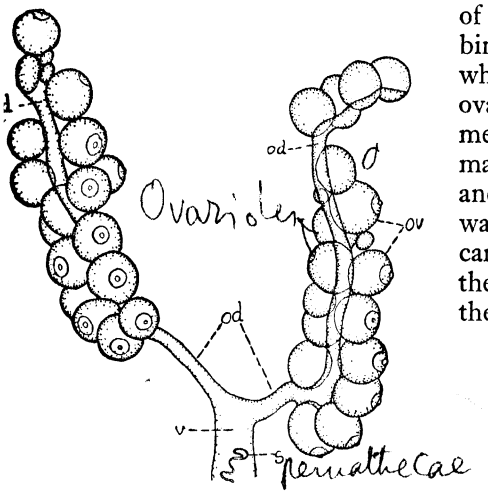


FIG. 156.—Female reproductive organs of *Forficula auricularia*

od, oviduct; *ov*, ovarioles; *v*, vagina; *s*, spermatheca.

cavity. (2) The *germarium.* This forms the apex of an ovariole, below the terminal filament, and consists of a mass of cells from which are differentiated the primordial germ cells and, in many insects, the nutritive cells also. (3) The *vitellarium.* The vitellarium constitutes the major portion of an ovariole and contains the developing eggs and the nutritive cells (nurse-cells) when present. The epithelial layer of the wall of the vitellarium grows inwards in such a manner as to enclose each oocyte in a definite sac or follicle. The cells of the follicle secrete the chorion of the egg and in some cases serve to nourish the oocytes. Three principal types of ovarioles are recognized and are based upon the presence or absence of nutritive cells and on the location of these cells when present (Fig. 158).

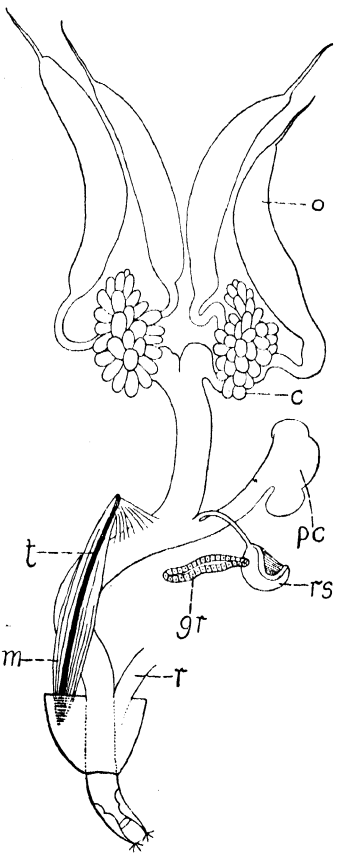


FIG. 157.—Female reproductive system of *Anthonomus pomorum*

c, egg-calyx; *m*, vaginal muscle and spiculum *t*; *o*, ovariole; *pc*, bursa copulatrix; *r*, rectum; *rs*, receptaculum seminis and gland *gr*. *After* Henneguy, *Les Insectes.*

(*a*) The *panoistic type.*—Nutritive cells are wanting. This type of ovariole is primitive and is found in *Japyx*, the Orthoptera, Dictyoptera, Isoptera, Odonata, Siphonaptera and others.

(*b*) The *polytrophic type.*—Nutritive cells are present and alternate with the oocytes. In many cases (Neuroptera, Coleoptera-Adephaga and Hymenoptera) the nutritive cells are grouped together so as to lie in chambers, each chamber being separated from that containing an oocyte by a well-marked constriction; in others (Lepidoptera, Diptera) these constrictions are wanting.

(*c*) The *acrotrophic type*.—Nutritive cells are present and situated at the apices of the ovarioles (Coleoptera-Polyphaga and Hemiptera). In certain Heteroptera the nutritive cells are connected with the oocytes by means of protoplasmic cords.

Types (*b*) and (*c*) are often grouped as one type—*meroistic*, which is characterized by the presence of nutritive cells.

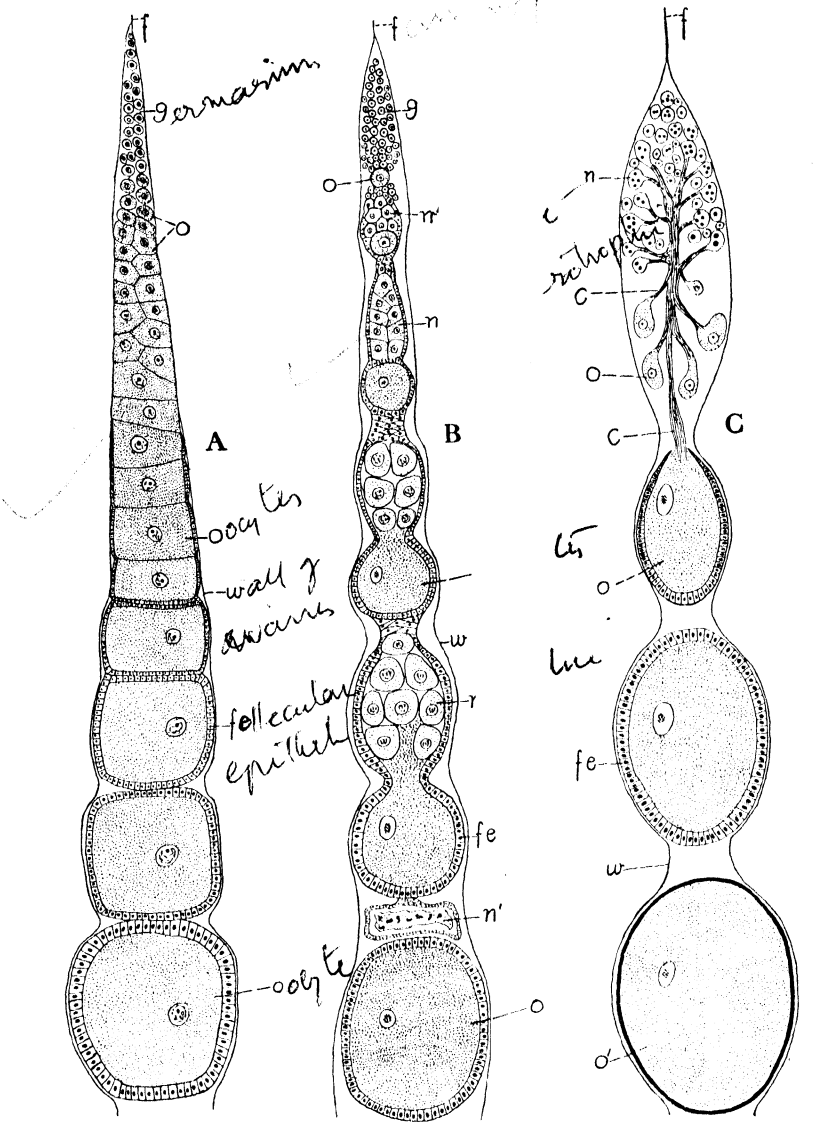


FIG. 158.—Schematic figures of three types of Ovarioles

A, panoistic. B, polytrophic. C, acrotrophic. *f*, terminal filament; *g*, germarium; *o*, oocytes; *o'*, mature oocyte with chorion; *n*, nutritive cells; *n'*, remains of same; *w*, wall of ovariole; *fe*, follicular epithelium; *c*, cord joining nutritive cells with oocyte.

In some insects a large number of eggs mature in the pupa or last nymphal stage and are ready to be laid soon after emergence and mating. In others, the ovary of the young adult female is small and a period of feeding and maturation is necessary to produce fully formed eggs. The mature eggs are discharged from the ovariole—an insufficiently studied process known as

ovulation—and are usually stored temporarily in the efferent ducts before being laid. After ovulation the cells of the empty follicle undergo condensation and disorganization to form the corpus luteum, a body of unknown function which is sometimes yellow or orange in colour and which finally degenerates before the next egg is discharged. In some species, if conditions are unfavourable to oviposition the mature egg is resorbed before ovulation (e.g. Flanders, 1942).

The Genital Ducts.—The lateral oviducts are paired canals leading from the ovaries and are usually formed from mesoderm at the hinder extremities of the embryonic gonads. The two lateral oviducts join the common oviduct, which is initially developed from an invagination of the body wall behind the 7th abdominal sternum but which generally becomes extended through the 8th segment to join the vagina, which arises from an infolding behind segment 8 (Fig. 159). In many adult insects there is no obvious distinction between

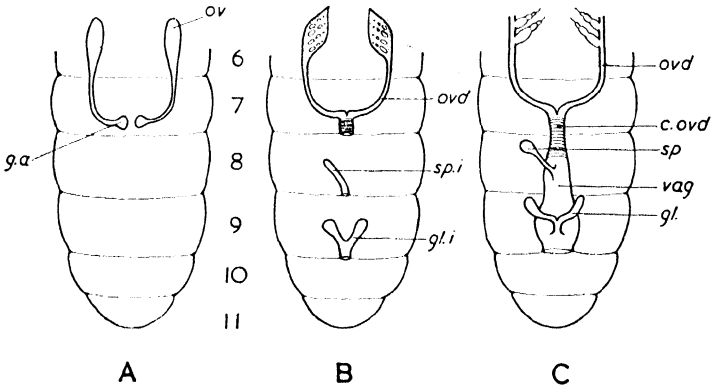


FIG. 159.—A, B. Stages in development of female reproductive ducts. C. Adult condition *c.ovd*, common oviduct; *g.a*, genital ampulla; *gl*, accessory glands; *gl.i*, invagination of developing accessory glands; *ov*, developing ovary; *ovd*, lateral oviduct; *sp*, spermatheca; *sp.i*, invagination of developing spermatheca; *vag*, vagina. 6–11, Abdominal segmentation.

these parts of the median reproductive duct but in certain viviparous insects (*Glossina*, *Melophagus*, etc.) the vagina is greatly enlarged to form a chamber or uterus for the reception of the developing larva or, in the more generalized insects, it forms little more than a shallow genital chamber into which the common oviduct opens. If present, the bursa copulatrix is a pouch-like development of the vaginal region and when, as often happens, the latter becomes extended into the 9th segment to open there by the definitive genital aperture, the bursa loses direct connexion with the exterior. In the Ditrysian Lepidoptera, however, the opening behind the 8th segment is retained as a copulatory aperture leading into the bursa while the opening of the vagina proper behind the 9th segment is the pore through which the eggs are laid. In the Anobiidae a pair of posteriorly placed vaginal pouches contain symbiotic yeasts which are smeared over the surface of the egg and pass to the young larva when it eats the egg-shell after hatching. In other insects the transmission of symbionts to the offspring occurs in different ways, including passage into the ovarial eggs (Buchner, 1953). Structurally the oviducts and vagina are composed of an epithelial layer, the cells of the ectodermal part secreting a cuticular lining which is continuous with the cuticle of the body-wall. The epithelial layer rests upon a basement membrane and outside the latter is a coat of powerful, and mainly circular muscle fibres.

The Spermatheca (*receptaculum seminis*).—This is a pouch or sac for the reception and storage of the spermatozoa and is absent in only a small number of cases. It varies greatly in form and usually opens by a duct (often reduced to a mere neck) into the dorsal wall of the vagina or genital cavity and in the Ditrysian Lepidoptera is connected by a fecundation canal with the bursa copulatrix. In many insects pairing only takes place once and, since the maturation of the eggs may extend over a prolonged period, the provision of a spermatheca allows for their fertilization from time to time. Although commonly ovoid or spherical in form, in some cases (certain Coleoptera) it is tubular, or even branched as in *Paederus*. As a rule the spermatheca is a single organ but in *Blaps*, *Phlebotomus* and *Dacus* there are two spermathecae and in *Culex*, the Tabanidae and most Calyptratae three. Since it is derived from the ectoderm the spermatheca is lined with cuticle which is sometimes darkly or brightly coloured. A stratum of columnar epithelium rests upon a basement membrane which is followed by a muscular coat. In some cases glandular cells are present in the wall of the spermatheca and in others a special *spermathecal gland* opens into the duct of the spermatheca, or near the aperture of the latter into the vagina.

The Accessory Glands.—One or two pairs of accessory (collaterial) glands are present in most insects and usually open into the distal portion of the vagina. They are large and important organs in many Orthoptera and Dictyoptera where they provide the material for the formation of the egg-pod or ootheca: in *Chironomus* they secrete a mucus-like substance which forms the gelatinous investment of the eggs, and in other cases they simply provide a cement-like secretion which serves to fasten the eggs down to the substratum upon which they are laid. The poison glands of Hymenoptera are modified accessory glands, but the nutritive glands associated with the uterus of some viviparous insects are perhaps separately evolved structures.

3. The Sex Cells and Sperm Transfer

The Eggs.—The cytoplasm of the mature eggs usually forms a reticulum in whose meshes occurs a large, centrally placed nucleus and abundant globules or granules of yolk. The latter, which provide nourishment for the developing embryo, consist of carbohydrates (especially glycogen), protein and lipoids (including fats, fatty acids, lecithin and cholesterol). The egg is invested by a delicate homogeneous vitelline membrane and a shell or chorion which is secreted by the follicle cells of the ovary. The chorion may be very thin, membranous and elastic, as in many parasitic Hymenoptera, or even absent (some viviparous insects), but more usually it is composed of two main layers (endo- and exochorion) and is relatively tough and rigid, protecting the contents and giving the egg its characteristic form. In the well investigated egg of *Rhodnius* the exo- and endochorion consist respectively of two and five distinct layers, some formed of relatively soft protein or lipoprotein and others rich in polyphenols and harder tanned protein. Beneath this chorion is the primary wax-layer, about 0·5 μ thick and a fertilization membrane to which material is later added by the serosal cells of the developing embryo (Beament, 1946; 1946a; 1948–49). Other complex types of egg-membranes are described by Slifer (1937–38), Davies (1948), Moscona (1950) and Matthée (1952).

In the greater number of insects the chorion exhibits some form of external sculpture: very commonly it is marked out into hexagonal areas which correspond with the overlying follicular cells. In the Lepidoptera the eggs of many species are conspicuously ribbed and in some Ephemeroptera

they are covered with fine processes resembling pile. The form assumed by the eggs presents innumerable variations (Fig. 160): one of the commonest types is the elongate-ovoid and slightly curved egg prevalent among Orthoptera, and in many Diptera and Aculeate Hymenoptera. Among Lepidoptera the eggs may be almost spherical, cake-like or somewhat cylindrical and flat-

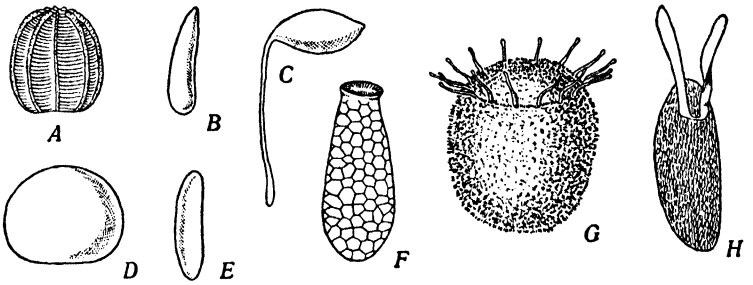


FIG. 160.—Eggs of various insects

A, butterfly, *Polygonia interrogationis*; B, *Musca domestica*; C, chalcid, *Bruchophagus funebris*; D, *Papilio troilus*; E, midge, *Dasyneura trifolii*; F, hemipteron, *Orius insidiosus*; G, hemipteron, *Podisus maculiventris*; H, *Drosophila melanogaster*. Greatly magnified. *After* Folsom, 1923.

tened at one end: in many parasitic Hymenoptera there is a tubular prolongation or pedicel. In some insects an operculum is formed as a special differentiation of the chorion at the anterior extremity. This structure is uplifted at the time of eclosion of the contained insect and is well seen in the Embioptera, *Cimex* and other Heteroptera, and in the Mallophaga and Siphunculata. In the Oestridae, the eggs are provided with flanges which attach them to the hairs of the host upon which they are laid.

The normal type of insect egg, surrounded by a relatively thick chorion, presents a number of physiological problems associated with (1) Respiration, (2) Water relations and (3) Sperm penetration. Respiratory exchange is facilitated by various devices described by Tuft (1950) and Wigglesworth & Beament (1950). These frequently involve the development of a porous, spongy, air-filled protein which may be distributed throughout the chorion (e.g. *Psylla*, *Calliphora*, *Drosophila*) or forms an inner chorionic layer which communicates with the atmosphere by special channels. These are sometimes also filled with a similar porous protein and may be restricted to certain areas of the shell—e.g. over 180 such channels occur in the rim of the egg-cap of *Rhodnius*. The loss of water from the egg in dry surroundings is restricted by the primary wax-layer (Beament, 1946) but many eggs absorb water actively from their environment as a normal part of their development. In Aleyrodid eggs this occurs through the stalk by which they are attached to the host-plant (Weber, 1931) and in Acridids the serosal cuticle of the developing egg is modified over a small area —the hydropyle—through which uptake or loss of water occurs (Slifer, 1938, 1949; Matthée, 1952). The hydropic eggs of some parasitic Hymenoptera (Flanders, 1942) are thinly chorionated, small and deficient in yolk when laid but increase enormously during development by absorption of food and water through their specialized embryonic membranes. Except in those cases where fertilization occurs in the ovary before an impenetrable chorion is laid down, some provision is necessary to enable the spermatozoa to gain admittance. One or more specialized pores or canals known as *micropyles* are present for this purpose, and are usually situated at the anterior or cephalic pole of the egg. Unfortunately, older workers sometimes described as micropyles what are now known to be respiratory channels. In *Rhodnius* the respiratory channels of the cap-rim are accompanied by about 15 rather similar true micropyles while in *Oncopeltus* the 'sperm cups' at the anterior end of the egg function both as micropyles and respiratory channels (Wigglesworth & Beament, 1950).

The Spermatozoa.—As in other animals these consist of a head largely made up of chromatin, a middle piece and a vibratile tail of variable and often complex structure (Depdolla, 1928).

Sperm Transfer.—In the normal methods of copulation the sperms are transferred to the genital tract of the female by the penis. In some cases, free spermatozoa are deposited directly in the spermatheca, the male possessing an elongate thread-like extension of the penis (flagellum) which passes along the spermathecal duct as in some Heteroptera (Bonhag & Wick, 1953). In other cases, free spermatozoa are deposited in the vagina or bursa or the sperms are enclosed in a proteinaceous sac or spermatophore composed of materials secreted by the male, but in some cases only assuming a definite form within the body of the female. Spermatophore formation is characteristic of the Orthoptera and Dictyoptera and is also found in the Lepidoptera and in many Coleoptera and Trichoptera, etc., but apparently never occurs in the Diptera (Khalifa, 1949). In the Lepidoptera, Trichoptera and Coleoptera the spermatophore is deposited in the bursa, in the Acrididae it is placed in the spermathecal duct while in Tettigonioids it remains protruding from the female gonopore after copulation (see, e.g. Khalifa, 1949a). The sperms which escape from the spermatophore or those deposited free in the bursa or vagina eventually reach the spermatheca which they later leave to fertilize the egg.

Several anomalous methods of sperm transfer have been described. In *Sminthurus* (Lie-Pettersen, 1899) the male produces a drop of semen and transfers it to the female gonopore with the mouthparts while in the Odonata (p. 299) the male has a secondary copulatory apparatus at the base of the abdomen. In the Cimicidae and in *Xylocoris* the sperms are deposited in Ribaga's organ (p. 434) and from there pass through the haemocoele to the ovaries (Jordan, 1922; Abraham, 1934; Carayon, 1952). Haemocoelic migration of sperms also occurs in *Hesperoctenes* (Hagan, 1931), *Lyctocoris* and in the Nabidids *Prostemma* and *Alloeorhynchus*; in the last three the migration follows the puncture of the wall of the genital chamber by the male at copulation (Carayon, 1952).

4. Types of Reproduction

Ordinarily reproduction among insects is dependent upon the meeting of the two sexes and the fertilization of the ovum by the spermatozoon. Most insects are oviparous or, in other words, they lay eggs which hatch after deposition. Exceptions to the above generalizations, however, are somewhat numerous and are separately dealt with below.

Viviparity.—Those species in which embryonic development is completed within the body of the female parent and which therefore produce larvae or nymphs instead of laying eggs are said to be viviparous. The phenomenon occurs in scattered representatives of many orders but is particularly characteristic of the parthenogenetic Aphidoidea, the Strepsiptera and the Diptera Pupipara and in a few striking cases it is associated with paedogenesis (q.v.). Viviparity may mean little more than the retention of the eggs in the reproductive tract and the expulsion of the young when they rupture the chorion but in other cases the structure and physiology of the parent and the mode of development of the embryo show elaborate adaptations to the habit and Hagan (1951), who reviews the whole subject, distinguishes four main types of viviparity:

1. *Ovoviviparity:* Here the eggs contain enough yolk to nourish the developing embryos which are deposited by the mother soon after hatching. No special nutritive structures have therefore been evolved though the chorion may be thin and the female may have a reduced number of ovarioles and a saccular vagina while fertilization sometimes occurs in the ovarioles. This type is found in various representatives of the Thysanoptera, Blattidae, Muscidae, Tachinidae, Coleoptera, etc. It may be noted that the term ovoviviparity is sometimes also used to denote a different condition, i.e. the laying of eggs containing embryos in an advanced state of development.

2. *Adenotrophic viviparity:* The thinly chorionated eggs are ovulated singly and the embryos develop at the expense of the yolk which they contain. After hatching, however, the somewhat degenerate larva—whose gut is closed posteriorly—is retained in the large, muscular vagina (uterus) of the mother where it feeds *per os* on the secretion of her hypertrophied uterine glands and moults twice, being deposited as a mature larva which soon pupates. This condition occurs only in the Diptera Pupipara and in *Glossina*.

3. *Haemocoelous viviparity:* This highly specialized type occurs in the Strepsiptera and the paedogenetic larvae of the Cecidomyids *Miastor* and *Oligarces*. In all these there are no oviducts and the ovaries lie free among the fat-body, breaking up readily when mature so that the eggs are dispersed in the haemocoele. The eggs have no chorion but become surrounded from an early stage by a trophic membrane through which nutrient materials are supplied from the maternal tissues. When development is complete the young larvae of the Strepsiptera escape through the brood canal, but those of the Cecidomyids first devour the tissues of the maternal larva before escaping through its integument.

4. *Pseudoplacental viviparity:* Here the embryo develops in an enlarged part of the maternal vagina from a practically yolkless egg which is almost always devoid of a chorion and, when not parthenogenetic, is fertilized in the ovariole. The embryo is nourished through placenta-like structures which are formed from maternal and/or embryonic tissues and which are either in close contact with or actually fused to the maternal tissues. Oral feeding does not occur. This type of viviparity is found in the Aphidoidea, Polyctenidae, *Arixenia*, *Hemimerus*, *Diploptera* (Blattidae) and *Archipsocus* (Psocoptera).

Parthenogenesis.—This phenomenon, in which eggs undergo full development without having been fertilized, is well shown by various insects (Vandel, 1931) though among the better-known orders it has not been observed in the Odonata and Heteroptera. It occurs occasionally in what are otherwise normal, bisexually reproducing species, many examples occurring in the Lepidoptera (Cockayne, 1938). As a regular feature of the life-cycle it is particularly characteristic of certain groups and as it may be associated with various unusual life-cycles, with a sex-determining mechanism and with atypical gametogenesis, various types of parthenogenesis have been recognized (White, 1945; Suomalainen, 1950). Thus, it may be facultative, when it coexists with bisexual reproduction, or obligatory when males are absent or extremely rare and perhaps functionless. Again, the parthenogenetically developing eggs may have either a haploid or a diploid set of chromosomes and may give rise to both sexes (amphitoky) or exclusively to males (arrhenotoky) or females (thelytoky). Furthermore, parthenogenesis may be combined in the life-cycle with paedogenesis and viviparity or may occur in alternation with a bisexual generation. It may be found throughout a relatively large systematic group, in one or a few species of otherwise bisexual groups or may even occur in only part of the geographical range of a single species. In some species a parthenogenetic 'race' or 'races' is known, but some of these cases probably involve sibling species. Some of the better investigated examples of parthenogenesis are cited below; further details are given in the systematic section of this book.

1. *Haploid facultative arrhenotoky:* The significance of this type of parthenogenesis is that it constitutes a sex-determining mechanism which, moreover, can be more flexible than the usual chromosomal type. Females lay fertilized (diploid) eggs which give rise to females and unfertilized (haploid) eggs which develop parthenogenetically into males. It is characteristic of all Hymenoptera in which males are at all frequent, of some Aleyrodids, the Iceryine Coccoidea, some Thysanoptera and the peculiar beetle *Micromalthus debilis* (see below).

2. *Facultative thelytoky:* This is well seen in one race of *Coccus hesperidum*. Oogenesis is accompanied by meiosis and if the eggs are fertilized they produce both males and females. The nuclei of those eggs which are not fertilized return to the

diploid condition by fusion with the second polar body and develop only into females (Thomsen, 1927; 1929). Comparable processes occur in some Tetrigidae (Nabours, 1929, etc.), some Phasmids and some Symphytan Hymenoptera.

3. *Obligate thelytoky:* This is a striking and frequent type of parthenogenesis, males being absent or extremely rare and, at least sometimes, non-functional. The eggs are often formed without meiosis or, when this occurs, there is a later doubling of the chromosome number, e.g. by fusion of cleavage nuclei, and some species with this type of parthenogenesis have achieved polyploidy in the germ-line. The main significance of obligate thelytoky is that it permits more rapid reproduction by allowing all the activity of the female to be concentrated on feeding and the production of young and by eliminating any competition for food which might otherwise have resulted from the presence of males. These apparent advantages are, however, offset by the absence of the genetic variability which results from bisexual reproduction. Among other cases, it occurs in some Curculionidae (Suomalainen, 1940; 1940a), many Psychids (e.g. *Solenobia triquetrella*, Seiler & Schaeffer, 1938; 1940) and such Phasmids as *Carausius*, *Clonopsis* and *Bacillus*. See also below under cyclical parthenogenesis.

4. *Cyclical parthenogenesis* in Aphids and Cynipids: Some Aphids and Cynipids are exclusively parthenogenetic and provide striking examples of obligate thelytoky. In the remainder, however, a bisexual generation is interposed in the colder part of the year between one or more parthenogenetic generations. In such Aphidoidea there are normally several parthenogenetic generations with obligate thelytoky but the sexupara generation immediately preceding the bisexual one either consists of one type of female which gives rise pathenogenetically to both males and females (obligate amphitoky, e.g., *Tetraneura*, Schwartz, 1932) or, as in *Phylloxera* (Morgan, 1912), is made up of two sorts of females which produce respectively males and females by parthenogenesis. In the Cynipid *Neuroterus lenticularis* (Doncaster, 1910–16; Dodds, 1939) there is one parthenogenetic and one sexual generation, the former consisting of two types of females which are respectively male- or female-producers. In some other Cynipids each parthenogenetic female produces both sexes or gives rise to families in which one or other sex predominates (Patterson, 1928). Cyclical parthenogenesis can combine the genetic advantages of bisexual reproduction with the greater reproductive rate of thelytoky.

Paedogenesis.—In a few cases, immature insects possess functional ovaries, the eggs of which develop parthenogenetically so that reproduction is effected by the immature organism, a condition known as paedogenesis. This is most clearly shown in *Micromalthus debilis* (Coleoptera) and in some Cecidomyids, of which the best known are *Miastor* and *Oligarces*. In the N. American form of *Micromalthus* Scott (1936–41) distinguishes adult males and females—which are not known with certainty to be capable of reproduction—and two types of paedogenetic larvae. One of these is the principal reproductive form and produces viviparously 4–20 young larvae, these consuming their parent before escaping to adopt a phytophagous life. They later develop either into adult females or into paedogenetic larvae like their parents or into a second type of paedogenetic larva. The latter lays a single egg from which a male eventually develops, the young male larva normally devouring its parent. If, for some reason, this male larva is not produced or if the parent escapes being eaten she then continues her reproductive life as a paedogenetic larva of the first type. In the S. African form of the species the males and male-producing larvae are absent (Pringle, 1938). In *Oligarces paradoxus* (Ulrich, 1936–43) the normal male and female are also not definitely known to be fertile and there are three types of paedogenetic larvae, all viviparous. The first type produces daughter-larvae which can develop, according to conditions, into any of the following: (*a*) adult females, (*b*) paedogenetic larvae like their parent, (*c*) purely male-producing paedogenetic larvae and (*d*) the third type of paedogenetic larvae whose offspring develop either into adult males or paedogenetic larvae of the first type. The parthenogenetic viviparous

aphids may also be described as paedogenetic in a sense since their earliest offspring begin embryonic development long before the mother is mature, some, in fact, before she has even been born (Uichanco, 1924). Similarly in *Hesperoctenes* (Polyctenidae) fertilization and the early stages of embryonic development take place in the mother before her last moult is carried out (Hagan, 1931). The cases of oviparous pupal paedogenesis reported for species of *Tanytarsus* (Chironomidae) by Grimm (1870) and Johannsen (1937) are probably better regarded as the laying of parthenogenetic eggs by a fully-formed adult which has not yet escaped from the pupal integument (Hinton, 1948).

Polyembryony.—This term denotes the production of two or more (often very many) embryos from a single egg. It has been reported as a rare abnormality in, for example, the Acrididae (Slifer & Shulow, 1948) and is described as a normal occurrence in the Strepsipteran *Halictoxenos* (Noskiewicz & Poluszyński, 1935) but is otherwise known only in certain parasitic Hymenoptera. Here it is found in several Encyrtidae (*Ageniaspis*, *Copidosoma*, *Litomastix*), in *Platygaster* (Platygasteridae), in the Braconids *Amicroplus* and *Macrocentrus* and in *Aphelopus theliae* (Dryinidae) while its occurrence is suspected in some others. Silvestri (1937) and Clausen (1940) review the subject and indicate the many similarities which exist in the development of polyembryonic species (see also Doutt, 1947). One or more of the poorly yolked parasite eggs, which may be fertilized or develop parthenogenetically, are laid in the egg of the host species and the polar bodies which arise in the maturation of the parasite egg are not thrown off. Instead, with some cytoplasm from the egg, their nuclei give rise to a membrane—the trophamnion (Fig. 161)—which invests and helps to transmit food to the developing embryonic part of the egg. This latter divides to form a number of morulae each of which forms an embryo and in some cases the whole structure also becomes surrounded by an adventitious sheath of cells derived from the developing host. When numerous, the embryos, surrounded by the trophamnion, form an elongate, irregularly shaped, sometimes branching mass known as an embryo-chain (Fig. 162). This later breaks up and the separate embryos give rise to first-stage larvae. Abortive embryos and larvae may occur and degenerate or, together with trophamniotic fragments, are eaten by the remaining larvae which otherwise feed on the tissues of the developing host

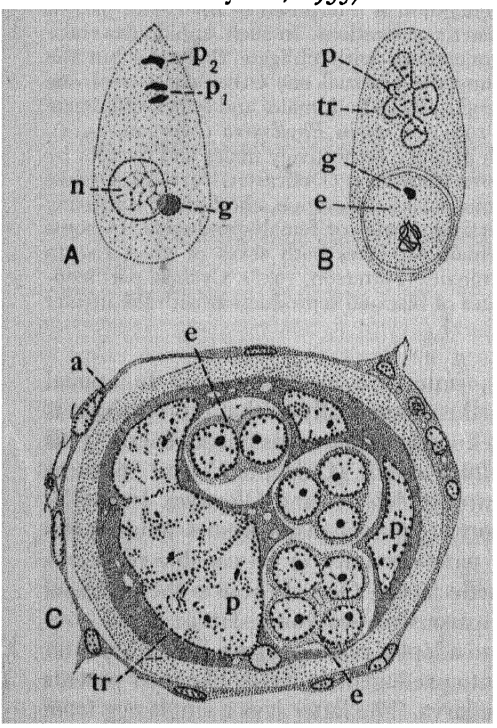


FIG. 161.—*Ageniaspis fuscicollis*, polyembryonic development

A, egg with 1st and 2nd polar bodies p_1, p_2; *n*, oocyte nucleus. B, division of egg into embryonic area *e* and trophamnion *tr* with paranucleus *p*; *g*, germ cell determinant. C, transverse section of polyembryonic mass; *a*, adventitious sheath; *e*, *e*, embryos. From Martin.

and reach maturity in its late larval, pupal or adult stage. In this way a single host may produce a brood of from 2 to about 3,000 parasites. The larger recorded broods are probably all due to the development of more than one parasite egg though each egg of *Copidosoma* and *Litomastix* may give rise to a thousand larvae. The brood from a single host may, as a result of superparasitism, consist of both sexes (as is usually the case in *Platygaster felti*) or

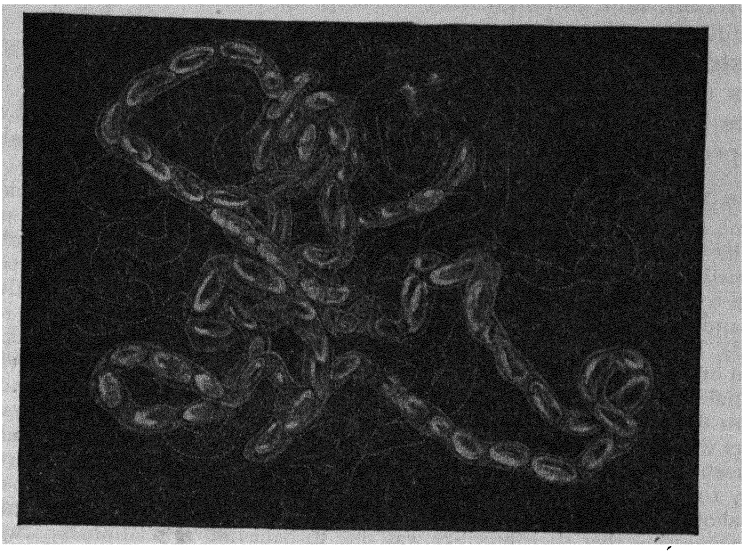


FIG. 162.—Two polyembryonic chains each derived from a single egg of *Ageniaspis fuscicollis* and contained in the same host

One of the chains is viewed by reflected light and the other is represented in outline only. *After* Marchal *Arch. Zool. exp.*, 1904.

be unisexual (e.g. most instances of *Copidosoma gelechiae*). Polyembryony clearly enables the species to achieve a high reproductive potential but its effects are partly offset by the fact that females of polyembryonic species tend to produce fewer eggs than do those of related monembryonic ones and Clausen (1940) says that field records do not indicate polyembryonic species to be particularly effective parasites.

Hermaphroditism.—Functional hermaphroditism is an extremely rare phenomenon in insects and seems to have been evolved only twice. In the scale-insect *Icerya purchasi* Hughes-Schrader (1927, 1930) found that in addition to the infrequent but normal males there are forms which are externally similar to the females of related species but which are actually functional hermaphrodites, true females being absent. The hermaphrodite reproductive system is not unlike the usual female condition but the gonad—which is formed by the anterior fusion of two originally separate organs—produces both spermatozoa and eggs. The outer cells of the gonad form ovarioles while the inner ones give rise to sperms. The eggs sometimes develop parthenogenetically into haploid males but are usually fertilized in the gonad by sperms from the same individual or, rarely, by sperms from the males with which the hermaphrodites mate. The hermaphrodites do not copulate with each other. In the Phorid *Termitostroma* Mergelsberg (1935) found each individual to have a pair of ovaries and a testis, each gonad with its own efferent duct and separate male and female gonopores. Hermaphroditism is probable in other Termitoxeniine Phorids; it is likely that the testis is functional before the

ovaries ripen and that though cross-fertilization is the rule self-fertilization can also occur.

Non-functional, accessory hermaphroditism is also very rare but is found in the stone-fly *Perla marginata.* Schoenemund (1912) has shown that all the males of this species possess a well-developed ovary connecting the anterior extremities of the testes. The eggs in this ovary show the male chromosome number (22), and although they develop up to a late period they neither mature nor function (Junker, 1923).

Castration.—Castration, in the broad sense, implies any process which inhibits completely or to a considerable extent the production of mature gametes by the organism, whose gonads may be greatly atrophied or well developed but not normally functional. Two types may be distinguished:

1. *Physiological castration:* This occurs as a normal phenomenon in social insects with one or more sterile castes. The processes leading to the production of sterile forms have not been fully investigated but probably differ in the different groups concerned. In the Isoptera, where the workers and soldiers are sterile representatives of both sexes, it is possible that a substance (ectohormone) is exuded by the sexual forms and inhibits the development of the gonads in those nymphs which receive it (p. 382). In many Hymenoptera (p. 675) it is not unlikely that differences in the amount or quality of the food received by the developing larvae help to decide whether the females to which they give rise are fertile (queen) or sterile (workers) and in *Apis mellifera* the diet of future workers is known to contain less 'royal jelly' though adult workers will develop ovaries and lay male-producing eggs if deprived of contact with the queen, from whom they normally receive an inhibitory substance (Hess, 1942; Butler, 1954). In *Polistes* (Vespidae) within 24 hours of the death or experimental removal of the queen, the previously sterile females in the nest start to lay unfertilized eggs, suggesting that their sterility was due to behavioural relationships within the normal colony rather than to more deeply seated physiological causes (Deleurance, 1946).

2. *Parasitic castration:* The development of various parasites within an adult insect may induce sterility which is, in some cases, accompanied by changes in the secondary sexual characteristics of the host. The phenomenon is well shown in Aculeate Hymenoptera and Auchenorrhynchan Homoptera parasitized by Strepsiptera where it is known as 'stylopization' (p. 828). The adult stylopized host often differs in many features from normal specimens (Salt, 1927, 1931; Clausen, 1940; Lindberg, 1949): There is a general loss of vitality and the rate of development may be accelerated or retarded; the ovaries are atrophied and though the testes are usually little affected, stylopized males may be sterile; in some host species, various changes also occur in the external genitalia and such secondary sexual characters as coloration and the structure of the antennae and pollen-collecting apparatus of the Hymenoptera. The stylopized host shows intersexual features, females tending towards maleness and vice versa. A somewhat similar phenomenon is shown by female Chironomids infected with Mermithid Nematodes (e.g. Rempel, 1940)—these show, to varying degrees, a number of male features in the external genitalia and reproductive system, even extending in extreme cases to the replacement of the ovaries by testes in which spermatogenesis takes place. Other Nematodes cause castration without affecting secondary sexual characters. For example, the frit fly (*Oscinella frit*) is attacked by females of *Tylenchinema oscinellae* (Goodey, 1930) while *Sphaerularia bombi* causes female sterility in *Bombus* through the production of a toxic substance which probably affects the ovaries through its action on the gonadotropic function of the corpora allata (Palm, 1948). Those insect hosts which live as adults following attack by Hymenopteran or Dipteran parasites are also partially or completely castrated. Clausen (1940) summarizes many examples attacked by representatives of the following parasitic families: Tachinidae, Braconidae (Euphorinae and Aphidiinae), Aphelinidae, Encyrtidae and Dryinidae. Male hosts attacked by the last-mentioned family tend to exhibit female external characters but the equivalent changes do not occur in castrated female hosts.

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Part II

DEVELOPMENT AND METAMORPHOSIS

Oviposition or egg-laying takes place among insects in diverse ways: the eggs are often protected in some manner or other, and are generally deposited in situations expressly adapted for the immediate needs of the subsequent offspring. In some cases the female simply drops the eggs at random while flying low, as happens for example in a few Lepidoptera whose larvae feed on grasses or their roots. In very numerous instances they are laid singly, or in clusters, on the leaves of the future larval food-plants (Heteroptera, Lepidoptera, certain Coleoptera): or they may be superficially inserted into plant tissues (many Tettigoniidae and Homoptera). When inserted more deeply, excrescences (galls) of the plant may arise (Tenthredinidae, Cynipidae). In the Chrysopidae the eggs are laid at the apices of stiff pedicels made of a hardened secretion. In certain other cases they may be glued to some surface or are laid beneath a web or a cottony covering. There are again insects which enclose their eggs in a firm capsule or *ootheca* (Blattidae, Mantidae) or a less compact pod (Acrididae). Many aquatic species surround the eggs with a gelatinous secretion which swells in water forming a jelly-like spawn (Trichoptera, *Chironomus*). A considerable number of insects lay their eggs beneath the soil (Gryllidae, many Coleoptera). Parasitic species usually oviposit on or within the bodies of the hosts which support their future offspring (Tachinidae, parasitic Hymenoptera): when the host is a vertebrate, the eggs are often fastened to the hair or feathers (Mallophaga, Siphunculata, Oestridae).

Embryonic development may take place entirely after oviposition, or partly while the eggs are still within the parental body, or the whole phase may be passed within the latter in viviparous species (p. 189). Almost every transition between these conditions may be found, notably among the higher Diptera. The duration of the egg state (after oviposition) is very variable. In some of the Sarcophaginae it is only momentary, the larva emerging immediately: in *Musca domestica* it lasts about 8–12 hours, according to temperature. At the other extreme are certain Lepidoptera which pass about nine months in the egg, and among the Phasmidae this stage may last nearly two years.

Development may proceed without interruption from egg to adult or the onset of unfavourable climatic conditions—especially temperature—may result in hibernation or aestivation, when little or no development takes place. Growth may also be interrupted in some insects by the animal entering a condition of diapause. During this state—which may arise at any stage of the life-cycle—development is suspended and cannot be resumed, even in the presence of apparently favourable conditions, unless the diapause is first 'broken' by an appropriate environmental change (see p. 245).

In discussing the development of insects the subject falls naturally into two divisions: (*a*) embryology and (*b*) postembryonic development.

EMBRYOLOGY

DETAILED accounts of embryonic development in the Insecta are given by Johannsen & Butt (1941) and Hagan (1951) while the physiology of development is reviewed by Pflugfelder (1952).

In the eggs of most insects there is a distinction between the anterior and posterior poles which bears a definite relation to the position of the future embryo. The eggs are located in the ovarioles in such a position that the cephalic pole of each is directed towards the head of the parent: also, the dorsal and ventral aspects of the egg correspond with those of the parent and of the future embryo (Hallez, 1886). Exceptions to this rule occur in *Pyrrhocoris* (Seidel, 1924), *Pteronarcys* (Miller, 1939) and others.

The contents of the egg are made up of two portions, namely, protoplasm, and deutoplasm or yolk. The protoplasm forms a reticulum which pervades the substance of the egg and also forms a bounding layer, or *periplasm*, which lies just beneath the vitelline membrane, and completely surrounds the egg (Fig. 163). The *deutoplasm* is contained within the meshes of the protoplasm and consists of vitelline spheres and generally globules of fat: small refringent vitelline bodies are present within the vitelline spheres. In addition to these constituents, many eggs contain symbiotic micro-organisms which they receive from the mother and which may come to occupy a special organ, the mycetome, in later development (Buchner, 1953).

In the unfertilized egg the nucleus is situated in the central part of the yolk, enclosed in an island of protoplasm. During maturation the nucleus migrates towards the periphery of the egg where it undergoes division and the polar bodies are formed (Fig. 163). After fertilization the zygote nucleus passes inwards and there commences to divide into daughter nuclei.

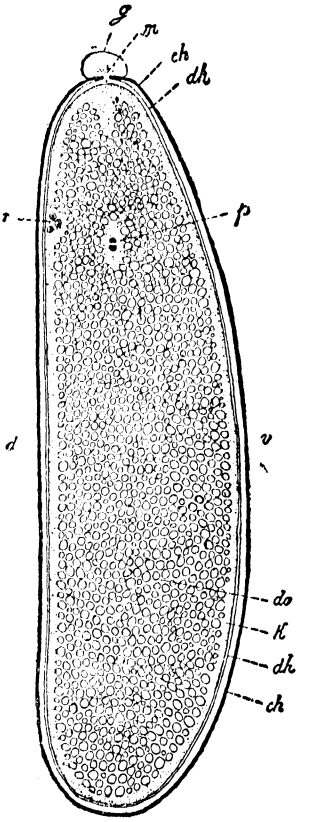


FIG. 163.—Longitudinal section of the egg of *Musca* in stage of fertilization

ch, chorion; *d*, dorsal, *v*, ventral side; *dh*, vitelline membrane; *do*, yolk; *g*, gelatinous cap over micropyle (*m*); *k*, periplasm; *p*, male and female pronuclei; *r*, polar bodies. From Korscheldt & Heider after Henking & Blochmann.

Cleavage and Blastoderm Formation.—The products of the division of the zygote nucleus are the cleavage nuclei, each of which becomes enveloped by a stellate mass of protoplasm. When a considerable number of cleavage cells have been

formed, the majority migrate to the periphery of the egg, where they become merged with the periplasm (Fig. 164). In this manner they form a continuous cellular layer or *blastoderm* surrounding the yolk (Fig. 165). At or about the time of blastoderm formation one or more of the cleavage nuclei of some insects become segregated at the posterior pole of the egg to form the future germ-cells (Fig. 165, *g*) but in other species this segregation is postponed somewhat.

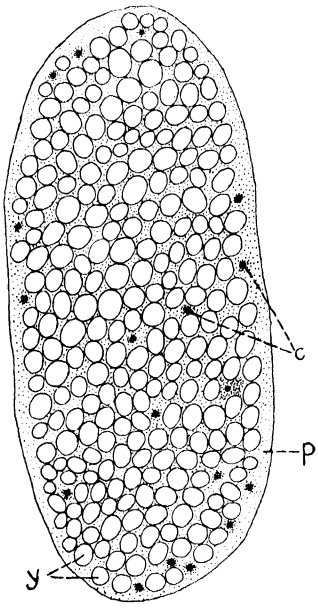


FIG. 164.—Longitudinal section of the egg of *Clytra laeviuscula*, 24 hours old

The cleavage cells (*c*) are seen migrating towards the periphery of the egg. *p*, periplasm; *y*, yolk spheres. *After* Lecaillon.

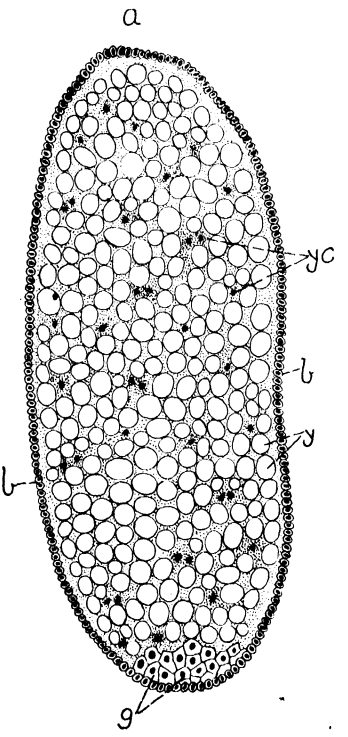


FIG. 165.—Median longitudinal section of the egg of *Clytra laeviuscula* at the time of completion of segmentation

a, anterior pole; *b*, blastoderm; *g*, genital cells; *y*, yolk spheres; *yc*, yolk cells. *After* Lecaillon.

At a slightly later stage the blastoderm consists of a layer of columnar cells (*ventral plate*) on the ventral side of the egg and a flattened epithelial stratum over the remainder (Fig. 165A). Those of the cleavage cells which remain in the yolk form the *primary yolk cells* or vitellophags, which become augmented by *secondary yolk cells* derived by the immigration of cells from the blastoderm. In some cases it appears that the yolk cells are only derived from the latter source. Among several orders of insects, notably Orthoptera, Lepidoptera and Coleoptera, the yolk undergoes secondary cleavage, becoming thereby divided into polyhedral masses each of which contains one or more yolk nuclei (Fig. 169). The function of the yolk cells is to liquefy the yolk and bring about its assimilation.

In a few insects the cleavage is total rather than peripheral as described above. This feature is exhibited among Collembola (e.g. *Anurida*) and certain of the endo-

parasitic Hymenoptera. In the former example the cleavage is slightly unequal and subsequently becomes peripheral: this condition resembles the one found in the Symphyla (Tiegs, 1940) and therefore may well be ancestral to the usual type found among insects. Among the parasitic Hymenoptera the cleavage is total and complete and has probably been secondarily acquired in relation to the almost entire absence of yolk.

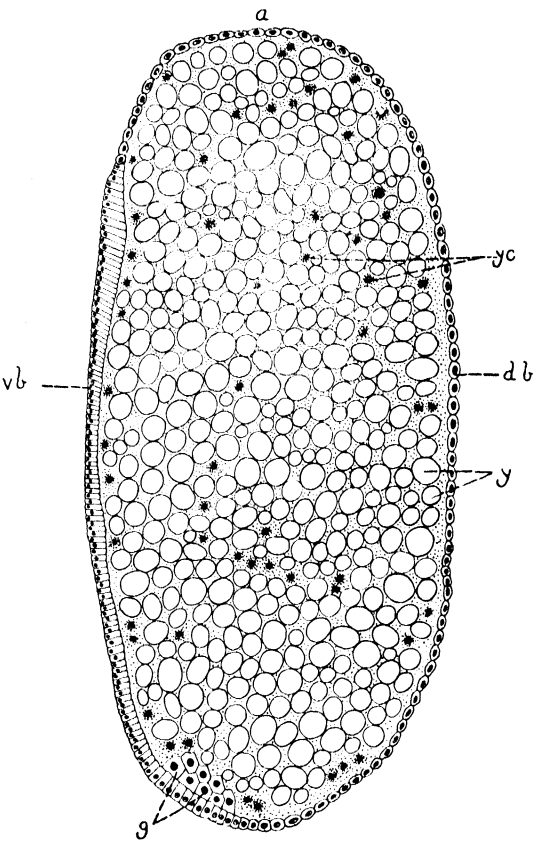


FIG. 165A.—Median longitudinal section of the egg of *Clytra laeviuscula* at the time of differentiation of the ectoderm

db, dorsal blastoderm; *vb*, ventral blastoderm. Other lettering as in Fig. 165. *After* Lecaillon.

Formation of the Germ-Band. — The *germ-band* makes its first appearance as the ventral plate already alluded to, the remainder of the blastoderm forming the extra-embryonic field. The germ-band forms an elongate or oval area which may increase considerably in length during development. Its early or later extent differs among different species but bears little relation to the form of the egg and is only of limited phylogenetic significance, its greatest extent varying inversely with the amount of yolk present. At about this stage in Collembola and *Campodea*, some of the dorsal blastoderm cells form the *primary dorsal organ* (Tiegs, 1942; 1942a). It is perhaps glandular and disappears in the later embryo. A comparable though less well developed structure occurs in a few Pterygotes.

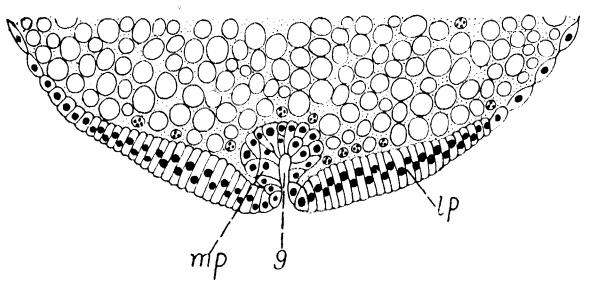


FIG. 166.—Transverse section of the germ-band of *Clytra laeviuscula* at the time of formation of the gastral groove (*g*)

lp, lateral plate; *mp*, median plate. *After* Lecaillon.

The next stage in development is the conversion of the single-layered germ-band into a two-layered structure, a process which can occur in one of three main ways. Commonly a pair of longitudinal folds appears on either side of the median line of the ventral plate and

thus cuts off a *middle plate* and two *lateral plates* (Fig. 166). In most insects (e.g. *Hydrophilus*, *Musca*, *Donacia*, etc.) a groove-like invagination (*gastral groove*) extends the whole length of the middle plate. The lateral folds grow over the middle plate and the groove becomes converted into a tube whose lumen later disappears: or, the overgrowth may take place in such a way that the cavity of the groove is wholly, or partially, obliterated. In other insects (e.g. *Apis*, *Pieris*, *Gastroidea*, etc.) the middle plate remains flat, and is overgrown by the lateral folds, without any invagination being formed (Fig. 167) while in a third type the inner layer results from a simple proliferation along the median line of the ventral plate (Apterygota and Orthoptera) and may, or may not, be accompanied by the formation of a gastral groove.

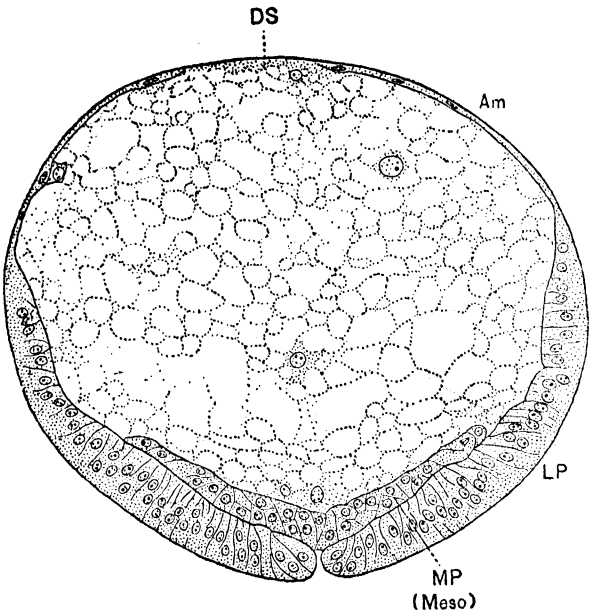


FIG. 167.—Transverse section of egg of the honey bee

MP, middle plate; *LP*, lateral plate; *Am*, amnion; *DS*, dorsal strip of blastoderm. *After* Nelson, 1915.

There is much disagreement over the relationship of the processes just described to those which take place in the embryonic development of other animals and over the application of the germ-layer theory to the embryology of insects; the difficulties are further discussed on p. 213. Provisionally one may interpret the formation of the double-layered germ-band as a modified form of gastrulation, the outer layer forming ectoderm while the inner layer gives rise to mesoderm and endoderm.

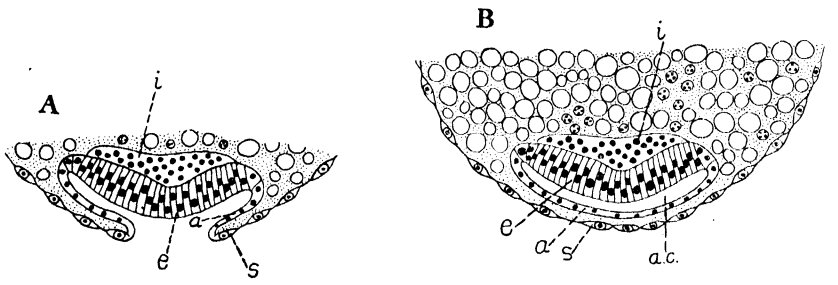


FIG. 168.—A, Transverse section of the germ-band of *Clytra* at the time of formation of the amniotic folds. B, at the time of fusion of the amniotic folds

a, amnion; *ac*, amniotic cavity; *e*, ectoderm; *i*, inner layer (mesoderm); *s*, serosa. Based on Lecaillon.

The Embryonic Envelopes and Blastokinesis.—It is characteristic of insects that the germ-band does not remain freely exposed on the surface of

the yolk but becomes covered by *amniotic folds* arising from its edges. These folds grow towards one another, usually meeting and fusing, with the result that they enclose a space or amniotic cavity containing the germ-band (Fig. 168). It will be observed from reference to Fig. 168 that the germ-band becomes covered by a double cellular envelope composed of the *amnion* and *serosa*. The *amnion* or inner envelope is continuous with the margins of the germ-band, while the *serosa* is an extension of the undifferentiated blastoderm covering the surface of the yolk, and forms the outer envelope to protect the developing embryo.

The formation of the embryonic envelopes and the closely associated movements of the embryo known as *blastokinesis* present many variations which are dependent upon whether the germ-band is invaginated into the yolk, simply immersed in the latter, or lies wholly superficially to the yolk.

Insects with an invaginated germ-band are exemplified by certain of the

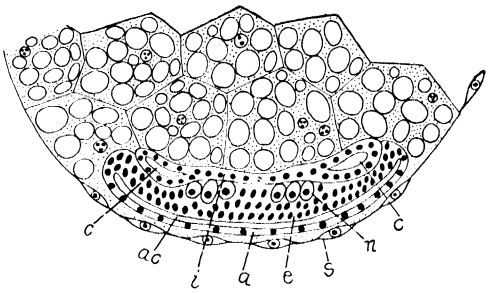


FIG. 169.—Transverse section of the germ-band of *Clytra* at the time of appearance of the neuroblasts (*n*) and coelomic cavities (*c*)

Other lettering as in Fig. 168. *After* Lecaillon.

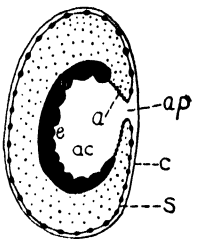


FIG. 170.—Diagram of the embryo and embryonic membranes in *Lepisma* according to Heymons

a, amnion; *ac*, amniotic cavity; *ap*, amniotic pore; *c*, chorion; *e*, embryo; *s*, serosa.

Thysanura, the Odonata, most Hemipteroid orders and some Orthoptera. In *Lepisma* the germ-band becomes segmented at the same time as it is being bodily sunk into the yolk, and the invagination, or amniotic cavity, remains permanently open by means of the amniotic pore (Fig. 170). The yolk is almost entirely covered by the serosa which is characterized by its large and widely spaced-apart nuclei. The inner walls of the cavity consist of ordinary flattened cells with normal nuclei and constitute the amnion. At a later stage the embryo becomes completely everted and superficial in position. In *Machilis* the embryo is very similarly invaginated and there is no closure of an amniotic cavity, the front half of the egg exhibiting the characteristic serosa cells, while the hinder half remains covered by cells with ordinary nuclei which represent the amnion. In the dragonfly *Agrion* the germ-band gradually sinks, at its hinder extremity, into the yolk and the space thus formed is the amniotic cavity (Fig. 171). As the germ-band sinks deeper, a portion of the undifferentiated blastoderm is drawn in with it, and forms the amnion. The part of the blastoderm not drawn into the cavity, but remaining around the yolk, constitutes the serosa. The invagination of the germ-band, or embryo as it now may be termed, proceeds in such a manner that its ventral surface comes to lie towards the dorsal aspect of the egg, and its posterior extremity is directed towards the anterior pole. The cephalic portion of the

embryo remains in its superficial position for a while, but it subsequently becomes enveloped by ventral folds of the amnion. The latter meet, completely enclosing the embryo, and at their point of union the amnion fuses with the serosa. Except just at the latter position, the two embryonic envelopes are separated by yolk. When the process is complete the original position of the whole embryo is reversed, and it will be observed that the dorsal and side

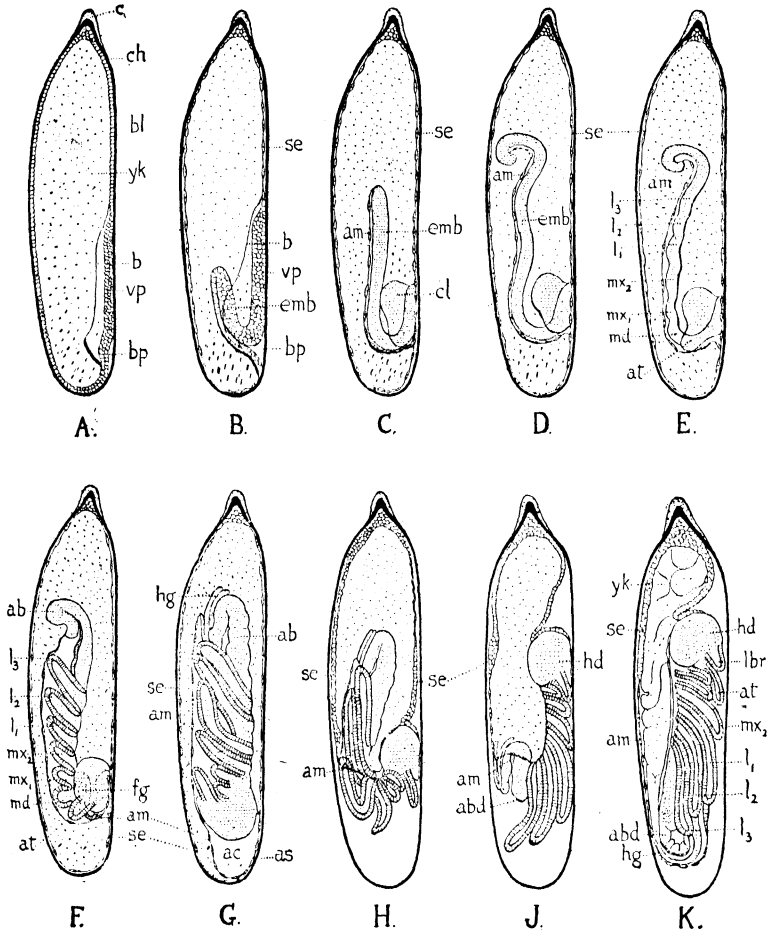


FIG. 171.—Stages in the embryonic development of *Agrion*

Lateral view, ventral surface to the right. A, Formation of ventral plate. B–D, Invagination of embryo in yolk. E–G, Formation of appendages. H–K, Rupture of amnion and reversion of embryo. *ab*, abdomen; *ac*, amniotic cavity; *am*, amnion; *as*, union of amnion and serosa; *at*, antenna; *b*, lateral border of ventral plate; *bl*, blastoderm; *bp*, blastopore; *c*, cap or pedicel; *ch*, chorion; *cl*, cephalic lobe; *emb*, embryo; *fg*, stomodaeum; *hd*, head; *hg*, proctodaeum; l_1–l_3, legs; *lbr*, labrum; *md*, mandible; *mx*, first maxilla; mx_2, labium; *se*, serosa; *vp*, ventral plate; *yk*, yolk. From Tillyard, *Biology of Dragonflies*, *after* Brandt.

walls of the amniotic cavity are formed by the amnion while the ventral wall is formed by the embryo itself. At a later stage the embryo undergoes further changes in position during which great alterations take place in the amnion and serosa. The latter contracts and thickens, drawing all the yolk towards the anterior pole. The consequent increase of pressure, together with the growth of the embryo, causes the amnion to rupture at the point of its fusion with the serosa. As the latter goes on contracting, the head of the embryo protrudes through the split and, turning round, becomes directed towards the anterior

pole of the egg. The rest of the embryo follows in due course, and it eventually comes to lie in its original ventral position. To recapitulate the account of the blastokinetic movements, the germ-band always arises on the ventral surface of the yolk, and it moves through an arc until its position is completely reversed on the dorsal surface. Here it rests for a while, and again passes through the same arc to its original ventral position. Blastokinesis, though sometimes with movements rather different from those described above, is characteristic of the Exopterygota whose eggs are rich in yolk, and the germ-band is often invaginated therein: in eggs poorer in yolk the process is usually less marked or wanting.

In a second type of development the embryo is not invaginated, it retains its ventral position and blastokinesis is usually wanting. The embryonic envelopes are formed as overfolds of the germ-band arising from the edges of the latter at its anterior and posterior extremities: the cephalic and caudal folds are generally connected later by side folds. When the folds come into apposition their intervening walls fuse, and two continuous embryonic membranes are formed which enclose an amniotic cavity on the ventral aspect of the embryo. This type of development is well exhibited, for example, in Nematoceran Diptera and Siphonaptera.

In Lepidoptera the envelopes are usually said to develop in a similar manner, but the germ-band subsequently sinks bodily into the yolk and the latter enters between the amnion and serosa. In this manner the immersed type of germ-band is produced. Christensen (1943; 1943a), however, claims that in Lepidoptera the serosal cells first cover the germ-band and the amnion is formed independently of the serosa by proliferation from the edges of the germ-band.

Among some Coleoptera (*Hydrophilus*, *Gastroidea*, *Chrysomela*) and some other insects the development is intermediate between that of *Agrion*, with a completely invaginated germ-band, and the wholly superficial type. The posterior extremity of the germ-band becomes invaginated after the manner already described for *Agrion*, bending round dorsally and becoming immersed in the yolk. Both anterior and posterior amniotic folds develop and fuse in the usual manner, thus enclosing the embryonic area. Finally the posterior extremity becomes drawn out of the yolk and regains its superficial position. This migration of the germ-band is to be regarded as a vestige of the process of blastokinesis, and the type of development is probably derived from ancestors in which the whole germ-band was invaginated. It is likely that the invaginated germ-band is the primitive one, while the superficial type, which is wholly overgrown by amniotic folds, is a secondary condition. With the acquisition of the latter blastokinesis becomes no longer evident.

In the Tettigoniidae a third envelope or *indusium* appears as a disc-like thickening of the blastoderm, just in front of the future head (Fig. 172). It develops into a membrane which pushes its way between the serosa and the yolk, finally becoming an inner envelope next the yolk and only separated from the embryo by the amnion. When fully formed it comprises an inner and outer indusium and the two membranes cover the whole surface of the egg except at the poles: they subsequently shrink and disappear with the growth of the embryo (Wheeler, 1893). An indusium is also present in the Flatid *Siphanta* (Muir & Kershaw, 1912) and somewhat similar, though less well developed, structures occur in a few other insects.

In addition to the foregoing there are certain anomalous types. An amnion and serosa are not differentiated in the Diplura and Collembola, the extra-embryonic

part of the blastoderm giving rise to the so-called amnioserosa which does not cover the embryo in any way. In *Apis* there is a single membrane which represents the serosa (Nelson, 1915) and in some ants the amnion is absent and the serosa rudimentary. The Strepsiptera have only an amnion and in the Cyclorrhapha both amnion and serosa are vestigial. In many parasitic Hymenoptera the embryo comes to be surrounded by a single membrane, the trophamnion (p. 192). It should also be mentioned that in the Acrididae the serosa secretes an outer non-cellular cuticle (p. 188) and that comparable layers are secreted by both the serosa and the inner indusium of the Tettigoniidae. In some Coleoptera a non-cellular subserosal layer is secreted by the inner surface of the serosa (Butt, 1936).

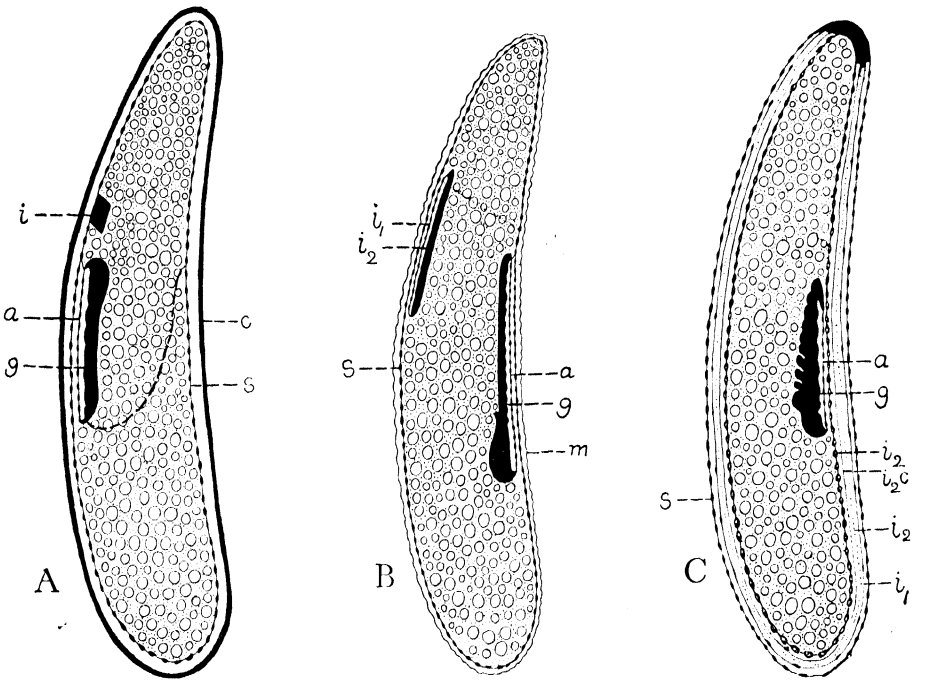


FIG. 172.—Figures illustrating the movements and envelopes of the embryo of *Xiphidium*

A, after closure of amnioserosal folds; the broken line shows the path of migration of the embryo. B, Embryo on dorsal surface. C, Shortening of embryo. *a*, amnion; *c*, chorion; *g*, germ-band; *i*, indusium; i_1, outer indusium; i_2, inner indusium; i_2c, cuticle and i_2s, granular secretion of inner indusium. *After* Wheeler, *J. Morph.*, 3.

Segmentation of the Embryo.—At an early stage in development the germ-band becomes divided by means of transverse furrows into a series of segments and, in this condition, it may be referred to as the embryo (Figs. 173–175). The segmentation may even occur contemporaneously with the formation of the gastral groove, as in *Hydrophilus* and *Chalicodoma*, but as a rule it does not become apparent until after the separation of the inner germ layer. The embryo is at first divisible into a *protocephalic* or *primary head region*, and a *protocormic* or *primary trunk region*. The protocephalic region is conspicuous on account of its large lateral lobes, which give rise to the *pre-antennary segment*. The latter bears evanescent *pre-antennary appendages* in *Carausius* (Wiesmann, 1926), but such organs have not so far been detected in any other insect. Immediately in front of the ocular segment is a median and often bilobed swelling which is the future *labrum*. It is not generally regarded as a true segment but rather as a pre-oral outgrowth—the acron of Heymons. The 2nd primary head segment is the *deutocerebral* or *antennary segment* which bears a pair of outgrowths representing the future antennae.

The 3rd segment is the *tritocerebral* or *intercalary segment*: in some cases it bears a pair of evanescent rudimentary appendages (Fig. 176, A) homologous with the Crustacean 2nd antennae and in *Campodea* vestiges of them are retained in the adult (Uzel, 1898). Immediately behind the labrum is a pit-like invagination of the ectoderm which is the beginning of the future stomodaeum. The first three of the primary trunk segments subsequently combine with the protocephalic region to form the future head. These segments are those which bear the developing rudiments of the mandibles, maxillae and labium. The *mandibular* and *maxillary segments* give rise to the hypopharynx and, in *Anurida* and *Campodea*, a pair of small protuberances situated near the

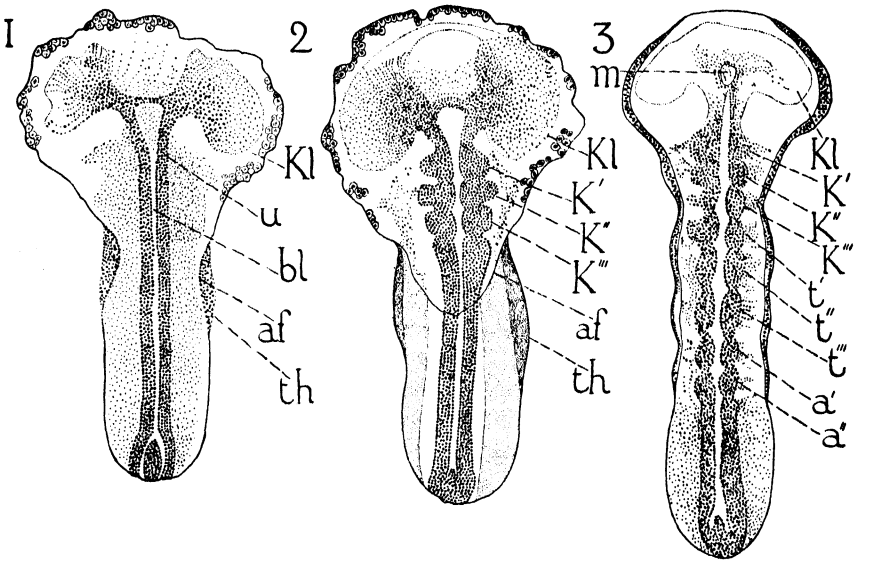


FIG. 173.—Three stages in the segmentation of the germ-band of a leaf-beetle (*Chrysomela*) *a′a″*, abdominal segments; *af*, amniotic fold; *bl*, blastopore; *K′–K‴*, gnathal segments; *Kl*, head-lobe; *t′–t‴*, thoracic segments. *After* Graber.

median line are the rudiments of the future *superlinguae* (Fig. 176, B). The appendages of the labial segment ultimately fuse to form the *labium*. The next three protocormic segments bear the rudiments of the future three pairs of *thoracic legs* and eventually form the thorax, while the remaining segments constitute the abdomen. In most insect embryos the latter region consists of ten segments, together with a non-segmental terminal region or *telson*, the latter bearing a median invagination which is the beginning of the proctodaeum. There is good reason to believe, however, that the primitive number of abdominal segments was 11 which, with the telson, make up a total of 12 divisions; this number has been recognized by Heymons in the embryos of Dermaptera, Orthoptera and Odonata, and by Nelson in that of the hive bee. All the abdominal segments may carry a pair of embryonic appendages and, in some orders, the first pair is frequently much more pronounced than those on the remaining segments and later may take on very different appearances in different groups. They are then known as pleuropodia and appear to be fitted for a variety of functions. In some insects they secrete an enzyme which helps to dissolve part of the egg-shell before hatching (Slifer, 1937; Miller, 1940) while in some viviparous species they form a sheath (*Hesperoctenes*) or a pair

of elongate filaments (*Diploptera*) and perhaps subserve respiration, excretion or the assimilation of food (Hagan, 1951).

According to the degree of development of the segmentation and appendages of the abdomen, it is possible to distinguish in the development of some insects three embryonic stages which succeed each other more or less clearly (Berlese, 1913). In the earliest or protopod phase (Fig. 173) segmentation is absent or indistinct and there are rudimentary appendages only on the head and thorax. The polypod phase (Fig. 175) has a clearly segmented abdomen and each segment of the body bears a pair of appendages, while the oligopod embryo is clearly segmented but lacks abdominal appendages (Fig. 174). There are, however, many deviations from such a pattern of development—e.g. the protopod phase is the only one in some parasitic Hymenoptera but is less well defined in many other insects while the polypod phase is absent from many Endopterygotes and the oligopod stage is apparently missing in others.

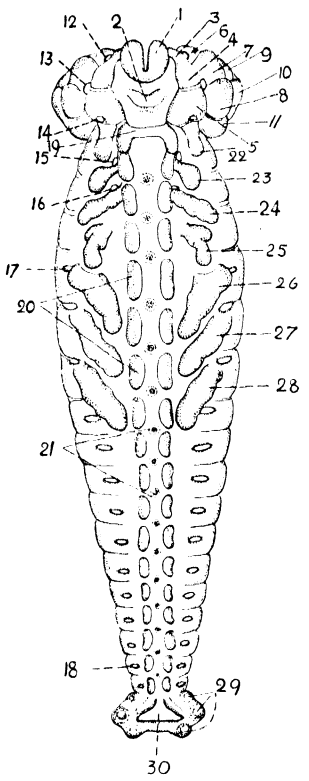


FIG. 174.—Embryo of *Leptinotarsa*

1, labrum; 2, stomodaeum; 3–5, brain segments; 6–8, segments of optic ganglion; 9–11, segments of optic plate; 12–16, tentorial invaginations, etc.; 17, 18, first and last spiracles; 19, tritocerebral commissure; 20, neuromeres; 21, middle-cord thickenings; 22, antenna; 23, mandible; 24, maxilla; 25, labium; 26–28, legs; 29, rudiments of Malpighian tubes; 30, proctodaeum. *After* Wheeler, *J. Morph.*, 3.

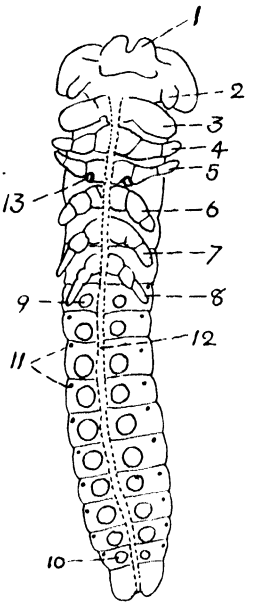


FIG. 175.—Embryo of silkworm

1, labrum; 2–5, head-appendages; 6–8, legs; 9, 10, first and last abdominal appendages; 11, spiracles; 12, neural furrow; 13, opening of silk gland on labium. *After* Toyama, *Bull. agric. Coll, Tokyo*, 5.

In general, some or all of the abdominal appendages degenerate and are lost before the end of embryonic development. The Apterygota retain at least one and usually more than one pair of pregenital abdominal appendages but the Pterygotes lose them unless it is considered that they are represented by the prolegs of Lepidopteran and Symphytan larvae or the gills of the Ephemeroptera, *Sialis*, etc. The appendages of the 8th to 10th segments form the external genitalia or disappear according to sex and species (p. 56) while those of the 11th segment are retained in many orders as the cerci.

Dorsal Closure of the Embryo and Degeneration of the Embryonic Envelopes.—As the embryo develops it grows round the yolk and the dorsal or non-embryonic portion of the former blastoderm becomes more and more restricted. The final closure of the embryo and the fate of the extra-embryonic membranes exhibit important differences among various insects which are classified below into four main types. It should be noted, however, that the

processes are somewhat different in insects with an anomalous arrangement of extra-embryonic membranes and that in all cases it is necessary to distinguish between the final or *definitive dorsal closure* of the embryo, which is accomplished by mid-dorsal junction of the upwardly growing ectoderm of each side and the *provisional dorsal closure* which may precede this and is brought about by the extra-embryonic membranes.

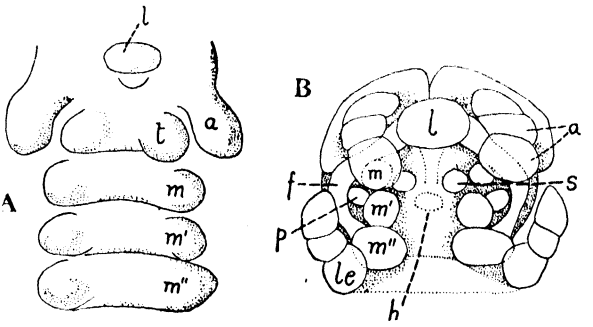


FIG. 176.—Cephalic region of embryo of *Anurida* showing developing appendages

A, at an early stage; B, later. *a*, antenna; *f*, oral fold; *h*, hypopharynx; *l*, labrum; *le*, leg; *m*, mandible; *m'*, maxilla; *m''*, labium; *p*, maxillary palp; *s*, superlingua; *t*, tritocerebral appendage. *After* Folsom, *Bull. Mus. Zool. Harvard*, 36 (redrawn).

1. Involution through the Formation of a Dorsal Amnioserosal Sac.—This process occurs in the more generalized orders of Pterygota but exhibits various modifications. The two envelopes rupture and, with the upward growth of the embryo, their contracted remains become carried on to the dorsal side of the yolk. Here they sink into the latter, forming a tubular sac known as the *secondary dorsal organ* (not to be confused with the primary dorsal organ, p. 203). Ultimately the secondary dorsal organ undergoes dissolution and the embryonic ectoderm completes the dorsal closure. In *Hydrophilus* the two flaps formed by the rupture of the amnion and serosa become carried to the upper side of the yolk, with a small contracted area of the original dorsal serosa between them. The flaps then overgrow the latter until their edges unite. By this means a tubular dorsal organ is formed, which sinks into the yolk and becomes enclosed by the developing mesenteron, while the embryonic ectoderm completes the dorsal closure (Fig. 177, A–E).

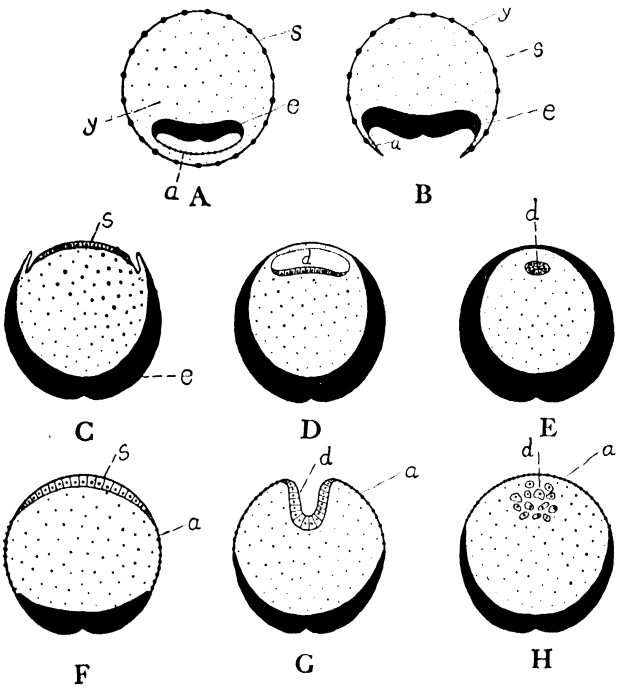


FIG. 177.—Diagrams illustrating the dorsal closure of the embryo and the fate of the embryonic membranes. A, B, General. C–E, *Hydrophilus*. F–H, *Oecanthus*

a, amnion; *d*, dorsal organ; *e*, embryo; *s*, serosa; *y*, yolk. Based on Ayers, Graber & Kowalevsky.

In *Oecanthus* the contracted serosa alone forms the dorsal organ, the amnion persisting, for a while, as a covering of the yolk (Fig. 177, A, B, F–H).

2. **Involution of the Amnion with the Retention of the Serosa.**—In *Leptinotarsa* and other Chrysomelids, the amnion ruptures ventrally and grows round the yolk so as to enclose it dorsally, becoming at the same time separated from the serosa. With the upward growth of the embryo the amnion becomes compressed into a small dorsal tract—the *dorsal organ*. The latter disintegrates in the yolk with the dorsal closure of the embryo. The serosa persists, until a late stage, as a complete membrane applied to the inner aspect of the chorion (Fig. 178, A–C).

3. **Involution of the Serosa with Retention of the Amnion.**—In *Chironomus* the serosa alone ruptures and contracts to form the dorsal organ, which becomes absorbed into the yolk. The amnion afterwards grows over this area, so as to entirely enclose the egg, and persists until the time of hatching (Fig. 178, D–F).

4. **Retention of both the Amnion and Serosa.**—In Lepidoptera and Tenthredinidae the amnion ultimately grows entirely round the yolk and becomes separated

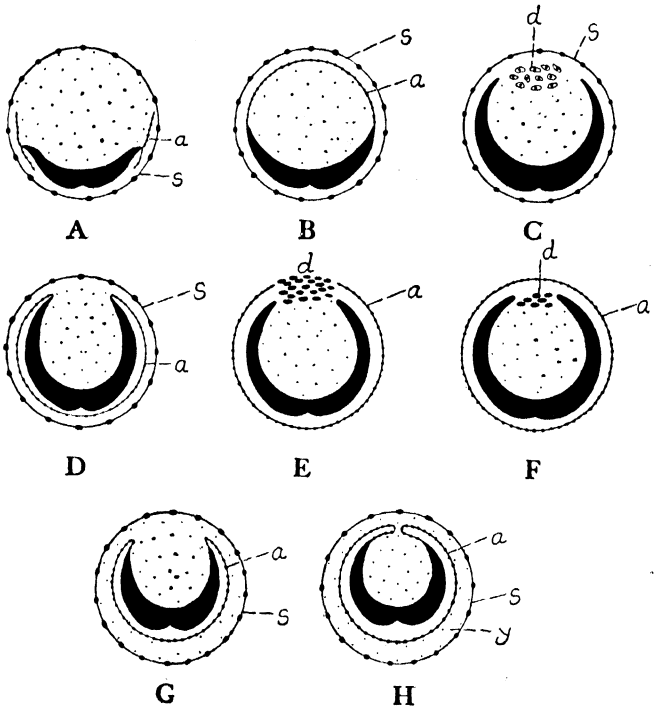


FIG. 178.—Diagrams illustrating the dorsal closure of the embryo and the fate of the embryonic membranes in A–C, *Leptinotarsa*: D–F, *Chironomus*: G, H, Lepidoptera
Based on Wheeler, Graber & Tichomiroff.

from the serosa. The egg is now enclosed by two complete envelopes up to the time of hatching, when they are ruptured. In Lepidoptera a quantity of yolk is retained between these two envelopes, and serves as the first food of the young larva (Fig. 178, G, H).

The Mesoderm.—According to which views one accepts on the origin of the endoderm of insects one may say that either the whole of the inner layer, or that part of it which does not participate in endoderm formation, gives rise to the mesoderm. The latter becomes arranged into two longitudinal bands, connected across the median line by a single layer of cells. These bands come to be constricted transversely, and consequently the mesoderm becomes divided into segments. These mesoblastic somites appear before or, less often, after the corresponding divisions of the ectoderm. In most insects some or all of the mesodermal somites form coelom sacs by acquiring paired

cavities, the coelomic cavities, which form either as clefts in the solid mesoderm or through a folding over of the lateral margins of the somites. In most insects there are coelomic cavities in the antennary and the three gnathal segments of the head, each thoracic segment and all abdominal segments except usually for the last one or two. Cavities occur in the preantennary segment of *Carausius* (Wiesmann, 1926) and in the intercalary segment of *Locusta* (Roonwal, 1936–37) but are otherwise rudimentary or absent in these regions. The labral coelomic cavities of *Carausius*, *Locusta* and others have been thought to demonstrate the existence of a true labral segment in the head but are more often regarded as a secondary phenomenon. Some other specialized conditions may be noted: In the Diptera the mesodermal somites remain solid, in *Apis* the coelomic cavities on each side of the body are confluent from their earliest appearance, thus forming a pair of longitudinal tubes, while in some Hemiptera the sacs remain open towards the yolk.

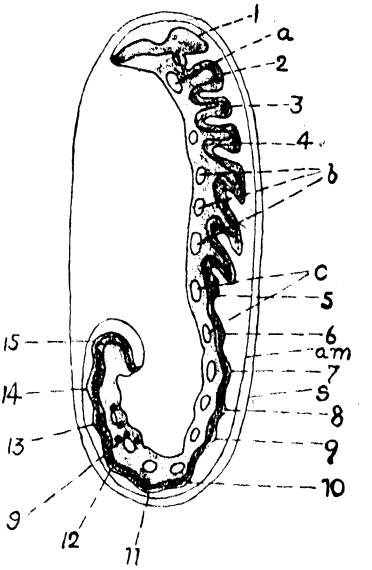


FIG. 179.—Diagrammatic sagittal section (a little to one side of the median line) of the embryo of *Donacia crassipes* showing coelom sacs

1–4, cephalic appendages; 5–15, abdominal segments; *a*, coelomic sac of intercalary segment; *b*, coelom sacs of thoracic segments; *c*, coelom sacs of abdomen; *am*, amnion; *s*, serosa; *g*, genital cells. Adapted from Hirschler, *Z. wiss. Zool.*, 1909.

The outer or somatic layer of the mesoblastic somites gives rise to the body muscles, dorsal diaphragm, and pericardial cells: from the inner or splanchnic layer the visceral muscles, genital ridges, and the greater part of the fat-body are produced. At the upper angles, where the somatic and splanchnic layers meet, are peculiar cells termed *cardioblasts* (Fig. 181) which take part in the formation of the heart. The middle layer of mesoderm, which unites the somites of the two sides of the body, appears in some insects to dissociate and form blood-cells.

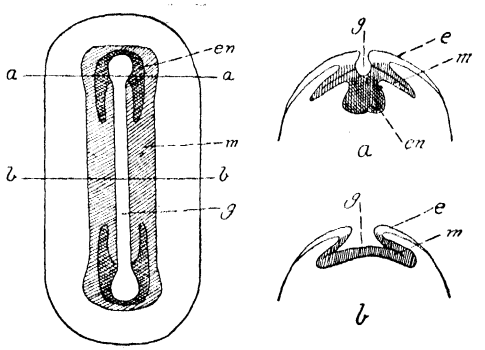


FIG. 180.—Diagram showing endoderm formation in *Leptinotarsa* according to Wheeler

The sections on the right are taken across the germ-band where the lines bear similar lettering. *e*, ectoderm; *en*, endoderm; *g*, gastral groove; *m*, mesoderm.

The Endoderm. — There has been much dispute over the recognition and origin of endoderm in insects, some authors finding grounds here for serious objections to the germ-layer theory. The subject is discussed fully by Eastham (1930) and Johannsen & Butt (1941) and turns around the mode of formation of the mid-gut epithelium, the only tissue for which an endodermal origin can be claimed. The view that the mid-gut epithelium of Apterygotes arises from the yolk cells is insufficiently established and there is now wide agreement that the epithelium has a

bipolar origin in all insects. In Hymenoptera, Diptera and some Coleoptera and Lepidoptera, a mesenteron rudiment arises at each end of the inner layer (Fig. 180). From each rudiment, cells grow towards each other in various ways. Often they first appear as paired ribbons but other methods are known and eventually the outgrowths from each rudiment meet and surround the yolk, being joined in some cases by cells liberated from the median part of the inner layer. In other Coleoptera and Lepidoptera and in the Orthoptera there is a comparable bipolar origin but the proliferating rudiments appear to arise directly from the apices of the stomodaeal and proctodaeal invaginations. Most of the difficulties arise from attempts at interpreting these processes in terms of the germ-layer theory. The mid-gut rudiments arising near the stomodaeal and proctodaeal invaginations have been held, for this reason, to be ectodermal while those formed from the middle and ends of the inner layer have been described simply as endodermal or gastrulation is thought of as proceeding in two or more phases, the primary yolk cells being first segregated as 'primary endoderm' while the inner layer gives rise to the so-called 'secondary endoderm'. It seems most likely that Eastham (1930) is correct in regarding the two methods of bipolar mid-gut formation as fundamentally similar, differing only in whether the stomodaeal and proctodaeal invaginations arise after or before the mesenteron rudiments are recognizable and Nusbaum & Fuliński (1909) have tabulated seven types of mid-gut formation which all conform to this view. Furthermore, one may consider that the mid-gut rudiments arise from cells which are not assignable to a germ-layer, being such as occur at the blastopore lip in other embryos. The two-layered germ-band is then regarded as a modified gastrula, the blastopore of which is hardly recognizable as such though its lip region is represented at first by the fold at the margins of the developing inner layer and later by the two groups of cells, with or without a median strand, from which the endodermal mid-gut rudiments later arise (Kowalewski, 1886). There are some difficulties in this interpretation (Eastham, 1930) but it seems to be the most useful way in which the apparently discordant data can be reconciled while conserving the main features of the germ-layer theory (Henson, 1946).

Alimentary Canal.—The alimentary canal is formed in three main sections of which the central part of the mid gut arises as described in the preceding paragraph. The remainder of the canal develops from a pair of invaginations from the extreme front and rear of the germ-band, known respectively as the stomodaeal and proctodaeal invaginations. The greater parts of these are ectodermal and give rise to the fore and hind gut but their innermost regions are probably to be regarded as endodermal (Henson, 1946) and form short additional sections of the mid gut. The establishment of a through passage, from the mouth to the anus, is brought about by the absorption of the apposed walls between mid gut and invaginations. The Malpighian tubes develop as paired outgrowths of the proctodaeum (probably its endodermal part), at a stage when the invagination is little more than a funnel-like depression (Fig. 174). At first they often open directly on to the external surface of the embryo, but become carried inwards with further growth. Two or three pairs make their appearance and, in cases where a larger number is present, the additional tubes usually arise postembryonically.

The Nervous System.—The beginnings of the central nervous system appear as a pair of longitudinal *neural ridges* of the ectoderm of the germ-band, about the time when the latter becomes segmented. They commence

at the sides of the stomodaeum, and continue backwards until they unite behind the proctodaeum. These ridges are separated by a median furrow—the *neural groove* (Figs. 175, 182). A chain of cells forming the *median cord* is separated from the ectoderm lining the neural groove. The ectoderm cells forming the neural ridges become segregated into two layers,—an outer thin layer of *dermatoblasts* which forms the ventral body-wall and an inner layer of *neuroblasts* which forms the nervous tissue (Fig. 169). When the embryonic appendages commence to appear the neural ridges become segmented into definite swellings at the bases of the former, and each pair of these swellings constitutes a *neuromere*. The intrasegmental portions of the median cord and neural ridges give rise to the definitive ganglia, while the intersegmental portions of the ridges form the connectives.

In the cephalic region the neural ridges expand into broad *procephalic lobes*, forming the future supra-oesophageal ganglion, and they become divided into three neuromeres corresponding with the three primary cephalic segments. These neuromeres are known respectively as the *proto-*, *deuto-* and *tritocerebrum* (vide also p. 73): since the first two lie in front of the stomodaeum, they are pre-oral in position, while the tritocerebrum is postoral since the commissure uniting its two halves (ganglia) passes below the stomodaeum. The optic lobes are formed by delamination (Orthoptera, Dermaptera) or invagination (Coleoptera, Hymenoptera) from the cephalic ectoderm and neuroblasts do not appear to participate in their formation.

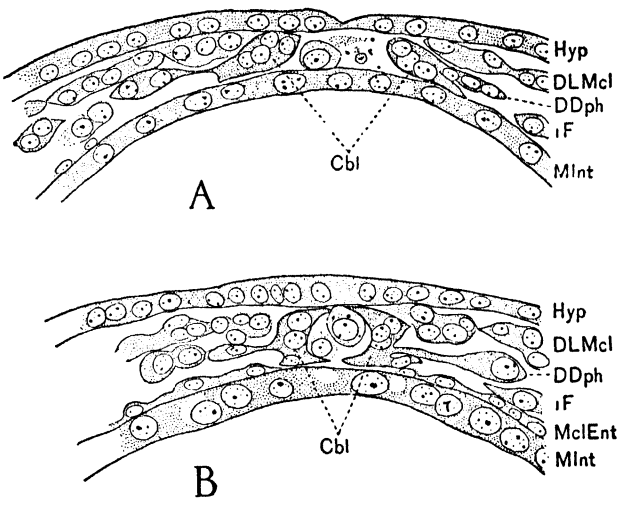


FIG. 181.—Transverse sections of dorsal region of 4th trunk segment of late embryo of hive bee × 600

Cb, cardioblasts; *DDph*, dorsal diaphragm; *DLMcl*, dorsal longitudinal muscles; *Hyp*, hypodermis; *IF*, fat-body; *MInt*, mid intestine and its muscles *MclEnt*. *After* Nelson, 1915.

The neuromeres of the first three protocormic segments fuse to form the suboesophageal ganglion, while the remaining neuromeres constitute the ganglia of the ventral nerve-cord. These latter are nine to eleven in number and subsequently undergo varying degrees of fusion in different insects.

The frontal ganglion and the remainder of the stomatogastric system develop as invaginations of the dorsal ectoderm of the stomodaeum.

The Tracheal System.—Shortly after the appearance of the neuromeres the tracheae appear as ectodermal invaginations lying just outside the bases of the appendages (Figs. 174, 184). As a rule, ten pairs are developed, and they occur on the last two thoracic and first eight abdominal segments. In a few species embryonic tracheal invaginations develop on the prothorax or 9th and 10th abdominal segments but close before hatching. In *Apis* there is a pair of invaginations on the labial segment of the head which forms the anterior prolongations of the main tracheal trunks and subsequently closes.

Each invagination gives rise to a T-shaped horizontal outgrowth, which extends longitudinally until it meets and fuses with those of the segment in front and behind, thus forming the main longitudinal trunks. The mouths of the original invaginations contract and form the spiracles. After the main tracheal trunks are laid down branches therefrom extend inwards and, at the ends of the finer vessels, certain cells separate from the tracheal epithelium and grow out in a stellate form towards the tissues. It is in these cells that the tracheoles develop as fine intracellular tubes: where the tracheoles invade the cells of different organs they are apparently formed by branches of the tracheal cells directly penetrating the cytoplasm.

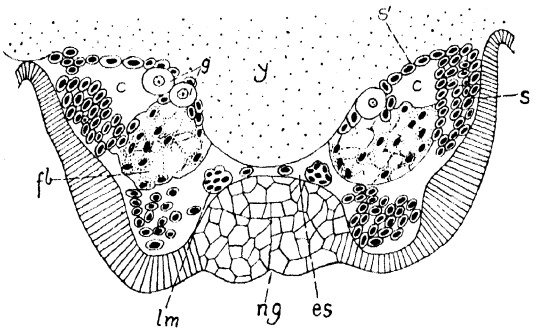


FIG. 182.—Transverse section of the abdomen of the embryo of *Blattella germanica*
For lettering, vide Fig. 184.

The Salivary Glands.—These appear as a pair of ectodermal ingrowths of the labial segment (Fig. 175). As they increase in depth their apertures approximate, and become drawn into the mouth where they finally open by a median pore.

The Body-Wall.—The body-wall is directly derived from the superficial ectoderm, and the essential parts of the organs of special sense are formed from the same layer.

The Body-Cavity and Dorsal Vessel.—The permanent body-cavity commences as a space—the *epineural sinus*—which is mainly produced by the separation of the yolk from the embryo, over the region of the ventral nerve-cord (Fig. 182). The process of separation extends laterally, and in some insects the walls of the coelom sacs are stated to break through in such a manner that their cavities become confluent, both with one another and with the epineural sinus; in other cases, however, the coelomic cavities are known not to unite with the epineural sinus. The developing haemocoele extends upwards along with the mesoderm, on either side, until the formation of the body-cavity is completed. The upward migration of the mesoderm carries the cardioblasts with it: the latter subsequently meet along the dorsal line of the

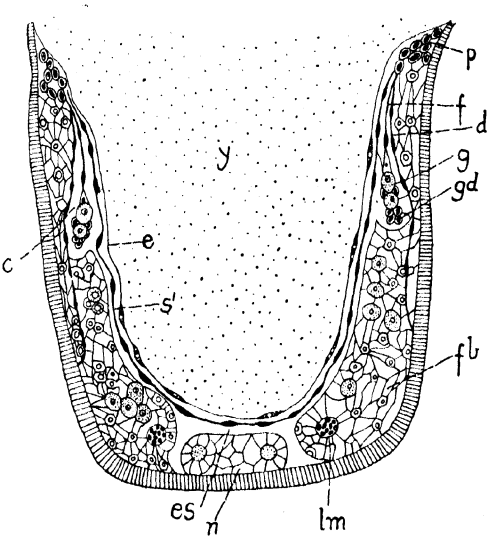


FIG. 183.—Transverse section of the abdomen of the embryo of *Blattella germanica* where the germband is beginning to grow around the yolk
For lettering, vide Fig. 184.

embryo, and arrange themselves in the form of a tube, which is the rudiment of the heart. A single layer of cells unites the cardioblasts to the somatic mesoderm on either side, and eventually gives rise to the dorsal diaphragm (Figs. 181, 183). The aorta is formed by the union in the mid-dorsal line of the two coelom sacs of the intercalary segment (*Donacia*), or of the antennary segment (*Forficula*, *Apis*, etc.): by its backward extension the developing aorta comes to unite with the heart.

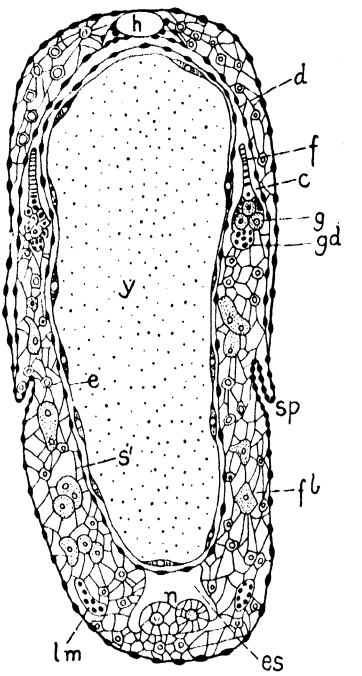


FIG. 184.—Transverse section of the abdomen of the embryo of *Blattella germanica*, after the yolk has become enclosed by the germ-band

c, coelom; *d*, dorsal diaphragm; *e*, endoderm; *es*, epineural sinus; *f*, filament plate; *fb*, fat-body; *g*, genital cells; *gd*, rudiment of genital duct; *h*, heart; *lm*, ventral longitudinal muscles; *n*, rudiment of nerve-cord; *ng*, neural groove; *p*, cardioblasts; *s*, somatic mesoderm; s^1, splanchnic do.; *sp*, spiracle. This and Figs. 182, 183 *after* Heymons (with different lettering).

The Reproductive System. — The primitive germ cells in some insects, including *Donacia*, *Chironomus* and *Miastor*, are derived from special 'pole cells' situated at the posterior end of the egg. In some cases these have been traced from a single original cell, distinguishable at an early stage of cleavage (vide Hegner, 1914). Among other insects the primitive germ cells are believed to be derived from the mesoderm, but it is probable that they are likewise segregated at a very early stage, only are not capable of being definitely identified until later. In any event they migrate to the splanchnic mesoblast, coming to lie in the walls of the coelom sacs—in the case of *Blattella* in those of the 2nd to 7th abdominal segments. The germ cells become surrounded by mesoderm, which forms the *genital ridges*, and the latter fuse into a cell-strand lying on each side of the dorsal wall of the coelom. The primitive germ cells give rise to the sex cells, while the enveloping mesoderm produces all other parts of the gonads and their primitive ducts. At an early stage

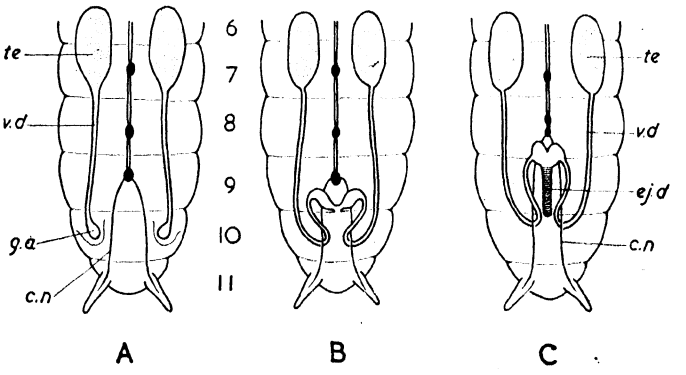


FIG. 185.—A, B. Stages in development of male reproductive ducts. C. Adult condition (*after* Snodgrass, 1941)

c.n, cercal nerve; *ej.d*, ejaculatory duct; *g.a*, genital ampulla; *te*, developing testis; *v.d*, vas deferens. 6–11, Abdominal segmentation.

a sheet of cells, the *filament plate*, is differentiated in female embryos, and connects the apex of the genital rudiment with the heart rudiment of the same side of the body. With the migration of the heart rudiments towards the mid-dorsal line, the genital rudiments follow. Their primitive metamerism becomes lost, and it is only in later embryonic stages that sexual differences can be recognized. In the female the filament plate divides into several strands or terminal threads, and these are connected with the divisions of the ovary which represent the ovarioles. The undivided basal portion of the genital rudiment gives rise to the efferent duct of its side. The paired mesodermal efferent ducts run posteriorly and each ends in a closed, dilated ampulla (Fig. 185). The genital ampullae of the male are found in the 10th abdominal segment, those of the female in the 7th segment; in both cases they represent the coelomic sacs of the relevant segment. The development of the median, terminal, ectodermal part of the reproductive system is largely a postembryonic process and is discussed on p. 186.

Sequence of the Developmental Stages.—Data concerning the rate of development, and the time taken to arrive at the principal stages, are given in great detail by several authors and those for *Hydrophilus* are quoted here. Heider (1889) divides the developmental period into three phases, occupying altogether 11 days, and the most important facts may be summarized as follows.

1ST PHASE

1st Day. Blastoderm completely formed.
2nd Day. Metamerization of the germ band; formation of amniotic folds, procephalic lobes, and middle plate.
3rd Day. Appearance of neural groove and antennae; closure of amniotic folds.

2ND PHASE

4th Day. Appearance of buccal and trunk appendages together with the stomodaeum, which is followed by the proctodaeum; appearance of tracheal invaginations.
5th Day. Elongation of appendages; mouths of tracheal invaginations reduced to rounded orifices representing the spiracles.
7th Day. Elongation of neural groove; embryonic membranes rupture, exposing the embryo.

During this phase the separation of the endoderm from the mesoderm takes place and the rudiments of the mid intestine are formed: the mesoblastic somites and body-cavity appear, and yolk cleavage occurs.

3RD PHASE

End of 7th Day. Appearance of dorsal organ.
8th Day. Dorsal organ completely formed.
9th Day. Pigmentation of the eyes.
10th Day. Eyes more pigmented; main tracheal trunks visible.
11th Day. Embryo becomes strongly pigmented and exhibits movements beneath the chorion.
12th Day. Eclosion of the larva.

This phase is one of histological differentiation and no new permanent organs are developed.

Physiology of Embryonic Development

The physiological processes which determine or co-ordinate some phases of embryonic development have been elucidated in experimental studies reviewed by Richards & Miller (1937), Krause (1939) and Pflugfelder (1952). Three centres have

been shown to control early development in a number of cases. Cleavage and nuclear migration begin at the *cleavage centre* which is situated in that part of the egg where the future head-rudiment normally develops. The mechanisms which ensure approximately synchronous division of cleavage nuclei and their peripheral migration are not known but the arrival of cleavage nuclei at the posterior pole of the egg causes the release from an *activation centre* there of a substance which diffuses forwards and determines the formation of a germ-band. Experimental elimination of this part of the egg by excision, ligaturing or ultra-violet radiation prevents the development of a germ-band though an extra-embryonic blastoderm can develop and yolk cleavage occurs. Once the centre has had time to exert its effect the posterior pole of the egg can be constricted off with a ligature without effect on the formation of the germ-band. Finally, there is a *differentiation centre* in the cortex of the egg near the future thoracic region of the embryo. This is stimulated by the products of the activation centre and is the region from which visible differentiation of the blastoderm proceeds. The differentiation centre apparently behaves as a localized zone where the yolk undergoes retraction from the chorion, the blastoderm nuclei assembling in the resulting space and forming the germ-band.

The earliest cleavage nuclei are isopotent, that is, any one of them can, under experimental conditions, give rise to tissues other than that into which it would normally have developed. The elimination of early cleavage nuclei by ultra-violet radiation therefore does not prevent the remaining nuclei from reorganizing to form a normal embryo. The early egg is thus capable of considerable regulation. After the differentiation centre has completed its function, however, the fate of the various parts is determined and the removal of part of the developing egg then causes corresponding deficiencies in the postembryonic insect. After determination the egg can be described as 'mosaic' and maps of the prospective organ-forming areas of a few species have been constructed. The stage at which determination is complete varies with the species and some regions are determined before others. The eggs of such Exopterygotes as *Platycnemis* (Seidel, 1926–35) and *Tachycines* (Krause, 1934–39) are capable of regulation up to the beginning of germ-band formation whereas those of *Drosophila* and other Diptera, for example, have been determined by the time they are laid (Geigy, 1931). Other Endopterygote eggs become determined at times between these extremes—e.g. *Apis* (Schnetter, 1934; 1934a), *Tenebrio* (Ewest, 1937), etc. In *Drosophila* (Geigy, 1931) and *Tineola* (Lüscher, 1944) the egg is first determined in respect of larval characters and then, shortly afterwards, in respect of imaginal features.

The causal analysis of later embryonic development and the phenomena of embryonic induction have been less fully studied in insects but Bock (1939; 1941; also Seidel, Bock & Krause, 1940) has shown in *Chrysopa* that the ectoderm forms a self-differentiating system and determines the differentiation of the underlying mesoderm.

Literature on Embryonic Development

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Bock, E. (1939). Bildung und Differenzierung der Keimblätter bei *Chrysopa perla* (L.). *Z. Morph. Oekol. Tiere*, **35**: 615–702, 105 figs.

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POSTEMBRYONIC DEVELOPMENT

A. Metamorphosis

Eclosion from the Egg.—The process of eclosion or hatching from the egg varies greatly in the different groups but usually begins with the swallowing of amniotic liquid so that air enters the egg (Sikes & Wigglesworth, 1931). The chorion and other embryonic membranes are then ruptured, the former either along a preformed line of weakness, such as surrounds the cap of some eggs, or in a more irregular manner. Lepidopteran larvae eat their way through the membranes but in other insects the muscular forces involved may be aided by the swallowing of air or the presence of special structures such as the blood-filled eversible *cervical ampullae* of some Orthoptera or the various types of *hatching spines* (egg-bursters). When present, the egg-bursters (van Emden, 1946) are solid tooth-like or spine-like cuticular outgrowths. They may be borne on the frontal region of the embryonic cuticle which is shed at or soon after eclosion (most Exopterygotes, Neuroptera, Trichoptera). Alternatively, comparable egg-bursters occur on the cuticle of the normal first-stage larva and are lost only when this moults (Lepismatidae, Nematoceran Diptera, Siphonaptera, Adephagan Coleoptera). Or again, the cuticle of the first-stage larva bears variously situated dorsal structures on the thorax or abdomen or both (many Polyphagan Coleoptera). In general, the egg-burster ruptures the chorion and embryonic membranes but in the Mallophaga and Siphunculata it is used only to break the inner membranes, the chorion splitting around a cap (Weber, 1939). The chorion of the uterine egg of *Glossina* is broken by the larva but then stripped off by a maternal organ, the choriothete (Jackson, 1948). Some insects hatch with the tracheal system still full of liquid, but in others the rise of osmotic pressure in the tissue fluids caused by muscular activity results in a withdrawal of the liquid and the appearance of air in the tracheae before hatching.

Instar and Stadium.—Every insect during its growth sheds its skin one or more times, this process being known as a moult or *ecdysis*, the cast skin being termed the *exuviae*. The intervals between the ecdyses are known as stages or *stadia*, and the form assumed by an insect during a particular stadium is termed an *instar*. When an insect issues from the egg it is said to be in its first instar: at the end of this stadium the first ecdysis occurs and the insect then assumes its second instar, and so on. The final instar is the fully mature form which is known as the adult or *imago*.

A distinction sometimes emphasized is that between the separation of the old cuticle from the hypodermis (which is held to mark the beginning of the new instar) and its subsequent rupture and casting off. There may be an appreciable interval between the two events, during which time the instar within the old cuticle is known as the *pharate instar* (Hinton, 1946). In most Exopterygotes, the Neuroptera and Trichoptera, the insect at eclosion is

enclosed in the so-called embryonic cuticle which is either shed during eclosion so that it remains behind in the egg-shell or is cast shortly after hatching is complete, the insect bearing it being variously known as the pronymph (Odonata), vermiform larva (Acrididae) or primary larva (Cicadidae). There

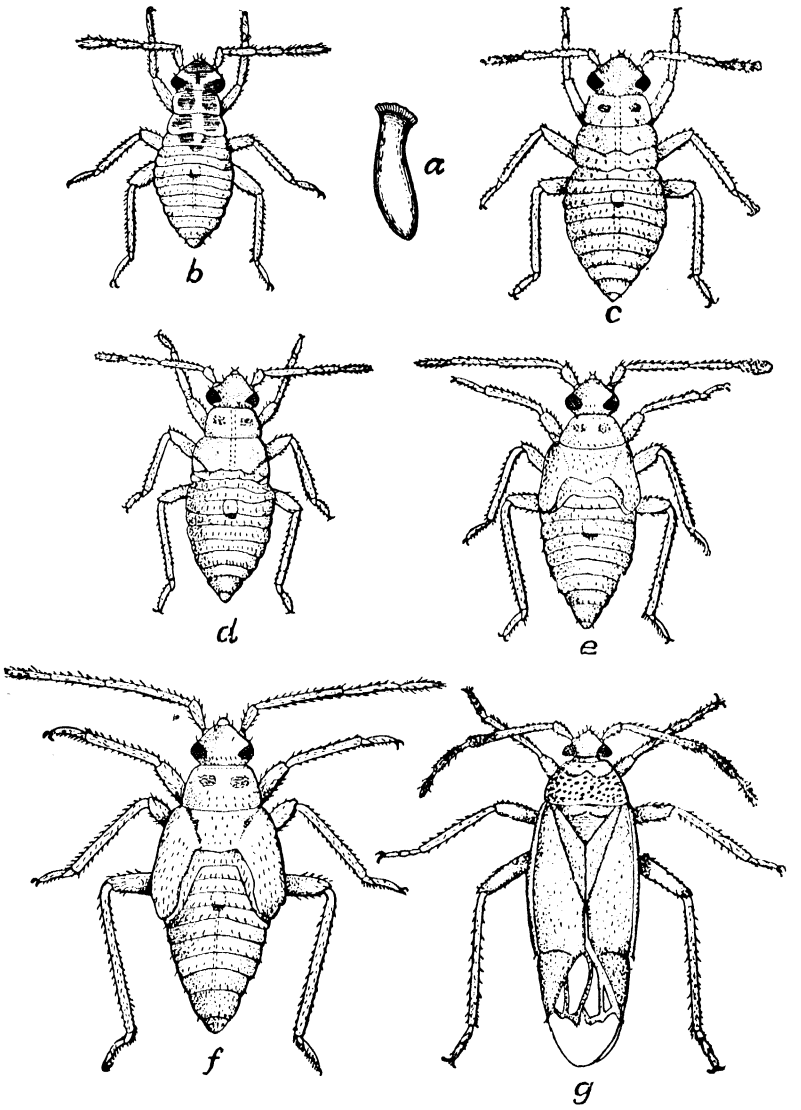


FIG. 186.—Metamorphosis of a Mirid (*Plesiocoris rugicollis*)

a, egg; *b–f*, nymphal instars (wing-rudiments minute in *d*, larger in *e* and *f*) × 20; *g*, imago × 8. From Carpenter, *after* Petherbridge and Husain.

seems little doubt that this stage represents a greatly abbreviated first instar (van Emden, 1946) though it is usually excluded from the system of numbering the instars in life-cycle studies.

Metamorphosis.—One of the most characteristic features of insects is the fact that they are almost always hatched in a condition morphologically different from that assumed in the imago. In order to reach the latter instar

they consequently have to pass through changes of form which are collectively termed *metamorphosis*.

Some insects emerge from the egg in a form which differs from the imago only in the undeveloped state of the reproductive organs and external genitalia and in morphologically unimportant details of shape or chaetotaxy and the segmentation of antennae and cerci. Such insects include the Apterygota and secondarily apterous Exopterygotes like the Mallophaga, Siphunculata, female Embioptera, etc. They are often regarded as having no metamorphosis, but the changes mentioned above are generally sufficiently marked to constitute a slight metamorphosis. The majority of insects, however, pass through a more or less profound metamorphosis. Among these forms it is convenient to distinguish two types of immature individuals, viz., nymphs and larvae, though many entomologists do not regard the distinction as a fundamental one (see p. 235) and the term 'larva' is often used to denote both instances.

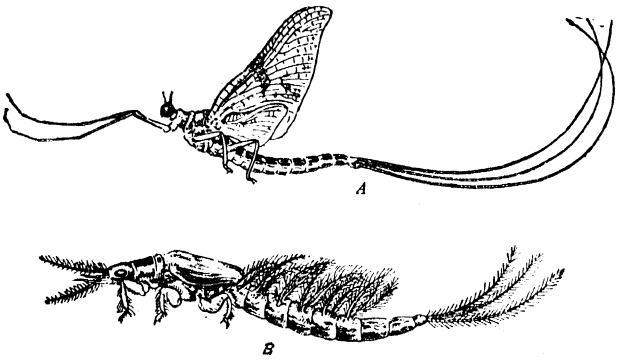


FIG. 187.—Metamorphosis of *Ephemera*
A, male imago. B, nymph. From Comstock *after* Needham.

A *nymph* is a young insect which differs mainly from the imago in that the wings and genitalia are only present in an incompletely developed condition. Wing rudiments are not usually discernible in the first instar but later become visible externally as wing-pads which gradually increase in size. The mouthparts exhibit the same general type of construction as in the adult, while the compound eyes are normal in form and function. The growth from the nymph to the imago is a simple one and is unaccompanied by a pupal instar though the changes at the last nymphal moult are usually greater than at preceding ones.

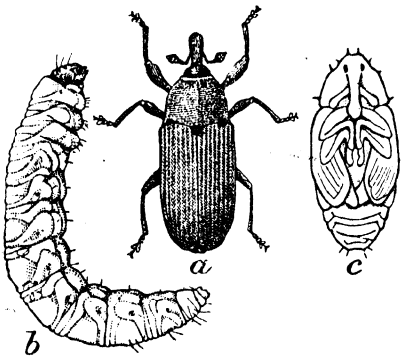


FIG. 188.—Metamorphosis of a weevil (*Trichobaris trinotata*)
a, imago; *b*, larva; *c*, pupa. *After* Chittenden, *U.S. Dept. Agric. ent. Bull.*, 33 (n.s.).

A *larva* differs fundamentally in form from the adult. The mouthparts usually differ greatly in construction from those of the adult and compound eyes, with scarcely any exceptions, are either wanting or non-functional. The growth from the larva to the imago is by means of a complex metamorphosis accompanied by a pupal instar.

Types of Metamorphosis.—The orders of insects exhibiting metamorphosis are often divided into two main groups: (1) Hemimetabola and (2) Holometabola.

1. HEMIMETABOLA.—This term is applied to members of the lower orders (or Exopterygota: p. 252) which pass through a simple metamorphosis often described as *direct* or *incomplete*. A pupal stage is wanting, and the immature insects are referred to as nymphs.

The degree of metamorphosis which prevails varies in different orders of Hemimetabola. In many cases the young resemble the adults in general form and mode of life (Fig. 186). Postembryonic development is consequently one of gradual growth, unaccompanied by any striking morphological change. The distinctive feature of this type of metamorphosis is the acquisition of wings and genitalia. Among the Plecoptera Odonata and Ephemeroptera (Fig. 187) the nymphs differ from the adults in possessing provisional organs. Since they live in water, while the imagines are aerial, these differences are of an adaptive nature and chiefly concern the respiratory and locomotory organs. The tracheal gills of the nymph are lost or, as in the Plecoptera, persist only as non-functional vestiges in the adult, which acquires open spiracles. The highly specialized labium of the Odonate nymph undergoes extensive remodelling to form the adult structure (Munscheid, 1933). The Ephemeroptera are unique in that the last immature stage, known as the subimago, possesses functional wings (p. 284). The Thysanoptera, Aleyrodidae, male Coccoidea and winged female Chermesids and Phylloxerids are regarded either as aberrant Hemimetabola or as Holometabola. The earlier immature stages are without wing rudiments and rather widely distinct in form from the adult while one or more quiescent or semi-quiescent stages recalling the Holometabolan pupa precede the adult stage. Further details are given in the relevant systematic sections.

2. HOLOMETABOLA.—This term is given to members of the higher orders (or Endopterygota, p. 252) which pass through a complex metamorphosis: the young are larvae and the imago is preceded by a pupal instar (Fig. 188). Such a type of metamorphosis is often referred to as *indirect* or *complete*.

Types of Insect Larvae.—Insect larvae assume an immense variety of forms, many of which are clearly adaptive and are discussed in detail in the systematic sections of this work (see also Peterson, 1948–51; Paulian, 1950; and Hayes, 1941). Several anatomical classifications of larvae are possible but the larger orders contain several different types of larvae so that transitional forms are not uncommon. In addition, special descriptive terms are widely used for the larvae of particular groups such as the 14 types of first-instar larvae recognized in the parasitic Hymenoptera by Clausen (1940), some of which are mentioned below and on p. 691. Berlese (1913) based a classification of insect larvae on the resemblances which they show to the three phases—protopod, polypod and oligopod—which sometimes succeed each other in embryonic development (Fig. 189; see also p. 210). He considered that, in general, the development of Endopterygote insects is temporarily arrested in one or other of these phases when eclosion from the egg takes place so that the larva is, so to speak, a protracted, free-living embryo. His theory has implications which are not generally accepted (p. 235) but it can provide a useful descriptive system. In the classification which follows, a fourth, apodous type of larva is also recognized and the oligopod and apodous types are respectively subdivided on the basis of their general facies or degree of cephalic development.

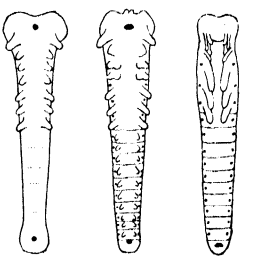


FIG. 189. — Embryonic phases

A, protopod. B, polypod. C, oligopod. *After* Berlese, *Redia*, 9.

1. PROTOPOD LARVAE.—This type is found in the primary larvae of certain parasitic Hymenoptera. The eggs of such species contain but little yolk and the larvae emerge while still in an early embryonic phase. Their survival is rendered possible from the fact that they occur in the eggs, or in the bodies,

of other insects where they develop immersed in a highly nutritive medium. Protopod larvae are characteristic of the Platygasteridae (Fig. 190) where, in *P. herrickii*, the larva is little more than a prematurely hatched embryo, devoid of segmentation in the abdomen and with rudimentary cephalic and thoracic appendages. The nervous and respiratory systems are as yet undeveloped, and the digestive organs are still largely in an embryonic phase. In the cyclopoid primary larva of other species of *Platygaster* (Fig. 191) and of *Synopeas* there is a greatly developed cephalothorax, powerful jaws and elaborate caudal outgrowths. The so-called eucoiliform larva of Figitidae is also a specialized protopod type with greatly developed thoracic appendages. Other examples include the first instars of Dryinidae and Scelionidae.

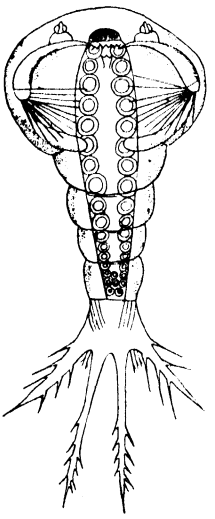


FIG. 191.—First larval instar (protopod) of *Platygaster*

After Ganin.

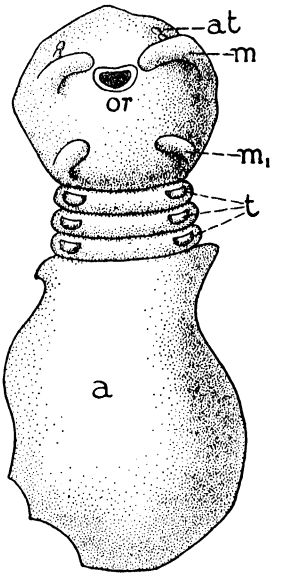


FIG. 190.—Protopod 1st instar larva of *Platygaster herrickii*

a, abdomen; *at*, antenna; *m*, mandible; m_1, maxilla; *or*, oral aperture; *t*, thoracic appendages. *After* Kulagin.

2. POLYPOD LARVAE.—Typical examples of this type (Fig. 192) are seen in the so-called *eruciform larvae* of most Lepidoptera, sawflies and scorpion flies. Their essential features are the well-defined segmentation, the presence of abdominal limbs or prolegs (whose serial homology with the thoracic ones is not, however, established with certainty) and a peripneustic tracheal system. The antennae and thoracic legs are present but little developed, and such larvae are relatively inactive, living in proximity to their food. The existence of a presumed though somewhat reduced polypod instar among endoparasitic Hymenopterous larvae is recorded in the Figitidae



FIG. 192.—Eruciform (polypod) larva of *Pieris brassicae*

where there are ten pairs of trunk appendages (James, 1928); in *Ibalia* where there are twelve pairs (Chrystal, 1930) and in the Proctotrupid *Phaenoserphus* where there are eight pairs of such organs (Eastham, 1929). In the Figitidae the polypod instar follows the protopod stage but, in the other examples, it is the first-stage larva. Owing to an endoparasitic mode of life the spiracles are undeveloped in these examples.

3. OLIGOPOD LARVAE.—These are characterized by the presence of more or less well-developed thoracic legs and the absence of abdominal appendages

except sometimes for a pair of cerci or similar caudal processes. The head-capsule and its appendages are usually well developed but otherwise there is appreciable variation in their general appearance though two common types can be distinguished: (*a*) *Campodeiform larvae* (Figs. 193, 194, A) are so called from their resemblance to *Campodea* and typically possess an elongate, more or less fusiform somewhat depressed body which is often well sclerotized, a markedly prognathous head, long thoracic legs and usually a pair of terminal abdominal processes. They are generally active predators with a well developed sensory equipment and are commonly regarded as the most primitive larval forms, differing mainly from exopterygote nymphs in the absence of compound eyes, dorsal ocelli and wing pads. Varying degrees of reduction occur and in some hypermetamorphic forms a campodeiform first instar is succeeded by more degenerate oligopod stages (e.g. Meloidae, Rhipiphoridae, *Aleochara*, etc., Fig. 194). Campodeiform larvae occur in the Neuroptera, some Coleoptera (especially Adephaga), Strepsiptera and Trichoptera. (*b*) *Scarabaeiform larvae* (Fig. 194, C) are stout subcylindrical, C-shaped larvae with shorter thoracic legs, a soft, fleshy body and no caudal processes. They are typical of the Scarabaeoidea but also occur, sometimes in a more reduced condition, in other Coleopteran families (e.g. Ptinidae, Anobiidae) and are evidently derived from the campodeiform type, leading a less active life in the presence of ample supplies of food.

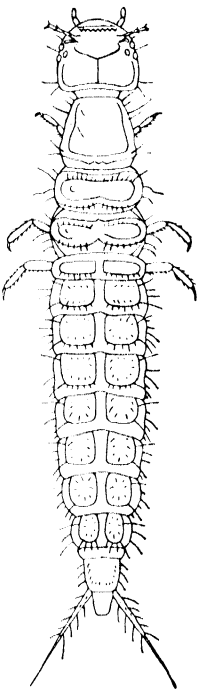


FIG. 193. — Campodeiform (oligopod) larva of a Staphylinid (*Philonthus nitidus*) *After* Schiödte.

4. APODOUS LARVAE.—In this type the trunk appendages are completely suppressed and, in the vast majority of cases, it is derived from the oligopod type. Among Coleoptera the apodous condition occurs in several families and, in the Bruchidae, it is preceded by a degenerate oligopod instar, while in the Curculionidae the last rudiments of thoracic limbs are retained as sensory protuberances in *Phytonomus* (Pérez, 1911). In the Hymenoptera the apodous condition occurs in almost all larvae of the Apocrita—traces of an oligopod stage have been detected in *Polysphincta* and certain other Ichneumonoidea and the few polypod types are mentioned above. In the Symphyta a long series of transitional forms occur from typical polypod types to oligopod forms, finally culminating in the apodous larva of *Orussus*. In Diptera the larvae are usually apodous but bear three pairs of sensory papillae in direct relation with the developing imaginal leg-buds—thus they occupy the positions of ancestral thoracic limbs of which they are the transformed vestiges (Keilin, 1915). Dipterous larvae are, therefore, probably to be regarded as highly specialized derivatives of the oligopod type. A clearly defined polypod phase has become obliterated from all stages in the ontogeny of most flies (but cf. the larva of *Atherix*). The apodous larvae may be divided into three types depending on the degree of development of the head. The eucephalous larvae (most Nematocera; Buprestidae, Cerambycidae; Aculeate Hymenoptera) have a more or less well sclerotized head-capsule with relatively little reduction of the cephalic appendages. In the hemicephalous larvae (Tipulidae, most Brachycera) there

is appreciable reduction of the head-capsule and its appendages accompanied by marked retraction of the head into the thorax while the acephalous larvae of Cyclorrhaphan Diptera have no obvious head-capsule or appendages though some cephalic structures contribute to the largely concealed buccopharyngeal apparatus.

Hypermetamorphosis.—When an insect in its development passes through two or more markedly different larval instars it is said to undergo *hypermetamorphosis* (Fig. 194). This phenomenon is accompanied as a rule

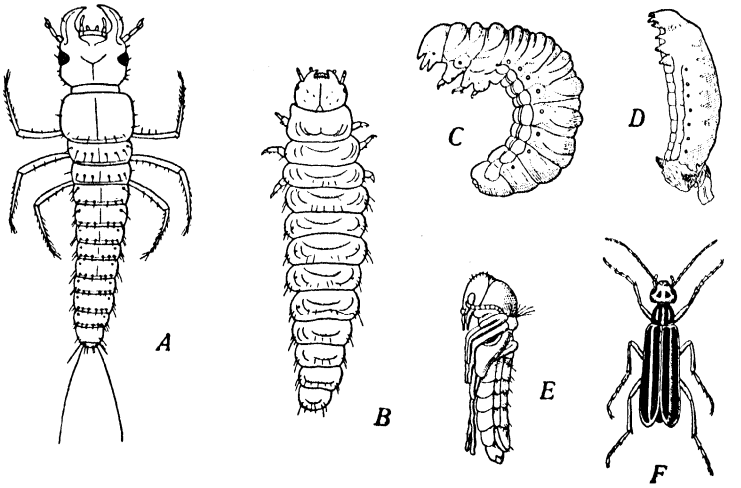


FIG. 194.—Hypermetamorphosis of *Epicauta*

A, triungulin; B, caraboid second instar; C, ultimate form of second instar; D, coarctate larva; E, pupa; F, imago. All refer to *E. vittata* except E, which is *cinerea* (F nat. size, others enlarged). From Folsom's *Entomology after* Riley.

by a marked change in larval life. In the majority of instances of hypermetamorphosis the first larval instar is campodeiform. During this stage it seeks out its future pabulum and having discovered it undergoes, in its subsequent instars, morphological transformations which adapt it to the changed mode of life.

Since various examples of hypermetamorphosis are described under the several families concerned they need not be discussed here, and only the principal instances are enumerated below.

NEUROPTERA. *Mantispa.*
COLEOPTERA. Carabidae (*Lebia scapularis*). Staphylinidae (*Aleochara* spp.). Meloidae. Rhipiphoridae.
STREPSIPTERA. All species.
DIPTERA. Bombyliidae. Acroceridae. Nemestrinidae. Some Tachinidae.
HYMENOPTERA. In all the chief groups of Parasitica.
HEMIPTERA. Coccoidea—*Margarodes* and allies.

Ecdysis.—The more or less rigid integument is ill adapted for accommodating itself to the increase in size of an insect that is consequent upon growth, and is therefore periodically shed. During each act of ecdysis not only the general cuticle investing the body and its appendages is cast off, but also the lining or intima of most of the tracheal system, fore and hind intestine, glands, etc. All these parts, together with hairs, scales, and similar structures, are renewed by the hypodermal cells underlying them.

The histological and other changes which accompany moulting are summarized by Richards (1951). The insect which is about to moult becomes less active and the process starts with an increase in the size of the hypodermal cells which usually also show mitotic activity. The cuticle then becomes detached through the retraction of the hypodermis and the cytoplasmic filaments in the pore-canals are said also to be withdrawn. The space beneath the old cuticle is filled with the moulting fluid (Passonneau & Williams, 1953) which is secreted by the hypodermal cells and contains a proteinase and a chitinase. These dissolve away the inner layers of the old cuticle by hydrolysis, the products of digestion being resorbed. At the same time the hypodermis and associated cells begin to deposit the new cuticle, the various components of which are laid down as described on p. 10. The way in which the new cuticle is protected from the effects of the moulting fluid is not clear though it is worth noting that the resistant epicuticle is the first part of the new integument to be formed. When an appreciable thickness of new cuticle has been laid down the remaining moulting fluid is absorbed through the general body surface and the old cuticular sheath is ruptured. This occurs along definite lines of weakness in the head-capsule and along the median anterodorsal part of the body, the precise sites being different in different species (Henriksen, 1932; Snodgrass, 1947). The pressure necessary to accomplish rupture is achieved through the insect swallowing air or water aided by muscular contractions and the transmission of the resulting pressure-changes by the blood. The new instar then gradually wriggles out of the old integument, probably assisted in some cases by the spines or other processes which it bears. The ecdysis is followed by a further increase in cuticular thickness and sclerotization and by the development of full pigmentation. Many of the changes of form which become evident at a moult are due to differential growth of the hypodermis but tonic muscular contractions probably play some role, especially in the formation of apodemes.

In some insects the old cuticle is not ruptured but remains as a protective covering for the new instar, as in the puparium of Cyclorrhaphan Diptera, the larval sac of Dryinids and a few other cases. In other instances the successive shrivelled exuviae are retained at the hind end of the body (e.g. the larvae of some parasitic Hymenoptera or Cassidine beetles) or are incorporated into the 'scale' of some Coccoidea. For information on the hormonal control of ecdysis, see p. 244.

Different insect species differ greatly in the number of moults which they undergo in the course of their life, and details are given in the appropriate systematic sections. Though little phylogenetic significance is to be attached to the number of moults it is broadly true that specialized forms have fewer instars than do more primitive ones. Among the Apterygota *Ctenolepisma* moults 14 times before reaching a mature state and then continues moulting at intervals without change of form until it dies. Similar moults occur after sexual maturity in *Campodea* and the Collembola but in no Pterygote insects do the adults ever moult. The nymphs of Ephemeroptera moult more than 20 times whereas most Plannipennian Neuroptera undergo 4 ecdyses in development (or 5 if one includes the throwing off of the embryonic cuticle at eclosion). Most other insects fall between these extremes. In some groups the number of moults is remarkably constant (e.g. 5 in the Heteroptera, 6 in the Psocoptera, both excluding the embryonic moult) while the Lepidoptera, for example, have from 2 to 9 larval instars according to species, with not infrequent variations between individuals of the same species. Under adverse

nutritional conditions the number of larval instars in some Coleoptera and Lepidoptera can be greatly increased, though there is little growth in size and sometimes even a decrease. In several species the sexes differ in the number of moults, the female commonly having more instars. Mention may finally be made of the concealed moult which occurs within the puparium of the Cyclorrhaphan Diptera where a 'prepupal cuticle' is thrown off from all or part of the body (Snodgrass, 1924; Fraenkel, 1938).

Growth.—The larval and nymphal periods are pre-eminently ones of growth. The rapidity with which this process takes place, and the great increase in size which accompanies it, are particularly evident in many holometabolous insects. A comparison of the weight of a mature larva with that at the time of eclosion from the egg has been made in several species. Thus Trouvelot found that the silkworm *Telea polyphemus* when fully grown is 4,140 times its original weight. In the larva of the bee *Anthophora retusa* the corresponding increase is 1,020 times (Newport); in the larva of *Cossus cossus*, which lives for three years, it is 72,000 times (Lyonnet); in *Sphinx ligustri* 9,976 times (Newport); in the silkworm *Bombyx mori* the increase varies according to racial and other factors between about 9,100 times and 10,500 times. Growth in weight is not, however, continuous but is interrupted at each ecdysis, though the habit of swallowing water in aquatic forms in order to split the old cuticle may obscure the interruption on a growth curve.

Growth of the tissues occurs partly through cell-division and partly by an increase in the size of individual cells, the latter process predominating in the brain and gut of *Popillia japonica* larvae, for example (Abercrombie, 1936). In *Aedes* larvae, Trager (1937) finds that some tissues, which are destroyed at pupation, grow by an increase in cell size whereas others, which persist into the adult stage, grow by cell-multiplication, and in *Calliphora*, where destruction of larval tissues at metamorphosis is very extensive, larvae develop only by growth of the cells without division.

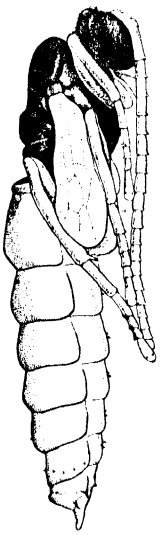
Dyar (1890) showed from observations on 28 species of Lepidopteran larvae that the width of the head-capsule increases in a regular geometrical progression in successive instars by a ratio of about 1·4 and the same is true for linear measurements of many cuticular structures in widely different insects (Teissier, 1936). Dyar's 'law' has consequently often been used successfully to determine the number of instars in a life-cycle, but there are many exceptions to it, the progression factor often changing in successive instars (Gaines & Campbell, 1935; Ludwig & Abercrombie, 1940). Richards (1949) found that in his examples the progression is regular only if account is taken of the fact that the different instars differ in duration, growth apparently proceeding in a uniform manner so that the longer the stadium the greater the amount of growth.

The various parts of the body tend to grow at rates which differ from each other and from the growth-rate of the whole body. In many cases, the phenomenon of allometric growth occurs (Huxley, 1932) in which the size of a part is a constant exponential function of the whole. This type of differential growth serves to explain such features as the relatively larger mandibles in male Lucanidae of greater absolute size. It also follows that taxonomic characters dependent on simple statements of the relative size of a structure may be unreliable if allometric growth occurs in the parts concerned (e.g. Boratynski, 1952).

The Pupa.—The term *pupa* is now used with reference to the resting inactive instar in all holometabolous insects. During this stage the insect is

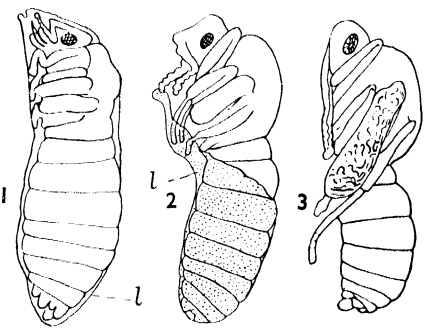
incapable of feeding and is quiescent. It is to be regarded as a transitional phase during which the larval body and its internal organs are remodelled to the extent necessary to adapt them to the requirements of the future imago. Though the term customarily denotes the whole of the pre-imaginal stage it must be recognized that for a varying period before adult emergence the 'pupa' actually represents a pharate adult (p. 222)—i.e. the more or less fully-formed adult lies separate within the old pupal cuticle and the limited degree of locomotion which pupae undertake is usually the result of movements by the pharate adult.

Among some Neuroptera including *Raphidia*, *Hemerobius* and *Chrysopa* the pharate adults are relatively active and are able to crawl about. Those of certain Trichoptera exhibit adaptive modifications which enable them to swim to the surface of the water to allow of the exit of the imagines. In the Culicidae and certain Chironomidae the pupae are active throughout the instar, and are capable of vigorous swimming by means of caudal movements. Movements of a less pronounced character are exhibited by many pupae which occur in the soil, in wood or in stems.



A

FIG. 195A.—Exarate or free pupa of a Hymenopteran (Ichneumonidae): lateral view



B

FIG. 195B.—External changes during prepupal and pupal instars of *Formica rufa*

1, prepupa; 2, change into pupa; 3, pupa; *l*, larval skin. *After* C. Pérez, 1902.

The following types of Endopterygote pupae are distinguished by Hinton (1946a), the primary division reflecting the way in which the pharate adult (late pupa) escapes from the cocoon or pupal cell before emergence of the adult occurs (see also p. 233).

1. *Decticous Pupae* (Fig. 445).—These have relatively powerful, sclerotized, articulated mandibles which are actuated by the musculature of the pharate adult when they are used to escape from the cocoon or cell. This is the primitive type of pupa and is always exarate—i.e. the appendages are not adherent to the rest of the body and can be used in locomotion. It occurs in the more primitive Endopterygotes—Neuroptera, Mecoptera, Trichoptera and in the Lepidopteran families Micropterygidae and Eriocraniidae.

2. *Adecticous Pupae.*—Pupae of this type have non-articulated mandibles which are often reduced and are not used in escaping from the cocoon or cell when this is present. Two main forms of decticous pupae are recognizable, though intermediates are known.

(*a*) *Exarate adecticous pupae.* As in the exarate pupae of the other main group, the appendages are free of any secondary attachment to the body (Fig. 195A). They are found in the Siphonaptera and Strepsiptera, most Coleoptera and Hymenoptera, and the Cyclorrhaphan and most Brachyceran Diptera.

(*b*) *Obtect adecticous pupae.* Here the appendages of the pupa are firmly pressed against its body and are soldered down to it by a secretion produced at the last larval moult; the exposed surfaces of the appendages are more heavily cuticularized than

those adjacent to the body. Such pupae are best known from all higher Lepidoptera (Fig. 196) but also occur in some Coleoptera, the Nematoceran Diptera and many Chalcidoids.

The so-called coarctate pupa of Cyclorrhaphan Diptera (Fig. 197) is clearly an adecticous, exarate pupa enclosed in a puparium which is formed from a preceding larval cuticle and which is functionally comparable to the cocoon or pupal cell of other forms.

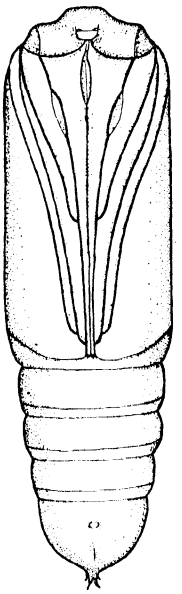


FIG. 196. — Obtect pupa of a Lepidopteron (Noctuidae): ventral view

The Prepupa.—This term is used in more than one sense but it refers in most cases to the pharate pupa. Near the end of the larval life the insect prepares for transformation into the pupa, usually constructing a cocoon, cell or other form of protection. Meanwhile the larval cuticle becomes separated from its hypodermis and the developing pupa, with everted wings and appendages, lies within the persistent larval cuticle. The changes in form which accompany the development of the pupa often cause the deformation of the persistent larval cuticle so that the prepupal phase differs somewhat in external appearance from the earlier larva. The body is commonly more depressed and the abdomen relatively shorter while the insect at this time is quiescent and does not feed. The phase does not, however, constitute a distinct instar and when the old larval skin is ultimately cast off it reveals the pupa (Fig. 195B). In the Cyclorrhaphan Diptera conditions are a little different in that the puparium is formed from the third-instar larval cuticle and the enclosed insect then sheds an additional thin cuticle from all or part of its body before eversion of the pupal head and appendages is completed (see p. 230). Though this thin cuticle is often referred to as the prepupal cuticle there seems no advantage in restricting the term 'prepupa' to the short-lived and, indeed, sometimes incomplete instar which produces it. Exceptionally among Endopterygotes there is an anatomically very distinct instar which precedes the pupa, e.g. of the hypermetamorphic Carabid *Lebia scapularis* and this is known as the prepupa (Silvestri, 1904). Finally, in male Coccoidea and in Thysanoptera the first instar in which external wing-pads appear is sometimes known as the prepupa or propupa.



FIG. 197. — Coarctate pupa of a Dipteron (Muscidae): dorsal view

Pupal Protection.—During transformation into the pupa and throughout the latter instar insects are particularly vulnerable. Since at these periods they are provided with exceedingly limited powers of movement and defence, special methods of protection are necessary. Most pupae are concealed in one way or another from their enemies, and also from such adverse influences as excess of moisture, sudden marked variations of temperature, shock and other mechanical disturbances. Provision against such influences is usually made by the larva in its last instar. Many Lepidopterous and Coleopterous larvae burrow beneath the ground and there construct earthen cells in which to pupate. The larger number of insects, however, construct cocoons which are special envelopes formed either of silk alone, or of extraneous material bound

together by means of threads of that substance. Thus many wood-boring larvae utilize wood-chips, larvae which transform in the ground select earth-particles: many Arctiid larvae use their body-hairs and Trichoptera use pebbles, vegetable fragments, etc., their larval cases functioning as cocoons. In these instances the substances are held together by means of a warp of silk and worked up to form cocoons. A large number of other insects, including some of the Neuroptera and Trichoptera, many Lepidoptera and Hymenoptera and the Siphonaptera, utilize silk alone in forming their cocoons. Great variations exist in the colour and nature of the silk and in the texture and form of the completed cocoons. The densest and most perfect types of cocoon are found in the Saturniidae, while the other extreme is met with in the Papilionoidea, where the pupa may be suspended by its caudal extremity, which is hooked on to a small pad of silk representing the last vestige of a cocoon. Among the Tenthredinidae cocoons of a parchment-like or shell-like consistency are frequent: in some cases the outer cocoon encloses an inner one of more delicate texture. In the Diptera Cyclorrhapha a cocoon, with very rare exceptions, is wanting, and the hard puparium forms the sole protection to the pupa.

Some specialized representatives of the Lepidoptera, Coleoptera, Diptera and Hymenoptera have pupae which are not protected by a cell, cocoon or puparium though they may be concealed in the integument of the host (Chalcidoidea) or are protected by being strongly sclerotized, obtect structures which are sometimes protectively coloured.

Emergence from the Cocoon.—Escape from the cocoon or cell is effected in a variety of ways, many of which are described by Hinton (1946; 1949). Most of the more primitive Endopterygotes escape as the pharate adult, the mandibles of their decticous pupae, aided sometimes by backwardly directed spines on the body, enabling them to cut open the cocoon or cell and burrow through the soil, rotten wood, etc., in which it lay. The pupal skin is then shed some distance from the cocoon. Insects with adecticous pupae have evolved many different methods of escape, especially in the Lepidoptera (p. 533) and the Diptera. In the latter order, the primitive method of escape is probably one in which the pupa, aided sometimes by body spines and sharp cephalic processes or cocoon-cutters, makes its way to the surface of the pupation medium from which its body projects while the adult escapes. Other special methods occur in forms with aquatic pupae and in the Cyclorrhapha where the newly emerged adult has an eversible cephalic sac, the ptilinum, to force open the puparium and escape from the surrounding medium (p. 587). In the Siphonaptera, Coleoptera, male Strepsiptera and Hymenoptera the adult emerges within the cocoon or cell and escapes by using its mandibles (including the special deciduous mandibular appendages of some Curculionids) or, in most fleas, by means of imaginal cephalic cocoon-cutters.

Eclosion of the Imago.—As the time for the eclosion of the imago approaches the pupa noticeably darkens in colour. In some of the more transparent pupae of the Papilionoidea the colours of the imago are distinctly observable a short period before its emergence. When the time for the latter arrives, the contained insect, by means of convulsive movements of its legs and body, succeeds in rupturing the pupal cuticle. A longitudinal fracture occurs down the back of the thorax, and there are often other fractures in the region of the legs and elsewhere. The insect withdraws its appendages from within those of the pupa or last nymphal instar and emerges completely formed except for the wings. It crawls up the nearest available support and there rests in such a position that the folded miniature wings are inclined

downwards. By the influx of blood from the body, and pressure exerted upon that fluid by muscular action, the complete expansion of the wings is rapidly acquired (Fig. 198). During this preliminary phase drops of liquid (the

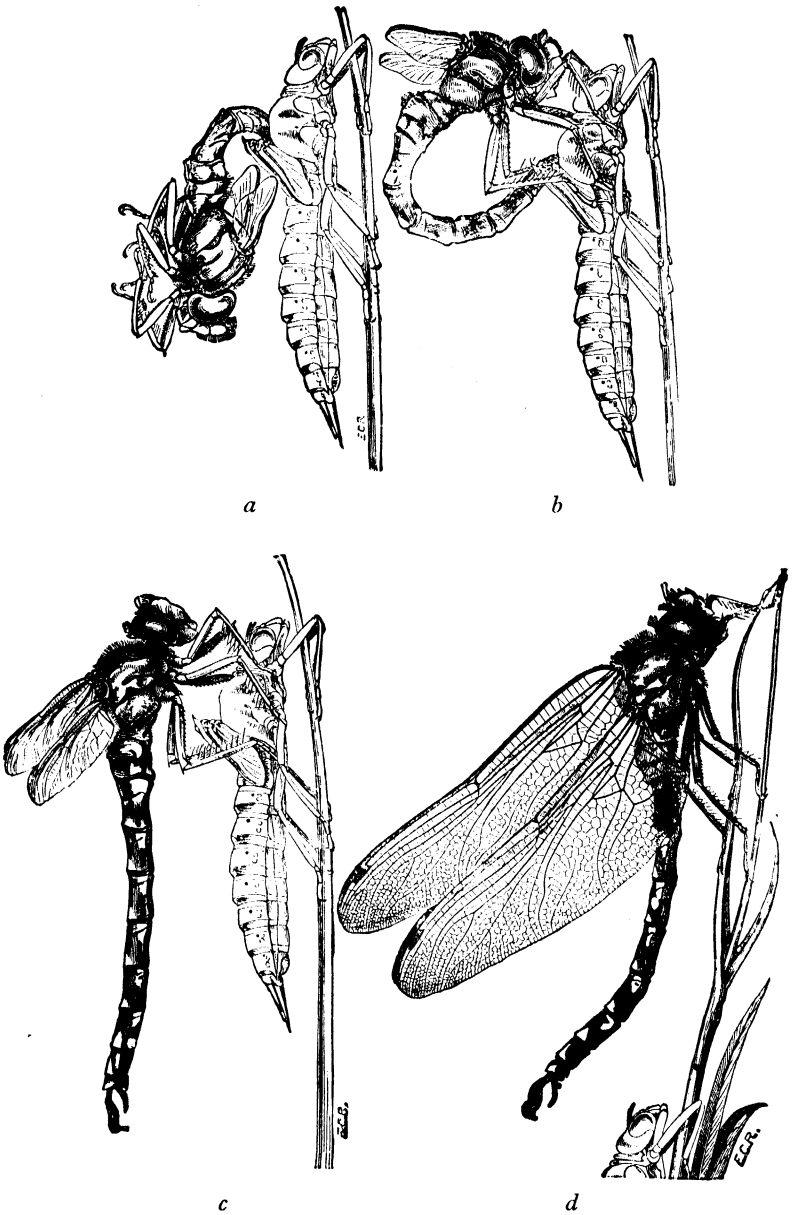


FIG. 198.—Stages in the emergence of a dragonfly (*Aeshna cyanea*)
a–c, from the nymphal cuticle; *d*, fully-formed imago. *After* Latter, *Nat. Hist. of Common Animals.*

meconium) are discharged from the anus: they represent the waste products of pupal metabolism, and in Lepidoptera are coloured with residual pigmentary matter which has not been utilized. A short period elapses after eclosion before the insect is able to make its trial flight. The time of emergence varies

greatly in different species. In some Lepidoptera, for example, it occurs in early morning and in others towards evening: at such times they may sometimes be observed resting upon tree trunks, etc., awaiting their normal hours of activity. Among certain aquatic insects the imago is able to take to the wing almost immediately after eclosion.

Origin and Significance of the Pupal Instar.—Several more or less distinct interpretations of metamorphosis have been proposed, accounting in different ways for the origin of the Endopterygote pupa. While it is clear that the pupa has considerable selective value in making possible a wide divergence in form and habits between the adult and larva and thus permitting the latter to exploit many habitats which have proved less accessible to Exopterygote nymphs, there is as yet no general agreement on the relationship between the typical Exopterygote and Endopterygote modes of development.

Berlese (1913) supposed that the Exopterygote nymph represents a post-oligopod stage of development whereas the larvae of the Endopterygotes evolved through eclosion occurring at a developmental stage corresponding to one of the preceding embryonic phases (p. 210). It follows that the larva is a sort of free-living embryo while the pupa represents the sequence of nymphal stages compressed, as it were, into a single instar. A fundamental distinction is thus made between larva and nymph, supported, it is claimed, by such characters as those mentioned on p. 224. On the other hand, Handlirsch (1928) recalls that even in the Exopterygotes there are commonly rather distinct changes during postembryonic development and supposes that by their accentuation and concentration towards the later part of development the larval stages arose as specialized nymphs and the pupa is a modified last-instar nymph whose quiescence accompanies the more extensive and abrupt changes now necessary for transformation into the adult. Such a view denies that there is any fundamental distinction between nymph and larva and regards those differences which exist as merely due to coenogenetic modification and to changes in the rate at which adult characters develop in the two types of metamorphosis. Among other things, Berlese's theory does not account satisfactorily for the fact that the Endopterygote pupa is always a single instar while Handlirsch's view tends to minimize the striking similarity in external form between the pupa and adult in the more primitive Endopterygotes. Hinton (1948), reviving and supplementing an earlier theory of Poyarkoff (1914), takes both these points into consideration by supposing that, while the nymphal and larval stages are equivalent, the pupa represents the first of two imaginal instars whose principal function it is to provide a cuticular 'mould' which ensures the adequate development of the skeletal musculature peculiar to the adult. The muscles then become attached to the adult cuticle when the latter is laid down beneath the similarly shaped pupal cuticle. The absence of such an 'imaginal moult' in the normal Exopterygotes is explained on the grounds that the differences between the musculature of their adults and immature stages are few and slight and the necessary changes are accomplished without the need for a moult to secure the simultaneous attachment of a large number of newly-formed muscles to the adult cuticle.

There is little doubt that the so-called pupae of the Thysanoptera, male Coccoidea, etc., mentioned on p. 225 have evolved independently of each other and of the Endopterygote pupa. Whether they are all equivalent in terms of Hinton's hypothesis is not clear though Mäkel's (1942) study of the skeletal muscles of *Pseudococcus* males is thought to indicate that the Coccoidea, at any rate, are fundamentally similar to the Endopterygotes.

B. The Development of the Imago

The culminating feature of metamorphosis is the formation of the imago. The characteristic distinctions between hemi- and holometabolous insects with regard to the manner of development of the perfect insect have already been pointed out. In the Hemimetabola it is accomplished through a gradual series of external and internal changes and alterations of form, which may be traced back to simple growth during the nymphal instars, though the changes at the last moult are generally greater than those at previous ones. In the Holometabola the transformation from the larva to the adult is accomplished largely during the quiescent pupal instar and a more detailed consideration of the complex changes which occur there is required. The extent of the transformation varies according to the species and the organs or tissues concerned

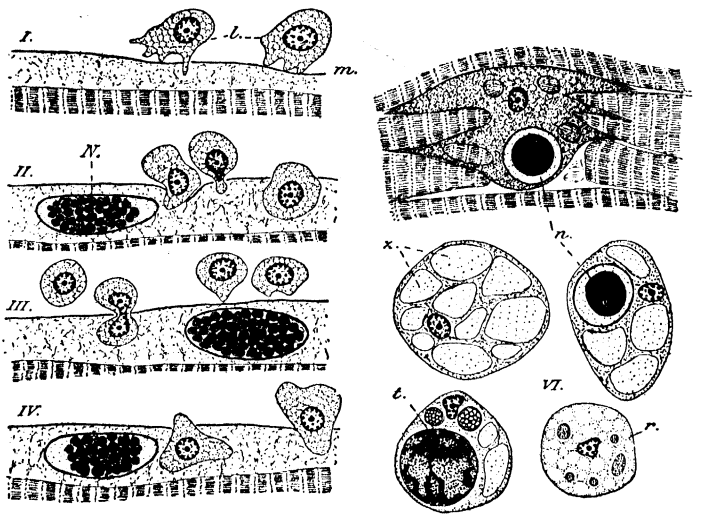


FIG. 199.—Phagocytosis of muscle in *Calliphora*

I–IV, stages in the immigration of phagocytes into a muscle. *V*, a phagocyte within a muscle; the nucleus of the latter has been ingested by the phagocyte. *VI*, diverse phases of the granular spheres. *l*, phagocytes; *m*, sarcollemma; *N*, muscle nucleus; *n*, do. within a phagocyte; *x*, sarcolytes or muscle fragments; *t*, other tissue engulfed by phagocyte; *r*, phagocyte which has almost digested its inclusions. *After* C. Pérez.

(Snodgrass, 1954). The simplest transition is effected when the cells of a particular larval tissue are carried over to form the corresponding tissue of the adult, the process being accomplished with relatively minor alterations due to differential growth and cellular differentiation. In other cases the larval tissue is largely or completely destroyed, a process known as *histolysis*, and the adult tissue which replaces it is developed by *histogenesis* from certain masses of formative cells known variously as *imaginal buds*, *imaginal discs* or *histoblasts*. The details of the histolytic processes differ in different insects but the first event is the death of the tissue concerned. This may then undergo simple fragmentation and autolysis with little intervention by phagocytic blood-cells or, in other cases, the latter may deal with the larger fragments or, again, the recently dead but intact tissues may be actively attacked by numerous phagocytes (Figs. 199, 209, 211). The cells of the centres of imaginal differentiation which carry out histogenesis are either indistinguishable or relatively inconspicuous during the earlier larval stages though they are constant in position for a given species and in the higher Diptera, for example, they are already

evident in the later embryo. They are best regarded as zones of persistent embryonic tissue whose capacity for growth and differentiation is largely suppressed during the larval stages and is fully realized only when the hormonal balance which controls metamorphosis is altered in the later part of larval life (see p. 244; also Henson, 1946). The different groups of Holometabolan insects differ considerably in regard to which larval tissues pass over to the adult without great change and which are destroyed and replaced. There are also variations in the mode of replacement and the following account summarizes the changes which can occur.

1. THE HYPODERMIS: The development of the imaginal hypodermis is a particularly important process since this tissue imparts to the pupa or adult the characteristic external form which distinguishes it from the larva. Associated with the hypodermal changes, therefore, are those processes which result in the formation of the segmental appendages and wings which become everted in the pupal stage, together with the elaborate alterations by which the highly differentiated imaginal head is formed in species whose larvae have a less well-developed cephalic region.

In the Coleoptera, much of the larval hypodermis passes without destruction into the adult (Poyarkoff, 1910; Murray & Tiegs, 1935; Patay, 1939). In Hymenoptera and Diptera, however, there is a gradual destruction of the larval hypodermis with accompanying replacement by the growth of cells from imaginal discs. The new hypodermis of the head and thorax arises from part of the imaginal discs of the cephalic appendages and legs, while that of the abdomen is formed from separate centres of regeneration—in *Drosophila*, for example, there are six such centres on each spiracle-bearing abdominal segment (Robertson, 1936).

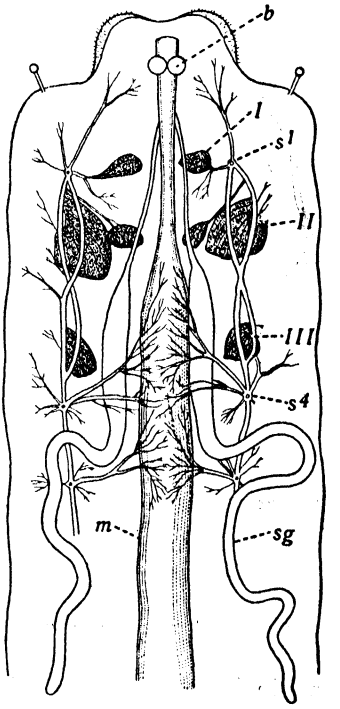


FIG. 200.—Fully-grown larva of *Pieris* dissected from above showing imaginal buds

b, brain; *m*, mid intestine; s^1, prothoracic spiracle; s^4, 1st abdominal spiracle; *sg*, silk gland; *I*, prothoracic bud; *II* and *III*, buds of fore and hind wings. From Folsom's *Entomology*, *after* Gonin.

In those lower Endopterygotes where the appendages of the larval head and thorax do not differ greatly from those of the pupa or adult, the latter develop within the larval appendages, often being folded until they are freed at the moult into the pupa. In other cases, the imaginal buds from which they differentiate are not always so closely associated with the larval structures (Fig. 34) though their position may be indicated externally by sensilla which lie on or replace the corresponding larval appendages (e.g. Eassa, 1953). They usually appear as evaginations from previously developed hypodermal pockets. The entrance to the pocket narrows or closes up, and the space surrounding the imaginal bud is the *peripodial cavity*, whose wall is known as the *peripodial membrane*: the latter is continuous with the general hypodermis (Fig. 34). As the imaginal buds develop the peripodial cavities enlarge accordingly and the peripodial membrane becomes attentuated. The mouths of the cavities eventually open and

the buds commence to protrude: with the assumption of the pupal instar they are completely everted and appear outside the body. A more detailed account of the development of the wing-buds is given on p. 44.

The imaginal buds are exhibited in a relatively simple condition in the larva of *Anopheles*. Those of the head appendages appear at the bases of the existing larval organs which they are destined to replace, and the imaginal head is formed within that of the larva. The largest buds are those of the antennae, and, of the buds of the mouthparts, the most conspicuous are those of the future labrum, maxillary palpi and labium. In the thorax two pairs of imaginal buds are present on each segment—a dorsal pair and a ventral pair. The dorsal imaginal buds give rise to the pupal respiratory horns, the wings and the halteres in their respective segments. Each pair of ventral buds forms the legs of its segment. In the abdomen there is a conspicuous pair of dorsal buds at the anal extremity which forms the pupal caudal lamellae.

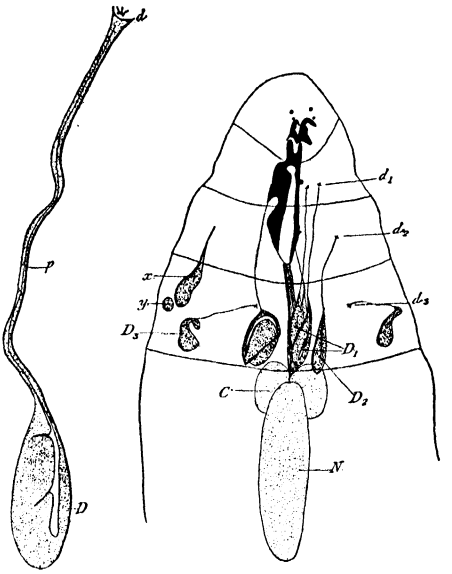


FIG. 201.—Imaginal buds of the larva of *Erioischia brassicae* showing the filamentous pedicels connecting them with the hypodermis

D_1–D_3, leg-buds; d_1–d_3, cutaneous sensory organs (vestiges of larval legs); *x*, wing-bud; *y*, bud of haltere; *C*, brain; *N*, ventral nerve-centre. × 36. On the left—imaginal bud *D* of the fore leg with its pedicel *p*. × 75. *After* Keilin, 1915.

The researches of Weismann (1864–66), Kowalevsky (1887), van Rees (1888), Pratt (1900), Vaney (1902), Pérez (1910) and others have shown that the imaginal buds attain increasing complexity in the passage from the lower to the higher members of the Diptera. In the Cyclorrhapha they are deeply sunk into the body, and it is often difficult to trace their connexions with the hypodermis owing to the peripodial membrane being reduced in each case to a greatly attenuated cord (Fig. 201). In *Melophagus* the buds, although superficial in position, become disconnected from the hypodermis (Fig. 202).

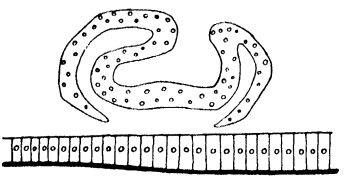


FIG. 202.—Thoracic bud of *Melophagus*

After Pratt, *Proc. Boston Soc. nat. Hist.*, 1900.

The most complex feature is exhibited in the imaginal buds of the head: the development of the latter is associated with the position of the cerebral ganglion in the larva, and the fact that the larval head is no longer able to accommodate the developing head of the imago. In *Chironomus* Miall & Hammond (1892) have shown that the cerebral ganglion lies in the larval prothorax, and the imaginal head is formed in relation with the former centre. In a larva about half an inch long, the hypodermis becomes infolded along two nearly longitudinal lines, corresponding to the margins of the larval clypeus. The imaginal buds of the compound eyes and antennae arise from the inner extremities of these cephalic folds and are thus far removed from the surface. The folds gradually extend backwards into the prothorax until the imaginal buds referred to become closely related to the cerebral ganglion. The posterior prolongation of the folds is accompanied by the formation of

a transverse fold which runs back from the junction of the larval head and prothorax (Figs. 203 and 204). During the change to the pupa the parts of the head, thus formed in the larva, assume their final exterior position by a process of eversion, with the result that the now evaginated folds form the wall of the imaginal head and carry the eyes and antennae with them.

In *Calliphora*, according to Weismann and van Rees (Fig. 205), the head becomes invaginated during the later embryonic period into the region which follows it, and its outwardly visible portion is reduced in the larva to a small apical papilla. The invaginated part of the head forms the so-called larval 'pharynx' and the true mouth opens into the posterior end of this pouch. A pair of cephalic buds extend as diverticula from the so-called pharynx to the cerebral ganglion (which is located in the metathorax), and the imaginal eyes and antennae develop from the inner wall of each sac. During the pupal stage the cerebral ganglion and cephalic buds move forwards until the former come to lie in the prothorax. At the same time the openings of the buds into the 'pharynx' widen, and ultimately both the pharynx and its diverticula become confluent, forming a single sac or *cephalic vesicle* (Fig. 205C). The latter is finally everted through the mouth of the pharynx, and becomes turned inside out to form the completed

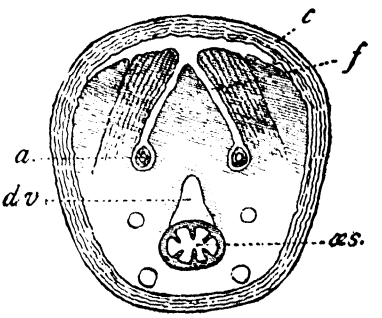


FIG. 203.—Transverse section through the junction of the head and prothorax of a *Chironomus* larva showing invaginations for imaginal head

c, larval cuticle; *f*, longitudinal fold; *a*, antenna of imago; *dv*, dorsal vessel; *oes*, oesophagus. *After* Miall & Hammond.

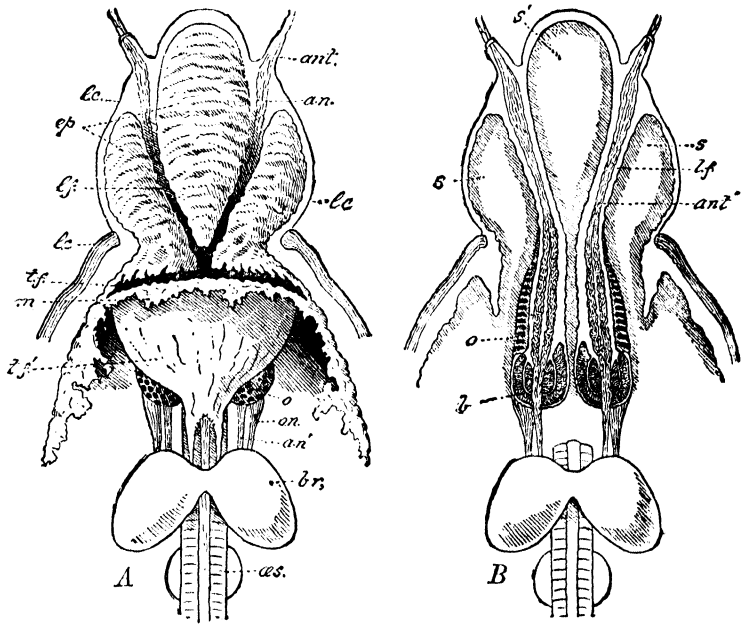


FIG. 204.—Formation of imaginal head in larva of *Chironomus*

A, The new epidermis thrown into folds which have been cut away in places. B, The same parts in horizontal section. *lc*, larval cuticle; *t.f*, transverse fold; *t.f'*, upper wall of ditto; *ep*, epidermis; *m*, cut edge of new epidermis; *ant*, larval antenna; *a.n*, nerve to ditto; *ant'*, antenna of fly; *l.f*, longitudinal fold; *o*, eye of fly; *on*, optic nerve; *a.n'*, root of antennary nerve; *br*, brain; *oes*, oesophagus; *b*, enlarged second joint (bulb) of antenna of fly; *s*, *s*, *s'*, blood-spaces. *After* Miall & Hammond.

imaginal head very much as in *Chironomus* (Fig. 205D). In the embryo of *Melophagus* Pratt states that the cephalic buds, which ultimately form the adult head, develop as paired dorsal and unpaired ventral thickenings which later on become

invaginated. The dorsal pair correspond to the cephalic buds of *Calliphora*: they are destined to form the dorsal and lateral portion of the imaginal head together with the compound eyes. The ventral cephalic bud has no counterpart in *Calliphora*: it forms the floor of the imaginal head together with the proboscis. Involution of the embryonic head takes place as in *Calliphora* and the cephalic buds become drawn into the secondary 'pharynx' thus developed (Fig. 206A and B). Owing to the early fusion of the dorsal buds the cavities of the latter open into the pharynx by a common connexion but they retain their paired formation posteriorly (Fig. 206, C and D). Finally the dorsal and ventral diverticula combine to form the cephalic vesicle, which subsequently becomes evaginated.

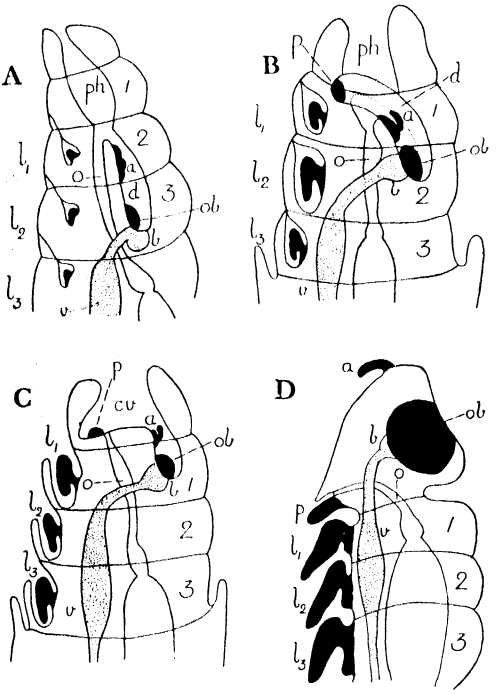


FIG. 205.—Development of imaginal buds in the Muscidae

A, larva; B–D, pupa. 1–3, thoracic segments; l_1–l_3, leg-buds; *ph*, 'pharynx'; *o*, oesophagus; *b*, brain; *cv*, cephalic vesicle; *v*, ventral nerve-centre; *d*, diverticulum of pharynx; *m*, mouth; *a*, antennal bud; *ob*, optic bud; *p*, proboscis rudiment. Based on Korschelt & Heider *after* Kowalevsky & van Rees.

The essential features of the development of the external form of the body in other orders proceeds very much after the manner described in Diptera. The imaginal buds, however, are not deeply invaginated as in the Muscidae, and the complex process which gives rise to the cephalic vesicle does not take place. Furthermore, the buds which form the pupal respiratory horns and caudal lamellae in *Anopheles* are unrepresented.

2. ALIMENTARY CANAL: The epithelium of stomodaeum and proctodaeum may pass from larva to adult with little change, as in the Coleoptera. In *Bombyx* (Verson, 1905) and *Malacosoma* (Deegener, 1908), this simple transition is supplemented by extension through the activity of cells which form the so-called imaginal rings at the inner ends of the stomodaeum and proctodaeum (cf. Fig. 207, *i*; Fig. 208, *a* and *c*). Finally, in *Mormoniella* (Tiegs, 1922) and the Cyclorrhaphan Diptera (Pérez, 1910; Robertson, 1936) the epithelium of the larval fore and hind gut is destroyed and replaced by cells proliferating from the imaginal rings and sometimes also from other centres. In all Endopterygotes the epithelium of the larval mesenteron is largely or entirely replaced. The remains of the old tissue is cast off into the lumen and a new pupal epithelium is formed either from the persistent replacement cells of the larval mid gut (Trichoptera, Lepidoptera, Diptera, Hymenoptera, many Coleoptera) or from histoblasts at the posterior end of the mesenteron, as in some Coleoptera (Mansour, 1927; 1934). In some insects there is a further destruction of the pupal epithelium and replacement to form the definitive adult mesenteron (e.g. *Cybister*—Deegener, 1904; *Leptinotarsa*—Patay, 1939).

3. MALPIGHIAN TUBULES: In the Diptera (Pérez, 1910), *Heterogenea* (Samson, 1908) and *Leptinotarsa* (Patay, 1939) the larval Malpighian tubules

are directly transformed into those of the adult without histolysis but in other species there is partial or complete destruction followed respectively by regeneration from replacement cells or the differentiation of new tubules from the extreme anterior end of the proctodaeum.

4. SALIVARY GLANDS AND SILK GLANDS: These glands degenerate and are

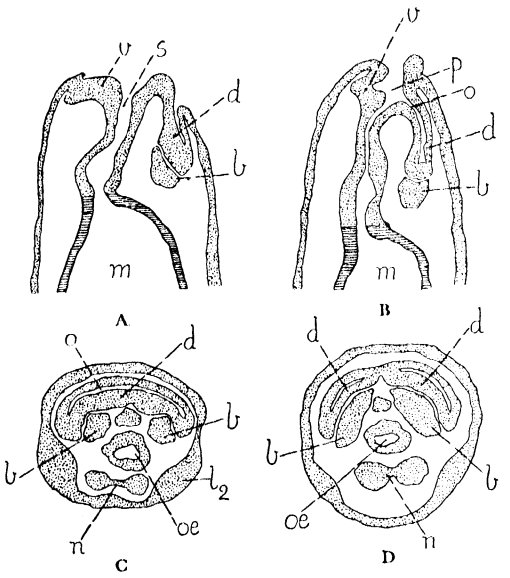


FIG. 206.—Development of the cephalic buds in *Melophagus* (ectodermal parts dotted, endodermal parts lined)

A, longitudinal section of an embryo when the dorsal buds become invaginated. B, later stage when the buds are drawn into the pharynx. C, transverse section of an embryo at stage B. D, do., taken further posteriorly. *b*, brain; *d*, dorsal cephalic bud; l_2, bud of 2nd leg; *m*, mesenteron; *n*, nerve-cord; *o*, mediar. opening of dorsal buds; *oe*, oesophagus; *p*, pharynx; *s*, stomodaeum; *v*, ventral cephalic bud. Adapted from Pratt, 1900.

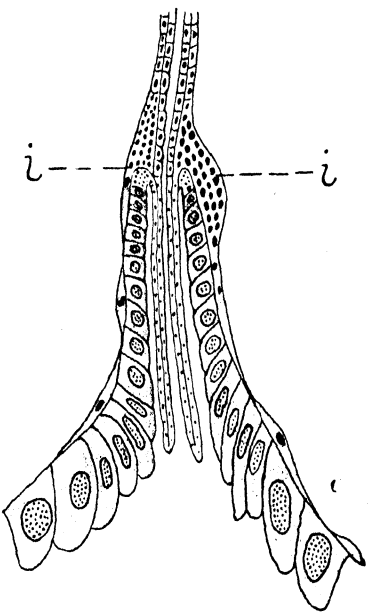


FIG. 207.—Median longitudinal section at the junction of fore and mid intestine of *Formica rufa*

i, annular imaginal bud of fore intestine. *After* C. Pérez.

usually destroyed by phagocytosis (Fig. 209). The imaginal glands are built up by a pair of annular buds situated at the junction of each gland with its duct (Fig. 208). In *Galerucella* Poyarkoff states that the new glands are formed as invaginations at the bases of the maxillae.

5. THE FAT-BODY: The extent to which the larval fat-body is destroyed is correlated with the extent of changes in the other tissues since its disintegration provides the materials necessary for histogenesis. In most Coleoptera there is little change in the larval fat-body whereas in *Calliphora* (Fig. 210) it is entirely replaced by imaginal tissue derived from mesenchyme on the inner surface of the hypodermis, the process being completed only after the emergence of the adult (Pérez, 1910).

6. OENOCYTES: Apparently a new imaginal complement is always formed by localized proliferation from the hypodermis, the larval oenocytes being histolysed.

7. TRACHEAL SYSTEM: The tracheal matrix cells are generally carried over from the larva without histolysis though modifications result from the proliferation of new branches and the opening of trunks to newly functional spiracles. Extensive replacement occurs in *Mormoniella* from special cells at the base of the larval spiracular trunks (Tiegs, 1922) and in *Calliphora*

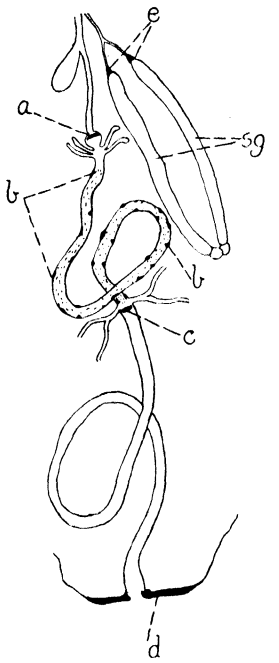


FIG. 208.—Alimentary canal and salivary glands (*sg*) of a Muscid larva showing imaginal buds

a, of fore intestine; *b*, of mid intestine; *c*, of hind intestine; *d*, of rectum; *e*, of salivary glands. *After* Kowalevsky.

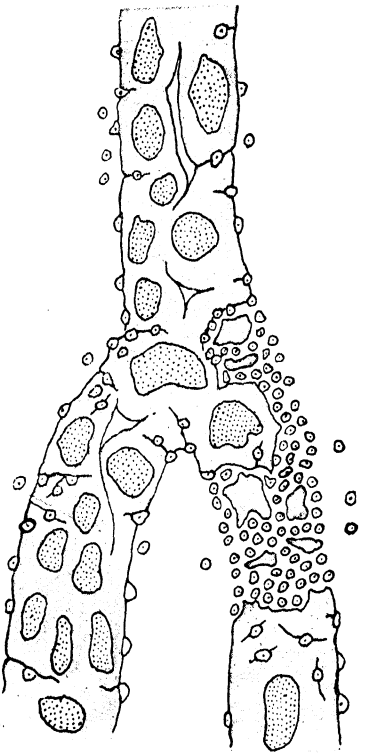


FIG. 209.—Histolysis of larval silk gland of *Formica rufa*

After C. Pérez.

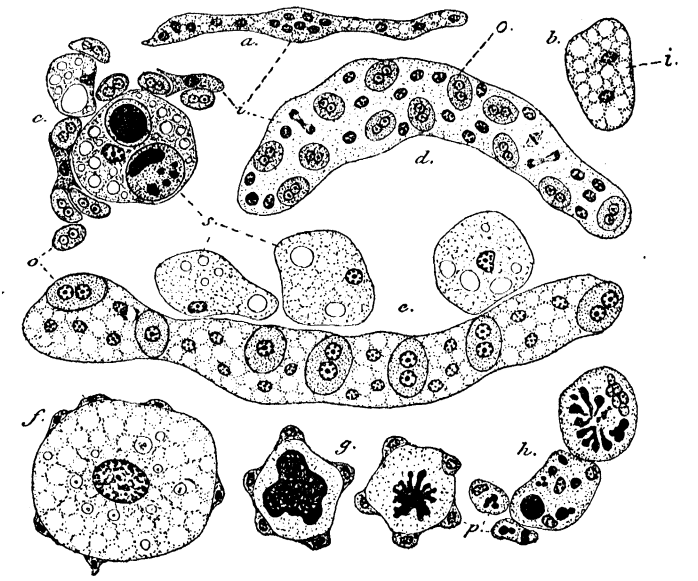


FIG. 210.—Origin of imaginal fat-body in *Calliphora*

a, *b*, in the head and thorax; *c–e*, in the abdomen in close relation with the imaginal oenocytes; *s*, granular spheres; *o*, oenocytes; *i*, initial cells of imaginal fat-body; *f–h*, destruction of remaining larval fat-body in the imago by phagocytes *p*. *After* C. Pérez.

some replacement is brought about by histoblasts scattered in the walls of the larval tracheae (Pérez, 1910).

8. DORSAL VESSEL: The dorsal vessel of the larva normally becomes that of the adult with very little change, the heart continuing to beat throughout pupation. In *Mormoniella* (Tiegs, 1922) there is degeneration of the larval cells and replacement from scattered histoblasts.

9. CENTRAL NERVOUS SYSTEM: The larval ganglia commonly become displaced by shortening of the connectives to give the more highly concentrated ventral chain of the adult. Little is known of the other changes though Bauer (1904) and Tiegs (1922) describe degeneration and reconstruction from neuroblasts.

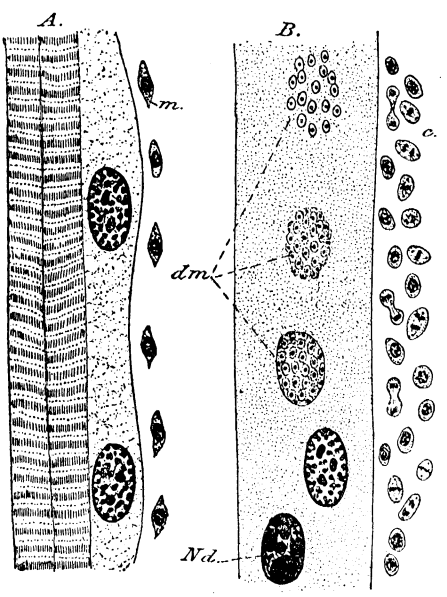


FIG. 211.—Metamorphosis of a muscle of *Calliphora* (semi-diagrammatic)

A, larval stage; *m*, myoblast. B, commencement of metamorphosis; *c*, mitosis of myoblasts; *dm*, multiple division of larval nuclei; *Nd*, degenerating nucleus. *After* C. Pérez.

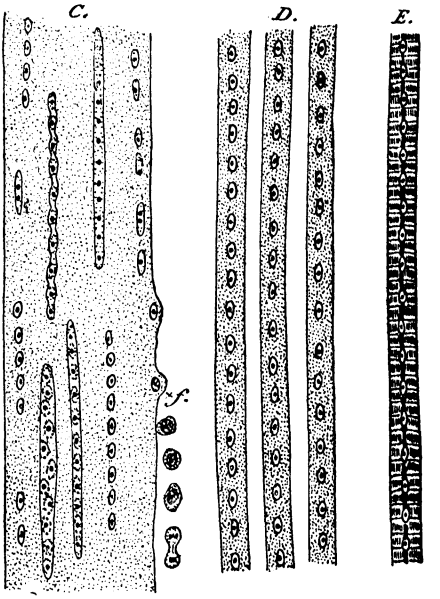


FIG. 212.—Metamorphosis of a muscle of *Calliphora* (later stages)

C, direct division, in chains, of imaginal nuclei; *f*, fusion of myoblasts with differentiated muscles. D, cleavage into separate fibres. E, final stage of imaginal muscle fibre. *After* C. Pérez.

10. MUSCULAR SYSTEM: There are great variations in the fate of this system at metamorphosis and different adult muscles arise in different ways. In general, five types of transformation may be recognized: (*a*) Some larval muscles pass unchanged into the adult; (*b*) some undergo reconstruction without complete histolysis to form the adult muscles; (*c*) some larval muscles are destroyed without replacement; (*d*) some are destroyed but replaced and (*e*) some muscles are peculiar to the adult and are formed for the first time in the pupa. The replacement muscles may arise either from small imaginal nuclei within or around the larval fibres (Coleoptera–Poyarkoff, 1910; Murray & Tiegs, 1935; Patay, 1939) or from myoblasts which previously lay freely outside the larval fibres (*Mormoniella*, Tiegs, 1922; Cyclorrhapha, Pérez, 1910). In *Calliphora* the adult muscles are either formed for the first time in the pupa by the aggregation and differentiation of previously scattered myoblasts or they arise through the reconstruction of larval muscles. The latter degenerate into a homogeneous mass which is then invaded by myoblasts and develops as shown in Figs. 211 and 212.

Postmetamorphic Development

Though the adult Pterygote insect does not moult it generally undergoes some further development after emergence. Coloration and hardening of the cuticle take a little time to be completed and in the majority of insects there is a period of some days during which the gonads and accessory reproductive glands attain their full size and become functional. In a few insects sexual maturity is accompanied by more striking changes. In the Isoptera (p. 376) the wings are shed, the mandibular and thoracic muscles degenerate and the ovaries undergo marked hypertrophy. Shedding of the wings also occurs in some Hippoboscidae and Streblidae and in the Zoraptera and Formicidae and degeneration of the thoracic muscles, with consequent loss of the power of flight, in some Aphididae and Culicidae (Johnson, 1953; Hocking, 1952). Physogastry, the distension of the abdomen by swelling of the ovaries or gut, is well shown in the flea *Tunga penetrans*, some Coccoidea, queen ants and many myrmecophile and termitophile Diptera and Coleoptera. The female of *Ascodipteron* (Streblidae) changes greatly in the adult stage (Jobling, 1939). After burying itself in the wound which its large mouthparts cause in its host (a bat), the legs and wings are cast off and a fold of the abdominal integument grows forward to surround the body, thus forming a flask-shaped structure. All that remains protruding from the body of the host is a small prominence bearing the spiracles and the conjoint opening of the rectum and vagina.

C. Physiology of Postembryonic Development

Two topics are discussed here, the hormonal control of growth and metamorphosis and the phenomenon of diapause.

(*a*) **Hormonal Control of Metamorphosis.**—As described on p. 173 the anterior part of the body of almost all insects contains a number of endocrine glands whose interacting secretions control postembryonic growth and differentiation in a way which is fundamentally very similar in both Hemi- and Holometabolan insects (Pflugfelder, 1952; Wigglesworth, 1954; Bodenstein, 1952). Both the growth and moulting of the larva or nymph and the final transformation into the pupa or adult require the presence of a 'growth and differentiation hormone'. This is secreted by the prothoracic glands or their analogues under the control of the neurosecretory cells of the brain. While the secretion of the corpora allata is also present in sufficient quantity, however, the latent imaginal characters (in respect of which the egg had already been determined) remain largely suppressed and development progresses through the normal series of larval or nymphal forms. In the last-instar nymph or larva the production of this 'juvenile hormone' by the corpora allata ceases temporarily and under the influence of the growth and differentiation hormone development is directed towards the formation of the adult. Experimental proof of this mechanism has been obtained in several ways. Thus, elimination of the brain prevents the growth and moulting of immature stages while extirpation of the corpora allata at an early developmental stage induces the premature appearance of adult characteristics. Again, the implantation of corpora allata from young nymphs of *Rhodnius* into mature nymphs causes one or two extra moults with a marked suppression of adult features. Furthermore the imaginal leg discs of mature blowfly larvae show little change when cultured in larval blood but unfold and differentiate when transferred to pupal blood.

(*b*) **Diapause.**—In a favourable environment the development of many insects will proceed without interruption and even if it is stopped temporarily by adverse conditions (e.g. low temperature) it is immediately resumed when these improve. On the other hand, many insects can, under certain conditions, pass into a state of diapause during which development is inhibited even though external circumstances appear suitable (Andrewartha, 1952). Diapause may consist merely of a retardation in growth for a few weeks or a cessation of development for several years but it is eventually 'broken' and the life-cycle then continues normally. Diapause occurs at a definite stage of the life-history which may be the egg, one of the other immature stages or the adult according to species. Some species enter diapause in every generation while others do so every other generation or less regularly; in some Lepidoptera different strains of the same species differ in this respect (e.g. *Bombyx mori*). Many external factors appear to be capable of inducing diapause, differing in different species and sometimes interacting. Unfavourable nutrition, desiccation and variations in illumination and temperature are variously known to be responsible. As their effects are often exerted some time before the onset of diapause and can even act through the female parent, the phenomenon often appears to originate with some semblance of spontaneity. During diapause there is a considerable depression of metabolism, the diapausing eggs of *Melanoplus*, for example, having only about a quarter of the normal oxygen requirement. This is probably connected with a disturbance of the cytochrome system since diapausing eggs of *Melanoplus* are relatively insensitive to hydrogen cyanide and pupae of *Platysamia* contain virtually no cytochrome C while in diapause. Diapause may be broken naturally or experimentally by a number of factors: exposure to low temperature is a common agent but mechanical injury and changes in illumination or water relations may also be effective, depending on the species. The immediate cause of postembryonic diapause is probably the absence of a growth hormone and Williams (see p. 178 for references) has shown that the diapause of *Platysamia* is broken by chilling, the effect of which is to stimulate the brain to produce a factor which activates the prothoracic glands whose secretion leads to renewed development.

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Part III

THE ORDERS OF INSECTS

THE CLASSIFICATION AND PHYLOGENY OF INSECTS

THE classification of insects has passed through many changes and with the growth of detailed knowledge an increasing number of orders has come to be recognized. Handlirsch (1908) and Wilson & Doner (1937) have reviewed the earlier attempts at classification and here we need only note that the foundations of a modern system were laid by Brauer (1885), who recognized the fundamental division of the class into two groups—the primitively wingless Apterygota and the winged or secondarily apterous Pterygota—and who also did much towards dividing the heterogeneous Neuroptera of older workers into sections of ordinal value. He did not, however, recognize the diversity of type within the Apterygota and included the Embioptera in his 'Orthoptera genuina' while his Corrodentia included Termites, Psocids and lice. Sharp (1899) did not allow the Dermaptera and Mecoptera the rank of orders but otherwise improved on Brauer's views by giving separate ordinal status to the Embioptera, Psocoptera, Isoptera, Mallophaga, Siphunculata and Strepsiptera. He also distinguished between the Collembola and the Thysanura but took the retrograde step of grouping together the secondarily apterous orders. Börner (1904) recognized the distinction between the ectognathous Thysanura and the entognathous Diplura and, except for his union of the Mallophaga and Psocids, produced a scheme which, with minor alterations, has been very widely employed (e.g. by Tillyard (1926) and in earlier editions of the present book).

In 1908 Handlirsch published a more revolutionary system, incorporating recent and fossil forms, which gave the Collembola, Thysanura and Diplura the status of three independent Arthropodan classes and considered as separate orders such groups as the Sialoidea, Raphidoidea, Heteroptera and Homoptera. He also split up the old order Orthoptera, gave its components ordinal rank and regrouped them with some of the other orders into a subclass Orthopteroidea and another subclass Blattaeformia. This system was modified somewhat by Handlirsch (1926) and as such has influenced Brues, Melander & Carpenter (1954), Weber (1933), Martynov (1938), Essig (1942) and Jeannel (1949). Handlirsch's recognition of the heterogeneous nature of the Orthoptera *sensu lato* is probably justified, but some of his other innovations seem less successful. Apart from the discovery since Handlirsch first wrote of the Protura, Zoraptera and Grylloblattidae, the most important other contribution to the major classification of insects has been that of Martynov (1925) who distinguished two groups of Pterygote insects which he named the Palaeoptera and Neoptera. The Palaeoptera—represented in the recent fauna by the Ephemeroptera and Odonata—are unable to flex the wings over the abdomen when at rest while all other recent orders form the Neoptera and possess such a wing-flexing mechanism (except for certain

Lepidoptera where it has been secondarily lost and for the secondarily apterous forms). Martynov (1938) has also subdivided the Neoptera into supra-ordinal groups but this aspect of his work is of less interest and in many respects his views are similar to those of Handlirsch.

The classification of recent insects adopted in this textbook is set out below; some of the problems involved are then discussed in connexion with the probable interrelationships of the orders recognized and the phylogeny of the class.

Subclass I: Apterygota. Apterous insects, the wingless condition presumed to be primitive. Metamorphosis slight or absent. Adult with one or more pairs of pregenital abdominal appendages. Adult mandibles usually articulating with the head-capsule at a single point.

Order 1. THYSANURA
Order 2. DIPLURA
Order 3. PROTURA
Order 4. COLLEMBOLA

Subclass II: Pterygota. Winged or secondarily apterous insects. Metamorphosis varied, rarely slight or wanting. Adults without pregenital abdominal appendages. Adult mandibles, unless highly modified, articulating with head-capsule at two points.

Division 1. **Exopterygota** (= **Hemimetabola**). Metamorphosis simple, sometimes slight. Pupal instar rarely present. Wings developing externally. Immature stages generally nymphs which usually resemble adults in structure and habits.

Order 5. EPHEMEROPTERA } Palaeopteran orders.
Order 6. ODONATA }

Order 7. PLECOPTERA
Order 8. GRYLLOBLATTODEA
Order 9. ORTHOPTERA
Order 10. PHASMIDA
Order 11. DERMAPTERA
Order 12. EMBIOPTERA
Order 13. DICTYOPTERA
Order 14. ISOPTERA
Order 15. ZORAPTERA
} Orthopteroid orders.

Order 16. PSOCOPTERA
Order 17. MALLOPHAGA
Order 18. SIPHUNCULATA
Order 19. HEMIPTERA
Order 20. THYSANOPTERA
} Hemipteroid orders.

Division 2. **Endopterygota** (= **Holometabola**). Metamorphosis complex and accompanied by a pupal instar. Wings developing internally. Immature stages are larvae which differ from adult in structure and habits.

Order 21. NEUROPTERA
Order 22. MECOPTERA
Order 23. LEPIDOPTERA
Order 24. TRICHOPTERA
Order 25. DIPTERA
Order 26. SIPHONAPTERA
} Panorpoid complex

Order 27. HYMENOPTERA
Order 28. COLEOPTERA
Order 29. STREPSIPTERA

The subclass Apterygota is a rather diverse, perhaps polyphyletic, assemblage, and only the Thysanura are likely to be near the main line of Pterygote evolution. It has even been argued that the other three Apterygote orders should not be regarded as insects at all. There seem, however, no satisfactory reasons for restricting the definition of the class so as to exclude them, though there is no doubt that they display some unusual features (e.g. the presence of only 9 postcephalic segments in the Collembola, the occurrence of anamorphosis in the Protura, the atypical tracheal system of the Diplura and the existence of flagellar muscles in the antennae of Diplura and Collembola). The primitive nature of winglessness in the Apterygota has also been disputed by Handlirsch and others who are inclined to regard them as neoteinic derivatives of winged forms, but the balance of opinion opposes this view and the Devonian *Rhyniella*, which is probably a Collembolan, certainly precedes all known Pterygote fossils.

Of the origins of the Pterygota, nothing certain is known but in the lower part of the Upper Carboniferous there are found the fossilized remains of the extinct orders Palaeodictyoptera (Fig. 41), Protodonata, Protoblattoidea and Protorthoptera (the latter two groups possibly connected by intermediates) together with wings of cockroaches (Dictyoptera: Mylacridae). The first two of these orders are regarded as Palaeopteran while the other three are Neopteran so that the primary phylogenetic bifurcation envisaged by Martynov must have occurred very early in the evolution of the Pterygotes. Later in the Upper Carboniferous, not only had the Palaeodictyoptera and Protodonata undergone further development (eventually to die out in the Permian) but two other entirely extinct Palaeopteran orders had arisen. These are the Megasecoptera, which persisted into the Upper Permian and the Protephemeroptera (Triplosobidae, Upper Carboniferous). Though the connexions of the Protephemeroptera and Protodonata with the recent Palaeopteran orders Ephemeroptera and Odonata are not entirely clear, it is at least likely that each of the extinct orders had a common origin with the corresponding recent forms. The gigantic Meganeuridae of the Upper Carboniferous and Lower Permian are probably to be regarded as among the earliest Odonata, though by some workers they are held to be Protodonata, while the Ephemeroptera arose in Lower Permian times. The Protohemiptera, represented by *Eugereon* (Lower Permian) is the last of the Palaeopteran orders; in spite of its name and the presence of elongate, presumably sucking, mouthparts, it has no close affinities with the Hemiptera. The recent Palaeoptera are thus seen to be the survivors of a relatively large and varied Palaeozoic fauna and though they share the archaic features of lacking a wing-flexing mechanism and retaining the anterior median wing-vein, they differ considerably in many other respects.

Turning now to the Neopteran line of descent, one sees that the Carboniferous strata contain only representatives of what may be considered broadly as an Orthopteroid group of insects—i.e. the Protoblattoidea, Dictyoptera and Protorthoptera. Viewed from the standpoint of the anatomy of recent forms, the Orthopteroid orders include the Dictyoptera, Isoptera, Zoraptera, Grylloblattodea, Orthoptera, Phasmida, Plecoptera, Dermaptera and Embioptera. They form an Exopterygote complex characterized by, or easily derivable from forms characterized by: (i) Unmodified mandibulate mouthparts; (ii) presence of a large anal lobe in the hind wing; (iii) presence of cerci; (iv) presence of numerous Malpighian tubules and (v) presence of several separate ganglia in the ventral nerve-cord. Of these orders, the Dictyoptera

probably had a common ancestry with the Protoblattoidea and though the latter died out in the Upper Carboniferous, the rich Palaeozoic Blattoid fauna gave rise to modern descendants. The anatomy of recent Mantids shows that they are undoubtedly close relatives of the cockroaches, but as the earliest indubitable fossil Mantids date only to the early Tertiary the details of their origin remain obscure. Comparative anatomy also makes it very probable that the Isoptera were originally little more than cockroaches which adopted a peculiar mode of social organization but the fact that no pre-Tertiary Isopteran fossils are known makes their precise origin uncertain. Tillyard (1937) has shown, however, that the mode of folding of the hind wing of *Mastotermes* resembles that of Palaeozoic cockroaches rather than recent ones. On anatomical grounds (Delamare-Debouteville, 1952), there is also some reason for allying the Zoraptera with the Dictyopteran-like forms, but no fossil Zoraptera are known and their affinities require further study.

Reverting to the Protorthoptera, it is likely that this order, which persisted only into the Upper Carboniferous, represented a stock from or near which arose, on the one hand, the Plecoptera and on the other the Grylloblattodea, Phasmida and Orthoptera (*s. str.*). The Plecoptera, which appeared first in the Upper Permian with forms referable to the still extant Eusthenidae, probably had as their immediate ancestors the order Protoperlaria (Lower–Upper Permian). The Grylloblattodea, known only from recent species, are certainly an unusually primitive group but no clear connexions between them and the Orthoptera are known, the latter order dating back to the Upper Carboniferous (Oedischiidae and Sthenaropodidae). The position of the Phasmida is obscure owing to the poor fossil record and it is the somewhat isolated position which they occupy among Orthopteroid insects which is the main justification for according them ordinal rank. Two further Orthopteroid orders which need consideration are the extinct Protelytroptera (Lower Permian) and the Dermaptera; these may be allied to each other but neither can yet be related satisfactorily to the Dictyopteran or Orthopteran lines of descent. Finally, the position of the Embioptera is also obscure though a Lower Permian form not unlike the recent *Clothoda* is known. So far as the recent orders are concerned, therefore, the more primitive Exopterygota form a group of Orthopteroid orders within which can be discerned (i) a Dictyopteran line of evolution (Dictyoptera, Isoptera and possibly Zoraptera), (ii) an Orthopteran line (Grylloblattodea, Orthoptera and Phasmida with the Plecoptera as a more isolated branch) and (iii) two orders—Dermaptera and Embioptera—which cannot readily be placed in the system.

The remaining Exopterygote orders are all extant today and form, on anatomical grounds, what might be called a Hemipteroid group defined, perhaps rather unsatisfactorily, as those which (i) possess specialized mandibulate or suctorial mouthparts; (ii) lack a large anal lobe in the hind wing; (iii) lack cerci; (iv) possess only a few Malpighian tubules and (v) show a more or less highly concentrated group of ganglia in the ventral nervous system. The distinction between the Hemipteroid and Orthopteroid groups is not sharp because the Zoraptera have a reduced wing-venation, few Malpighian tubules and a somewhat concentrated nervous system. Both anatomically and on palaeontological grounds, the Psocoptera may be regarded as the basal Hemipteroid stock, appearing first in the Lower Permian. Directly connected with them—though fossil lice are lacking—are the Mallophaga, which share with the Psocoptera a unique type of hypopharynx. The Siphunculata, in turn, are probably closely related to the Mallophaga, which

they resemble not only in many features of external and internal anatomy and in habits, but also in spiracular structure and in the mode of hatching from the egg. It may, indeed, be questioned whether the two groups of lice should not be united in a single order, but the great differences in the structure of the mouthparts are here held to justify the separation. The Hemiptera are first known from the Lower Permian, where Homopteran wings similar to those of Permian Psocoptera have been found. Many Homopteran families are known from the Permian and Mesozoic and Heteroptera—which, on the whole, are more specialized than the more primitive Homoptera—appear first in the Upper Triassic. The affinities of the remaining Hemipteroid order, the Thysanoptera, are obscure, though alleged representatives are known from the Permian.

In considering the Endopterygote insects one is faced immediately with the question of whether they are, in fact, a monophyletic group since the Hymenoptera and Coleoptera (with Strepsiptera) present considerable difficulties mentioned below. The remaining orders, however, since the classical work of Tillyard (1918–20; 1935) are generally considered to form the Panorpoid complex which is centred on the Mecoptera with the Neuroptera forming a somewhat distinct but related branch. Considering first the Neuroptera, there is no doubt that the Megaloptera (Upper Perm.–Rec.) include some of the most primitive recent Endopterygotes but the erection by Handlirsch of three separate orders to accommodate the Sialoidea, Raphidoidea and Plannipennia hardly seems necessary. The Mecoptera are first known from the Lower Permian and it is likely that from their primitive members there arose on the one hand the Diptera (with an unforked Cu_1) and on the other the Lepidoptera and Trichoptera with a terminally forked Cu_1. The position of the Micropterygidae is interesting in this connexion since although traditionally classed with the Lepidoptera, its members are actually more primitive than any other known Lepidoptera or Trichoptera and Hinton (1946) has therefore urged that it be given the rank of a distinct order (Zeugloptera). The Siphonaptera are very distinct in their imaginal structure but the larvae are not unlike those of some Nematoceran Diptera (Mycetophilidae) and it is likely that if not of early Dipteran origin they are at least derived from a Panorpoid stock.

With the Hymenoptera, Coleoptera and Strepsiptera one reaches unsolved phylogenetic problems, to which palaeontology has contributed very little since the few Mesozoic Symphytan wings are already relatively specialized and the fossil remains of the earliest (Lower Permian) beetles are mostly fragmentary elytra, impossible to relate to more generalized orders. Handlirsch attempted to derive the Hymenoptera from Protorthopteran stock, but his arguments are not convincing and the similarity of Symphytan larvae to those of Panorpoid insects, together with the fact that the wing-venation of the Symphyta can, without great difficulty, be derived from a Megalopteran pattern, inclines many to regard the Hymenoptera as having had a common ancestry with the Neuroptera and other Panorpoid orders. The Coleoptera have also been thought to have arisen independently of the other Endopterygote insects (either from a Protoblattoid-like stock or some earlier group) but there is little real evidence for this and other authorities favour a derivation from Neuropteran-like ancestors. The Strepsiptera (with no pre-Tertiary fossils) are generally considered to be related to the Coleoptera (in particular, to the Meloidae and Rhipiphoridae) though others have denied this and allied them to the Hymenoptera.

The above account is necessarily somewhat superficial and dogmatic. For a fuller account of the diverse views on phylogeny and fossil insects one should refer to Handlirsch (1908; 1937–39), Zeuner (1939), Martynov (1938, etc.), Laurentiaux (1953) and Hennig (1953), and to numerous papers published by Tillyard between 1917 and 1937 and by Carpenter from 1926 onwards.

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SUBCLASS: APTERYGOTA

THE Apterygota are universally distributed but, owing to their small size and concealed habits, probably the majority of the world's species have so far escaped discovery. About 2,300 species are known: without exception they are wingless insects and there is every reason to believe that this apterous condition is of a primitive and not a secondary origin. As a rule they retain the superlinguae in a more generalized condition than other insects, and the presence of pregenital abdominal appendages is a very characteristic feature. Except in the Lepismatidae the mandibles usually have only a single articulation with the head-capsule. Metamorphosis is always of a very slight and gradual nature or is more often absent. It is principally by a comparative study of some members of this subclass that it is possible to trace the origin and affinities of the Insecta as a whole. For a bibliography and general discussion of the Apterygota, reference should be made to papers by Crampton (1916), Imms (1936), Ewing (1942) and Wygodzinsky (1943). The extreme paucity of fossils in this group makes the study of its phylogeny rather speculative but it seems likely that the Apterygota is a somewhat heterogeneous assemblage of orders and that only the Thysanura are at all closely related to the Pterygote insects.

Order 1. **THYSANURA** (Bristle-tails)

Apterygota with ectognathous mouthparts, adapted for biting. Antennae many-segmented, but only the basal segment provided with muscles. Compound eyes present or absent. Tarsi with 2–4 segments. Abdomen 11-segmented with a variable number of lateral, styliform, pregenital appendages, a pair of many-segmented cerci and ending in a segmented median process. Tracheal system and Malpighian tubules present. Metamorphosis slight or wanting.

This order includes the most primitive of all insects and is very widely distributed; about 23 species have been found in the British Isles out of a total of about 350. Its members are ancient survivals of a formerly more extensive group and persist today largely owing to a concealed life in the soil, in rotting wood, under stones, or in the leaf-deposits of forest floors; a considerable number also live in the nests of ants and termites. Unlike many Collembola they are not usually found among living herbage. The 'silverfish', *Lepisma saccharina* (Fig. 213) and *Ctenolepisma longicaudata* occur in buildings in many parts of the world where they are destructive to paper, book-bindings, etc., while *Thermobia domestica* frequents the warmth afforded by bakehouses and kitchens. *Petrobius maritimus* (Fig. 214) inhabits rocky places on the British coasts, close to the edge of the sea. Although the order includes a number of minute forms, the majority of species attain a larger size than is found in the Collembola, though they do not exceed 2 cm. in length. Most species are brownish, grey or white in colour, and the scaled forms exhibit a metallic sheen.

External Anatomy.—The body is more or less spindle-shaped in outline, depressed in the Lepismatidae and somewhat compressed in the Machilidae. It is clothed with scales except in some Lepismatidae. The antennae are long and filiform, often consisting of 30 or more segments, the absence of muscles in the flagellar segments distinguishing them from those of the Diplura (Imms, 1939). Compound eyes are well developed in the Machilidae

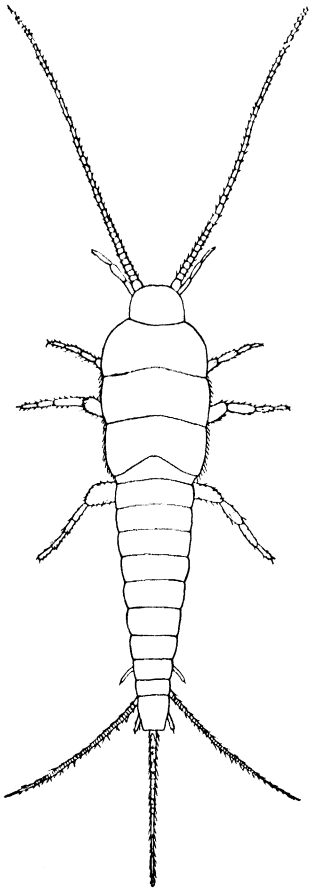


FIG. 213.—*Lepisma saccharina* (magnified). Britain
After Lubbock.

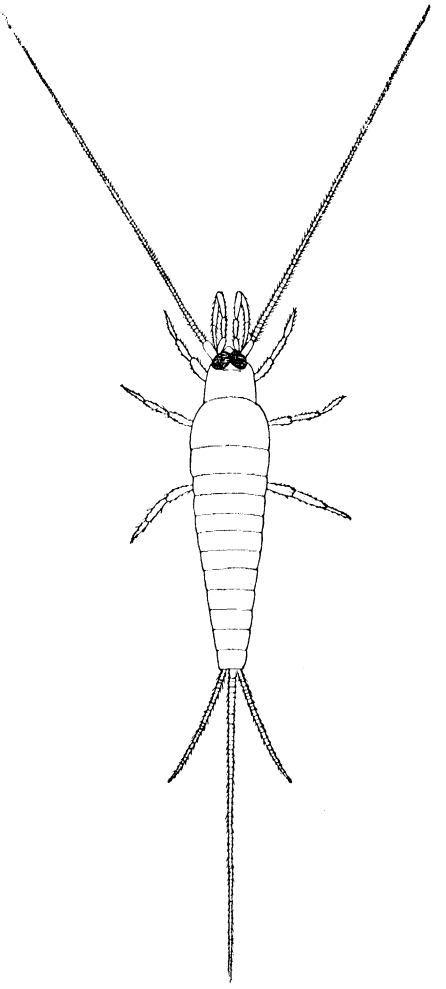


FIG. 214.—*Petrobius* (*Machilis*) *maritimus* (magnified). Britain
After Lubbock.

where they are approximated or contiguous dorsally, but in the Lepismatidae they are considerably reduced. The latter family also lacks ocelli but in the Machilidae median and paired organs of this nature are evident. They are variable in form but as the retinal cells form small groups surrounding a rhabdom-like structure they have been regarded as intermediate between simple and compound eyes (Hanström, 1940; Marlier, 1941). The head (Chaudonneret, 1951) often exhibits the epicranial suture and both the labrum and clypeus are well developed. The mouthparts (O'Harra & Adams,

1942; Chaudonneret, 1949) are normal and exserted and in *Petrobius*, which is selected as an example, they are of a primitive type (Fig. 11). The mandibles are elongated, pointed organs, with a transverse strengthening ridge which gives them a 2-segmented appearance and are each provided with a well-defined projecting molar area. In their general features they closely resemble those of certain of the higher Crustacea. The superlinguae are exceptionally well developed: each organ is attached by membrane to the base of the hypopharynx, and exhibits differentiation into two lobes together with a vestigial palp-like appendage. The maxillae are composed of the typical sclerites and their palpi are 7-segmented. In the labium the mentum and submentum are broad plates, the prementum is paired, and the palpi are 3-segmented. Paired glossae and paraglossae are present and the latter are longitudinally subdivided into three lobes. In *Lepisma* the mandibles are each provided with two cephalic articulations instead of the one found in Machilidae and in the labium the glossae and paraglossae are single organs on either side.

The legs have 3 tarsal segments in the Machilidae and 2–4 in the Lepismatidae; paired pretarsal claws are always present. In some Machilidae (Fig. 215) the coxae of the 2nd and 3rd pairs of legs each bear a small, movable, unsegmented style, but in other members of this family they are absent or occur only on the posterior pair of legs.

The abdomen is composed of 11 segments. The 10th segment is reduced and bears no appendages while the 11th is also small but carries the cerci and its tergum is prolonged into the median cerciform appendage. The abdominal sterna (Fig. 215) are exhibited best on the pregenital segments (1–7 inclusive) where each may be divided transversely, as in *Nicoletia*, or be composed of a small triangular sternum with, in some cases, a pair of laterosternites. Typically, each segment possesses a pair of laterally placed appendages made up of a basal, plate-like coxite and a small terminal style. These appendages are probably serial homologues of the thoracic legs but the extent to which they are developed varies considerably in different genera. In the Machilidae coxites and styles are present on segments 2–9 inclusive but styles do not occur on the 1st segment. In the Lepismatidae styles are found on segments 2–9 in *Nicoletia* but other genera have fewer, *Lepisma* and its allies rarely having more than 3 pairs (segments 7–9). In some cases the coxites are fused with the sternal plate to form a compound coxosternum. Each appendage of the pregenital segments may be provided medially with one or two *eversible vesicles* (Fig. 215). The latter can be extended by blood-pressure and retracted by special muscles: their function is uncertain but may conceivably be

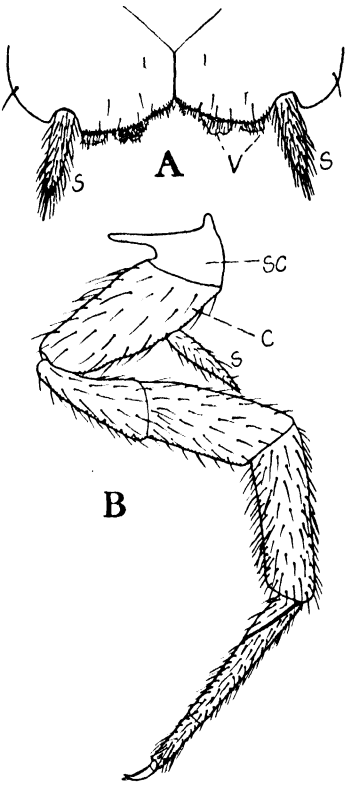


FIG. 215.—*Petrobius maritimus*. Britain

A, hind margin of 5th abdominal segment showing vesicles *v* and styli *s*. B, left leg of 3rd pair; *c*, coxa; *s*, stylus; *sc*, subcoxa.

respiratory. The vesicles are absent from many Lepismatidae but *Nicoletia* has 6 pairs (segments 2–7). They are always present in Machilidae (almost invariably on segments 1–7) and in some genera (e.g. *Machilis* and *Petrobius*) segments 2–5 each carry two pairs.

The 8th and 9th abdominal segments are modified through the development of external *genitalia* (Figs. 47 and 50). In the female, both segments bear a pair of coxites and styles and articulated basally with each coxite is a long, annulated gonapophysis. The four gonapophyses fit together to form the ovipositor. In the male the genital segments likewise usually possess a pair of coxites and styles and in a few Machilids (e.g. *Machilis*) there is a pair of small gonapophyses on the 8th segment. In all other cases, however, it is only the 9th segment of the male which bears a pair of small gonapophyses ('parameres') and between them lies the median penis. The genitalia of the Thysanura are of considerable morphological interest because of the light they are believed to throw on the homologies of these organs in Pterygote insects (Gustafson, 1950).

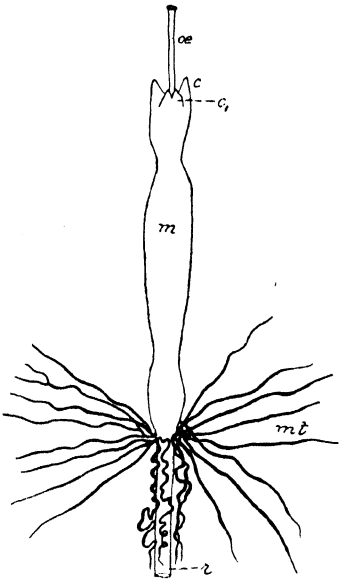


FIG. 216.—Alimentary canal of *Petrobius*

oe, oesophagus; *c*, large coeca; c_1, smaller do; *m*, mid intestine; *mt*, Malpighian tubes; *r*, rectum. *After* Oudemans.

Internal Anatomy. — The *alimentary canal* (Fig. 216) is a simple straight tube, except in *Lepisma* where the hind intestine presents a single convolution. There is a large gizzard in *Lepisma* and in this genus and in *Machilis* enteric caeca are present. Salivary glands appear to be universally present while the Malpighian tubes are well developed and number 12 to 20 in the Machilidae, and 4 to 8 in the Lepismatidae. The *nervous system* (Hilton, 1917) is exhibited in a generalized condition since there are 3 thoracic and 8 abdominal ganglia, and the longitudinal connectives retain their double nature throughout the length of the ventral nerve-cord (Fig. 68A). The *tracheal system* exhibits differences in the two families. In the Machilidae there are 9 pairs of spiracles: the 1st pair is located between the pro- and mesothorax, the 2nd pair is placed near the hinder border of the mesothorax, and the remaining pairs are placed on the 2nd to 8th abdominal segments. The tracheae associated with most spiracles remain unconnected with those of adjacent segments. In the Lepismatidae there are 10 pairs of spiracles which belong to the 2nd and 3rd thoracic and the first 8 abdominal segments. In this family the tracheal system is relatively highly developed; there is a common longitudinal tracheal trunk passing down either side of the body, and there is a transverse trunk in each segment uniting the tracheae of opposite sides (Sŭlc, 1927).

The *heart* in *Machilis* (Bär, 1912) extends from the 10th abdominal segment into the mesothorax, passing anteriorly into the aorta. There are 11 pairs of dorsally situated ostioles and, in the 8th and 9th segments, two pairs of ventral ones. 11 pairs of alary muscles are said to be present.

The *reproductive system* (Fig. 217) exhibits some differences in the two families. In the female, the panoistic ovarioles number 5 on each side in

Lepismatidae and 7 in Machilidae. In the latter family the ovarioles join a lateral oviduct one behind the other so as to present a metameric appearance, though a strict segmental disposition does not seem to be preserved. The two oviducts join to form a short vagina which, according to Gustafson (1950) opens behind the 7th abdominal segment in *Lepisma* and *Neomachilis* and behind the 8th in *Nicoletia*. In the Lepismatidae a spermatheca and a pair of accessory glands (unpaired in *Nicoletia*) are present, but the Machilidae do not possess them. In the male the testes comprise a group of lobes, each apparently made up of several follicles. The number of lobes varies considerably (many in *Nicoletia*, 6 in *Lepisma*, 3 in *Petrobius*). The vasa deferentia are more or less convoluted and in *Petrobius* each is double throughout the greater part of its length, the two canals thus formed being united by a series of 5 transverse connecting tubes (Fig. 217, A). According to Gustafson (1950) in *Lepisma* and *Ctenolepisma* the vasa deferentia of opposite sides do not join but extend separately into the penis on which they open by a pair of gonopores. In other cases there is a short median ejaculatory duct.

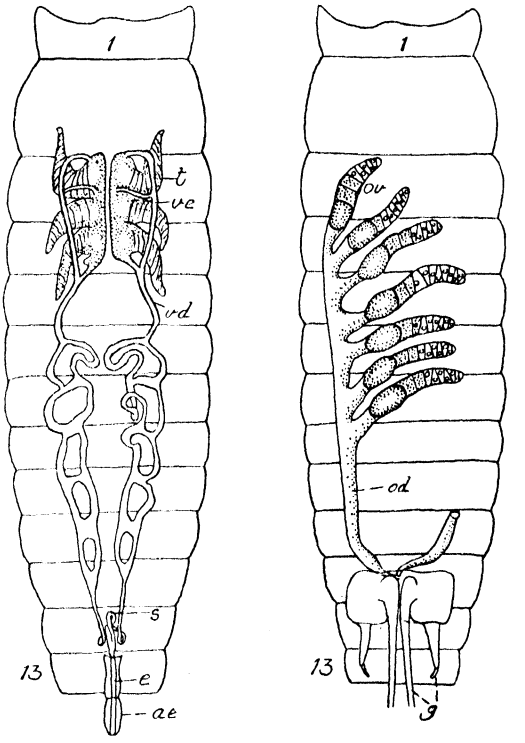


FIG. 217.—Reproductive organs of *Petrobius*. Ventral side

A, male; B, female. 1, 1st thoracic segment; 13, 10th abdominal do.; *t*, testis; *ve*, vas efferens; *vd*, vas deferens; *e*, ejaculatory duct; *s*, blind sac; *ae*, aedeagus; *ov*, ovariole; *od*, oviduct; *g*, genitalia. Adapted from Oudemans.

Postembryonic Growth.—Postembryonic development has been studied in the Machilidae by Heymons & Heymons (1905) and by Verhoeff (1910; 1911). There appear to be at least six instars, including the adult, and in the first two the young insects are devoid of scales, the genitalia are as yet undeveloped, and there are no styli on the thoracic coxae. In the third instar scales are evident and small coxal styli are present. In the fourth instar the gonapophyses are apparent, though short, and in the female their jointed character does not develop until later. Other changes are evident in the mouthparts, and the completed details of their structure are not assumed until after the final ecdysis. The changes undergone are less profound than those of the Orthoptera, but their simplicity is largely correlated with the absence of wings. The postembryonic growth of the Lepismatidae has been investigated for *Thermobia domestica* by Sweetman & Whittemore (1937) and Sweetman (1938) and for *Ctenolepisma longicaudata* by Lindsay (1940). Both species agree in moulting regularly throughout their long life (up to seven years in *Ctenolepisma*). *Thermobia*,

which moults every 12–13 days at 37° C., may thus have 45–60 instars although sexual maturity is reached after about 12 moults. At each moult the cuticular lining of the spermatheca is lost, together with its contents, so that copulation has to occur in each adult instar in order that fertile eggs may continue to be laid. The early nymphs have no scales, no abdominal styles and no external genitalia.

Literature: Apart from the references quoted in the text the following deal with the morphology and systematics of the Thysanura. General: Grassi (1888), Wygodzinsky (1941). Machilidae: Oudemans (1888). Lepismatidae: Escherich (1904). For the British species, see Delany (1954).

Classification.—The order is divisible into two families as follows:

FAM. 1. MACHILIDAE.—*Compound eyes large, ocelli present. Abdominal segments 1–7 with exsertile vesicles: styli usually present on thoracic coxae and on abdominal segments 2–9. Petrobius, Machilis, Praemachilis,* etc.

FAM. 2. LEPISMATIDAE.—*Compound eyes small, ocelli absent. Abdomen usually with exsertile vesicles: styli absent from thoracic coxae and usually present on abdominal segments 7–9, or 8–9. Lepisma, Acrotelsa, Nicoletia,* etc.

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Order 2. **DIPLURA**

Apterygota with entognathous mouthparts. Antennae many-segmented, flagellar segments provided with muscles. Compound eyes and ocelli absent. Tarsi 1*-segmented. Abdomen with lateral styliform appendages on most or all of the pregenital segments and ending in paired cerci of variable form. Terminal median filament absent. Tracheal system present; Malpighian tubules vestigial or absent.*

Like the Thysanura, with which they were formerly united in a single order, the Diplura are a group of widely distributed insects living in concealed situations under stones, in dead wood, among fallen leaves or in soil. The Campodeidae are well represented in the Holarctic region while the other two families occur mainly in the tropics and subtropics of all regions. About 400 species are known, of which 11 species of *Campodea* (Fig. 218) are British (Delany, 1954). The Diplura are usually small insects, the largest forms occurring in the genus *Heterojapyx* (Fig. 219) where *H. soulei*, for example, measures up to 50 mm. in length.

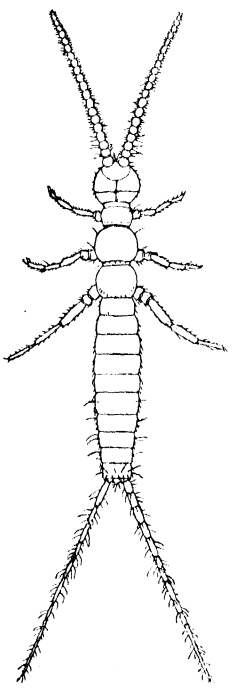


FIG. 218.—*Campodea* (× *circa* 15). Britain
After Lubbock.

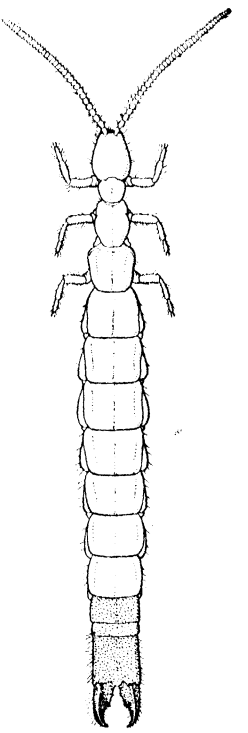


FIG. 219.—*Heterojapyx* sp. Australia (× 3)

External Anatomy.—The integument is generally thin and pale and scales occur only in a few Campodeidae (e.g. *Lepidocampa*). The head-capsule is oval or quadrangular in outline and is subdivided in some forms by epicranial and postoccipital sutures while the clypeus and labrum are distinct sclerites. The antennae are more or less elongate structures with 20 to 40 or more segments, all except the last being provided with intrinsic muscles (Imms, 1939). The reduced mouthparts (Fig. 220) are partially sunk into the head-capsule and resemble those of the Collembola (Snodgrass, 1952). The mandibles are elongate, apically toothed structures with a conical base fitting loosely into a corresponding socket on the head-capsule and in *Campodea* and

the Projapygidae a prostheca is present. In the maxilla the cardo is small, the stipes rather elongate and a small 1- or 2-segmented palp is also found. A lacinia and galea can be recognized, the former often serrated. The labium is sub-divided into pre- and postmentum and bears a pair of small papilla-like palps (absent in *Parajapyx*) and a ligula which is divided into glossae and paraglossae. Lateral to the prementum is a pair of sclerites of uncertain homologies—the admental plates of Silvestri (1933). A well-developed hypopharynx occurs with large superlinguae.

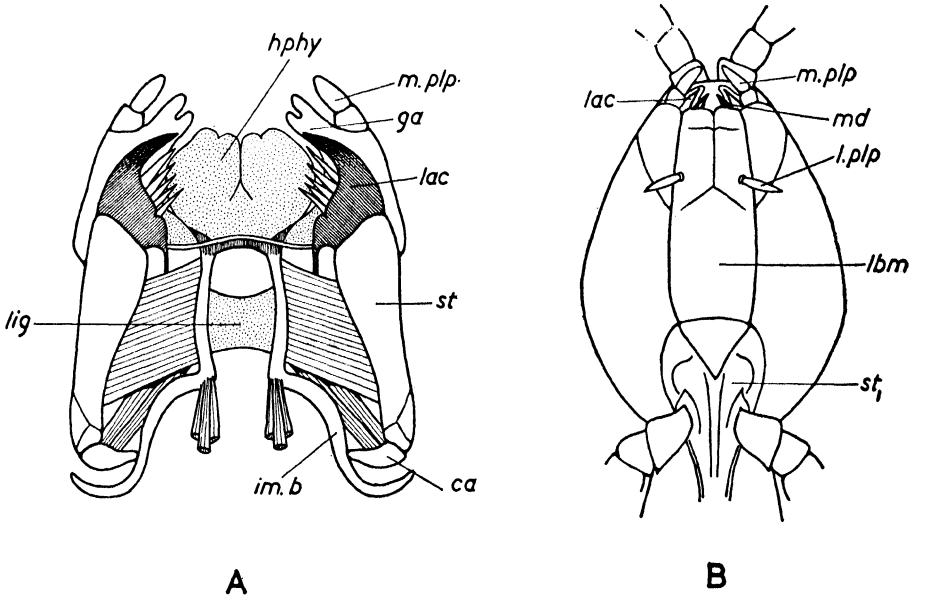


FIG. 220.—Mouthparts of *Heterojapyx* (*after* Snodgrass, 1952). A. Maxilla & Hypopharynx. B. Ventral view of head.

ca, cardo; *ga*, galea; *hypy*, hypopharynx; *im.b*, intermaxillary brachium; *lac*, lacinia; *lbm*, labium; *l.plpi*, labial palp; *lig*, interbrachial ligament; *md*, mandible; *m.plp*, maxillary palp; st_1, first thoracic sternum; *stp*, stipes.

The 3 thoracic segments are clearly separated, the prothorax being the smallest (Verhoeff, 1903). The sterna and sometimes also the terga are subdivided by transverse sutures but there is no general agreement on the homologies of the sclerites so delimited. The pleural sclerites are reduced but indications of the primitive anapleural and coxopleural arcs are to be seen in some genera. The 3 pairs of legs differ little, the tarsi are 1-segmented and there are usually 2 pretarsal claws, though an additional median claw-like appendage occurs in *Japyx*, *Anajapyx* and *Lepidocampa*.

The abdomen is composed of 10 well-developed segments and a small 11th segment which bears the cerci. The abdominal sterna, at the front of which narrow transverse presternites are sometimes delimited, bear a variable number of lateral styliform appendages. These occur on segments 1–7 in the Japygidae and Projapygidae and on 2–7 in the Campodeidae, the 1st segment in the latter family being provided with a pair of larger, lobe-like appendages which may show sexual differences. Paired eversible vesicles resembling those of the Thysanura are found on the 2nd to 7th abdominal segments of the Campodeidae and *Anajapyx*, on the 2nd and 3rd sterna of *Parajapyx* and on the 2nd alone in other Japygids; in *Projapyx* there are no vesicles. In some

Japygidae the cuticle of the 1st abdominal segment is differentiated just medial to the styles to form a pair of setose 'subcoxal organs' between which may lie an unpaired glandular structure. External genitalia are absent or vestigial in the Diplura. The cerci assume very different forms in the three families. In the Campodeidae they are long, many-segmented, antenna-like structures and the Projapygidae also retain segmented cerci though they are here short, robust organs perforated apically by the opening of a gland. In the Japygidae the cerci are represented by stout, strongly sclerotized forceps which the insects use in catching their prey (Kosaroff, 1935).

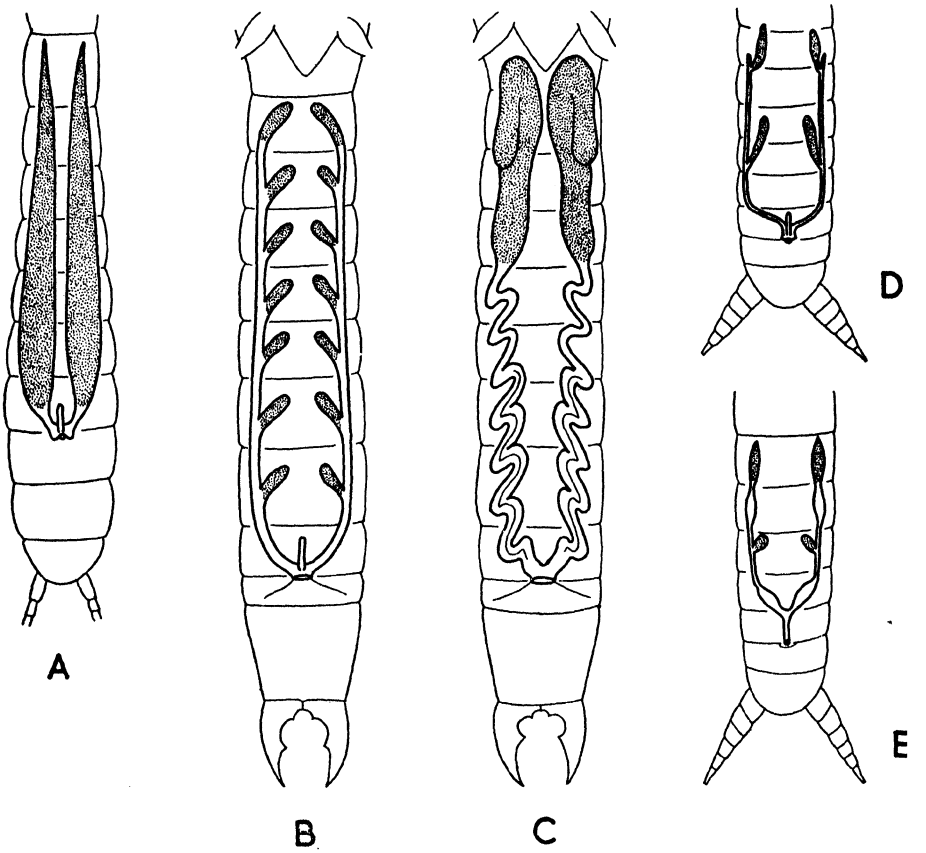


FIG. 221.—Reproductive systems of Diplura. A. Female *Campodea*. B. Female *Japyx*. C. Male *Japyx*. D. Female *Anajapyx*. E. Male *Anajapyx*. (Based on Grassi and Silvestri)

N.B. The gonads are stippled, the efferent ducts unshaded.

Internal Anatomy.—The *alimentary canal* is a straight tube. In *Anajapyx* the mid gut is very short but the oesophagus is of great length, extending into the 4th abdominal segment. *Campodea* has a large rectum which can be extended by dilator muscles. Philiptschenko (1908) distinguishes a number of paired cephalic glands (4 in *Campodea*, 3 in *Japyx*) the functions of which are uncertain but at least one pair may be salivary while another—the so-called tubular glands similar to those of Collembola and Thysanura—are probably excretory ('labial kidneys'). Malpighian tubules are represented in some Diplura by small papillae of which *Campodea* has 16, *Projapyx* 5 and *Anajapyx* 6, but in *Japyx* these structures are entirely absent.

The *nervous system* shows little concentration, the ventral cord comprising 8 ganglia in *Japyx* and 7 in *Campodea* and *Anajapyx*. A sympathetic nervous system with paired corpora cardiaca and corpora allata has been described in *Japyx* by Cazal (1948) (see also Hanström, 1940). The *respiratory* system shows several unusual features. In *Campodea* it is poorly developed and opens by means of 3 pairs of thoracic spiracles (2 on the mesothorax and 1 on the metathorax). The tracheae from each spiracle remain unconnected with those from the others, the tracheal intima lacks spiral thickenings (Marten, 1939) and the whole system is said to be absent from newly-hatched nymphs. Abdominal spiracles are absent in *Campodea*. In *Heterojapyx* and *Japyx solifugus* (Fig. 107) there are 11 pairs of spiracles, of which 4 are thoracic and 7 abdominal. The 1st, 2nd and 4th pairs correspond with the 3 pairs of thoracic spiracles of *Campodea*: the 3rd pair is situated on the metathorax in front of the 4th pair. A longitudinal trunk unites the tracheae on either side of the body into a single system, but there is only a single delicate transverse commissure which is situated near the junction of the 9th and 10th abdominal segments. In *J. isabellae* there are 9 pairs of spiracles; those homologous with the 2nd and 4th pairs of *J. solifugus* being unrepresented. In *Projapyx* there are 10 pairs—3 thoracic and 7 abdominal: in *Anajapyx* there are 9 pairs of which the 1st and 2nd correspond with the 1st and 3rd of *Japyx solifugus*.

The *dorsal vessel* is notable on account of the extension of the heart into the mesothorax. In *Japyx* the heart is composed of 10 chambers and in *Campodea* Marten (1939) found 9 pairs of ostia. A pair of *posterior glands*, possibly of a repugnatorial nature, opens at the apices of the cerci in the Projapygidae and is possibly homologous with similar glands in the Symphyla and Diplopoda.

The reproductive organs (Fig. 221) differ considerably within the Diplura. In the females, *Campodea* has a single pair of large polytrophic ovarioles but in other members of the order they are panoistic. *Japyx* has 7 metamerically arranged ovarioles on each side (1st to 7th abdominal segments) while *Anajapyx* has 2 pairs. In all cases the vagina is extremely short and the two oviducts combine immediately before opening by the gonopore on the 8th abdominal sternum. A small spermatheca is present but no accessory glands are known. In the male, *Campodea* has a single pair of large testes with a very short vas deferens on each side. *Anajapyx* has 2 testicular lobes on each side, arranged as are the ovarioles of this genus, while *Japyx* has 1 pair of testes with long, convoluted vasa deferentia. The ductus ejaculatorius, when present, is always short, there are no accessory glands and the male gonopore is situated on the posterior part of the 8th sternum.

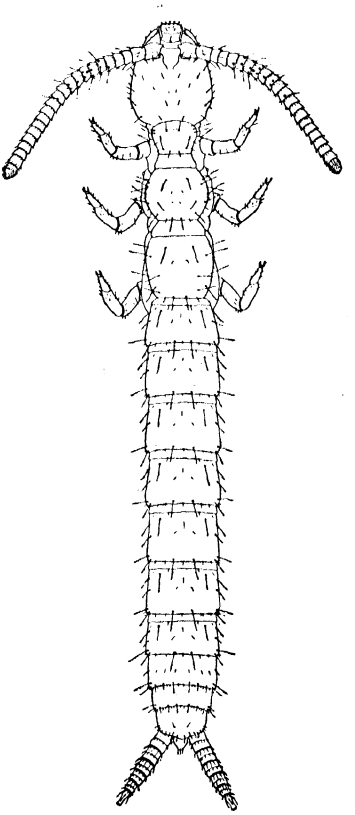


FIG. 222.—*Anajapyx vesiculosus* (magnified) Italy

After Silvestri, 1905.

Postembryonic Growth.—Little is known of the postembryonic development of the Diplura but the external changes involved appear to be slight. In *Campodea* the first instar is of very short duration, the 'embryonic cuticle' being shed soon after eclosion (Condé, 1946). In the Japygidae Silvestri states that the eggs and young forms are protected by the body of the mother and that the nymphal forceps, which are toothless and straight in the first instar, resemble those of the adult after the first moult.

Affinities.—The Diplura were formerly included in the order Thysanura as a suborder (Entognatha). Their elevation to separate ordinal status by most modern authorities is based mainly on the distinctive mouthparts, the intrinsic flagellar musculature of the antennae and the atypical arrangement of thoracic spiracles, the latter feature being unique among the Insecta. Although among the Apterygota it is the Thysanura which approach most closely to the Pterygote insects, the Diplura are of considerable phylogenetic interest because of their resemblance to the Symphyla (Imms, 1936). Thus *Anajapyx* and the Symphyla agree in the possession of abdominal styli, eversible vesicles and anal glands opening on the cerci as well as in the structure of the mouthparts, antennal musculature and legs. The fact that the Symphyla are progoneate is not considered by Imms (1936) or Tiegs (1945) to preclude the likelihood of the insects having originated from primitive Symphylan-like stock.

Literature.—The principal taxonomic papers on this group are by Silvestri who has also (Silvestri, 1949) catalogued the Japygidae and Projapygidae. Apart from authors cited in the text, the major morphological works are by Grassi (1888), Silvestri (1902; 1903; 1903a; 1905), Verhoeff (1903), Marten (1939) and Wygodzinsky (1941).

Classification.—3 families may be recognized:

FAM. 1. CAMPODEIDAE.—*1st abdominal segment without styli but with lobe-like appendages; abdomen ending in long, slender, many-segmented cerci which are imperforate apically. Campodea, Lepidocampa,* etc.

FAM. 2. PROJAPYGIDAE.—*1st abdominal segment with styli; cerci short, stout, composed of a few segments and perforate apically. Projapyx, Anajapyx* (Fig. 222), *Symphylurinus.*

FAM. 3. JAPYGIDAE.—*1st abdominal segment with styli; cerci modified into sclerotized forceps. Japyx, Heterojapyx,* etc.

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Order 3. **PROTURA (Myrientomata)**

Minute insects with entognathous piercing mouthparts; antennae and compound eyes wanting. Abdomen composed of 11 *segments and a well-developed telson; first three segments each with a pair of small appendages. Tracheal system present or absent. Malpighian tubes represented by papillae. Metamorphosis slight, chiefly evident as an increase in number of the abdominal segments.*

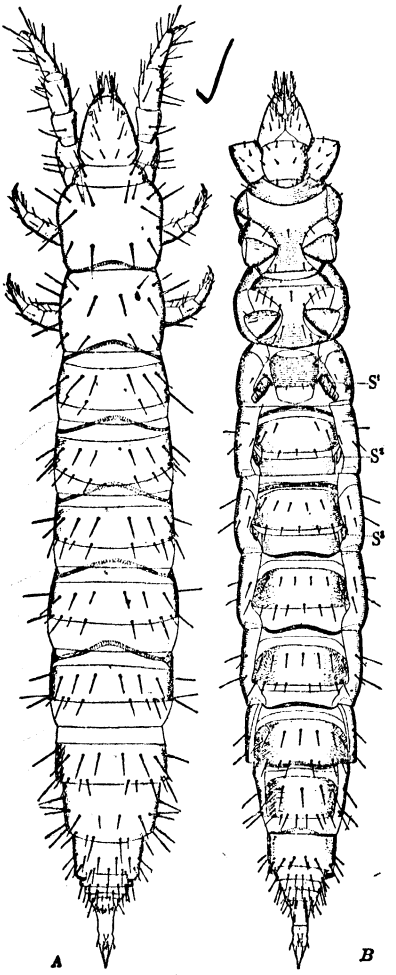


FIG. 223.—*Acerentomon doderoi* (highly magnified). Europe

A, dorsal; B, ventral. *S*, styli. *After* Silvestri, 1907

The Protura are minute whitish organisms—the largest species scarcely attain 2 mm. in length, and the majority are usually much smaller. They have been reported from all parts of the world. Owing to their very small size Protura are easily overlooked, but they are not rare in certain types of moist soil, in peat, deciduous woodland litter and in turf: they have also been met with under stones and beneath bark. The order was first recognized by Silvestri in 1907, from Italy, and has since been very fully studied by Berlese (1909) whose monograph is accompanied by a wealth of anatomical detail. Owing to the absence of antennae, the Protura have the habit of walking with the fore legs held upwards in front of the head, these appendages probably functioning as tactile organs.

Reference should be made here to *Protapteron indicum* which Schepotieff (1909) described as a Proturan with antennae and other unusual features. While the exact nature of his specimens remains obscure it is now commonly agreed that either this organism is not a Proturan or that Schepotieff was mistaken in his account of its anatomy.

External Anatomy (Prell, 1913; Tuxen, 1931).—The head is pyriform, narrowing anteriorly. There are no visual organs but on either side there are a pair of minute structures termed by Berlese *pseudoculi* which are perhaps homologous with the postantennal

organs of Collembola (vide p. 275), though Tuxen, after an account of their structure, innervation and musculature, concludes that they are vestigial antennae. The *labrum* is in the form of a pointed projection or is vestigial, while the mandibles and maxillae are withdrawn into the head (Fig. 224). The former appendages are stylet-like, adapted for piercing and are each attached to the head by a single articulation. The maxillae are divided into an outer and an inner lobe, and the palpi are 3- or 4-segmented: either the inner or both lobes are modified into piercing organs (Fig. 225). The labium comprises an elongate, basal submentum and paired mental and premental sclerites while the ligula is composed of a pair of pointed structures. The labial palpi are short and 2- or 3-segmented. Superlinguae appear to be absent, but from the hypopharyngeal region and the front of the head arises a complicated tentorium-like structure resembling that of the Collembola.

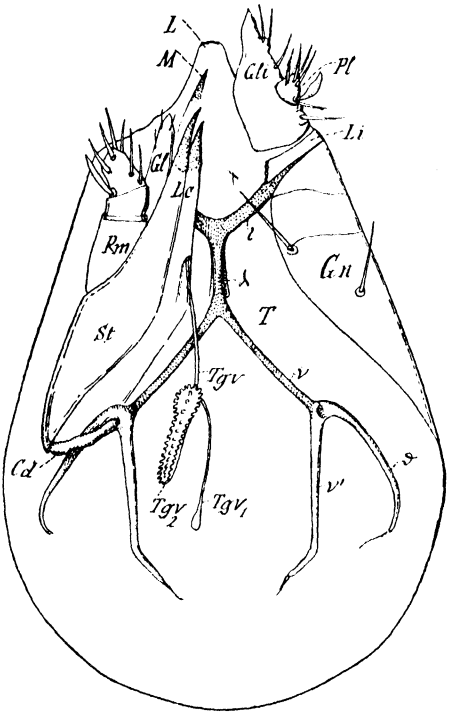


FIG. 224.—*Acerentulus tiarneus*. Ventral view of head showing right maxilla, left lobe of labium (*Gli*) and tentorium-like apodemes (*T*)

Cd, cardo; *Gl*, galea; *Gn*, gena; *L*, labrum; *Lc*, lacinia; *Li*, basal sclerite of labium; *M*, apex of mandible; *Pl*, labial palp; *Pm*, maxillary palp; *St*, stipes; *Tgv*, tubules of maxillary gland. *After* Berlese, *Redia*, 1909.

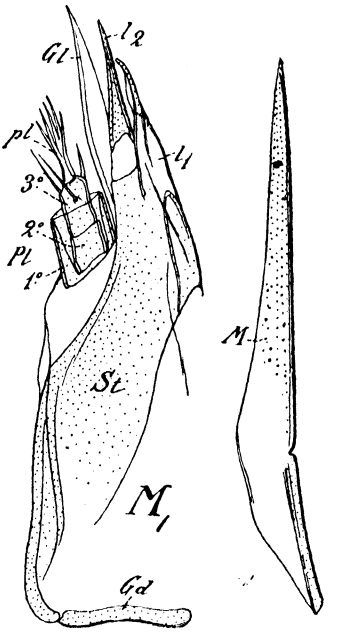


FIG. 225.—*Acerentulus confinus*

M, right mandible; M_1, left maxilla; *Cd*, cardo; *St*, stipes; *Pl*, palp; *Gl*, galea; l_1, l_2, lacinia. *After* Berlese, *Redia*, 1909.

The thorax is clearly defined with the first segment considerably reduced: the legs are long with 1-segmented tarsi, each of which is terminated by a single claw and an empodial appendage which may be absent. The abdomen is very long and slender: in the newly-hatched insect it is composed of 8 segments and a telson and, during postembryonic development, three more segments are added by intercalary growth between the telson and the last segment. This anamorphosis, or increase in the number of segments after emergence from the egg, is a generalized Arthropod character. The first three abdominal segments each carry a pair of small appendages (Fig. 230):

in the Eosentomidae they are 2-segmented, the second segment being reduced and provided with a protrusible vesicle. In other genera either the first pair or first two pairs are 2-segmented and the others consist of a single minute lobe. Cerci are absent in the order, and the name Protura is derived from the simple telson. Small external genitalia of an unusual form surround the gonopore in both sexes.

Internal Anatomy (Fig. 226).—The alimentary canal is a simple straight

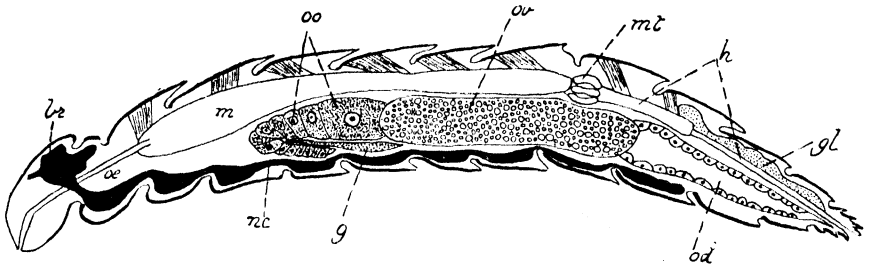


FIG. 226.—*Acerentulus confinus*, female: general anatomy

br, brain; *g*, germarium; *gl*, abdominal gland; *h*, hind intestine; *m*, mid intestine; *mt*, excretory papillae; *nc*, nerve cord; *od*, oviduct; *oe*, fore intestine; *oo*, oocytes; *ov*, mature ovum. Adapted from Berlese, *Redia*, 1909.

tube and its most extensive region is the large cylindrical mid gut. Two pairs of maxillary glands and a pair of labial (salivary) glands are present. The Malpighian tubes are represented by six uni- or bicellular papillae disposed in two groups of three. The nervous system consists of the brain and fused suboesophageal and prothoracic ganglia, while there are separate ganglia in the remaining thoracic and the first six abdominal segments. The connectives throughout are double. The terminal ganglion is larger than those preceding and there is a supplementary ganglion on each pedal nerve at the bases of the legs. In *Eosentomon*, which alone possesses a *tracheal system* (Fig. 227), the latter communicates with the exterior by means of two pairs of spiracles—one pair on the mesothorax and the other pair on the metathorax. There is no communication between the tracheae associated with the spiracles of one side or of opposite sides of the body and the tracheae are absent from the first-stage nymph (Tuxen, 1949). The *reproductive system* in the female consists of a pair of panoistic ovaries and oviducts; the latter combine to form a short vagina which opens by a median pore between the 11th abdominal segment and the telson. Each ovary extends, when mature, from the metathorax into the 9th abdominal segment and is homologous with a single panoistic ovariole in other insects. The germarium is situated in the reflexed apex of the ovary and from it is derived a single chain of egg-cells. In the male the testes are a pair of elongate sacs which are united anteriorly about the level of the mesothorax. The vasa deferentia are closely coiled tubes which enter the aedeagus separately: the latter organ is protruded between the 11th segment and the

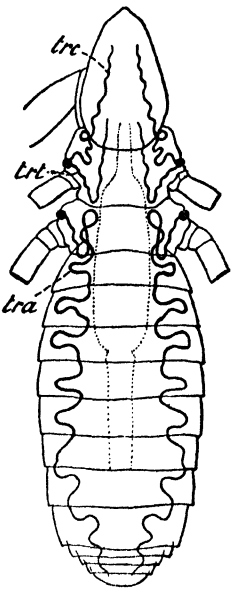


FIG. 227.—Tracheal system of *Eosentomon* (much retracted)

trc, cephalic trachea; *trt*, thoracic do.; *tra*, abdominal do. *After* Berlese, *Redia*, 1909.

telson. The germarium is apical and the remainder of the testes contains spermatozoa in various stages of development. The *circulatory system* has not been adequately studied. Berlese considered that the position of the dorsal pulsatory vessel was occupied by a longitudinal trough-like filament (*pericardial cord*) but Aubertot (1939) claims to have discovered a functional heart with seven pairs of ostia in *Acerentomon*.

Postembryonic Development.—Tuxen (1949) has described five nymphal stages in *Acerentulus danicus* and *Eosentomon armatus*. The 4th instar is the first to possess the full number of abdominal segments and external genitalia are developed in the last nymphal stage.

Affinities.—The systematic position of the Protura cannot be regarded as being settled and is, at present, largely a matter of opinion. Berlese and others maintain that they form a class of their own—the Myrientomata. On the other hand, Silvestri and Börner place them among the Insecta. The mouthparts are insectan in character and are not unlike those of suctorial forms among Collembola. The differentiated thorax and three pairs of legs are also insectan features, together with the reduction of the abdominal appendages. Those who maintain the view that the Protura represent a class of their own, base their conclusions mainly upon anamorphosis, the absence of antennae, and the position of the genital aperture. It is noteworthy that the absence of antennae is probably a secondary feature, and these organs are reduced to the condition of minute papillae in many insect larvae. The number of abdominal segments, furthermore, agrees with the primitive number found in embryo insects, and the most important non-insectan character is the occurrence of anamorphosis.

Classification.—43 species are listed by Mills (1932) and keys to the genera are given by Tuxen (1931) and Ewing (1936). The 17 British species are dealt with by Womersley (1927–29) and Bagnall (1934–36), while Ewing (1940) has monographed the N. American forms.

The three families recognized by Ewing (1940) may be distinguished as follows:

1. Tracheae and spiracles present; all abdominal appendages 2-segmented; 8th abdominal segment without dorsolateral combs . . . EOSENTOMIDAE
–. Tracheae and spiracles absent; 3rd abdominal appendage 1-segmented; 8th abdominal segment usually with combs 2

2. Typical abdominal terga each with 1 transverse row of setae and without transverse grooves or laterotergites; combs on 8th abdominal segment reduced or absent . . . . . PROTENTOMIDAE
–. Typical abdominal terga each with 2 transverse rows of setae, with 1 or 2 transverse grooves and laterotergites; combs not reduced . . . ACERENTOMIDAE

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Order 4. **COLLEMBOLA** (Spring-tails)

Mouthparts entognathous, principally adapted for biting; antennae usually 4-segmented, the first 3 provided with muscles; compound eyes absent. Abdomen 6-segmented, usually with three pairs of appendages, i.e. a ventral tube on segment I, a minute retinaculum on III, and a forked springing organ on IV. A tracheal system is usually absent and there are no Malpighian tubes. Metamorphosis absent.

Collembola are small insects rarely exceeding 5 mm. in length, and occur in almost all situations. They are found in the soil, in decaying vegetable matter, among herbage, under bark of trees, etc. A few species frequent the nests of ants and termites, others occur on the surface of fresh water and several are littoral or marine: *Anurida maritima*, for example, is daily submerged by each tide. The only condition which seems essential for their welfare is a certain amount of moisture, for they are rare in very dry situations. The order is world-wide and is remarkable for the extensive distribution of many of its genera and species (Salmon, 1949).

Collembola vary very much in coloration. Many are of a uniform dull blue-black, as in *Anurida*: others are green or yellowish with irregular patches of a darker colour: a few species are banded, some are all white, one or two are bright red while metallic forms are not infrequent. In habits they are saprophagous or phytophagous, pollen grains and fungal spores or mycelium often being eaten.

External Anatomy (Figs. 228–231).—In the greater number of species the body is clothed with hairs but some genera, notably *Tomocerus* and *Lepidocyrtus*, are scaled. The hairs vary in shape, often on different regions of the body: they may be simple and tapering, clavate, flattened and partially resembling scales, or plumose. The head (Denis, 1928) is pro- or hypognathous with the labrum distinctly marked off and sometimes also the clypeus and frons. The antennae vary greatly in length and the distal segments may be secondarily annulated. They are typically 4-segmented: the maximum number of six is found in *Orchesella*. In the Neelidae the antennae may be shorter than the head, while in some of the Entomobryidae they are longer than the whole body. Sensory organs of varied types are usually present on the last two segments and take the form of cones, rods, pits or papillae. A variable number of ocelli is generally present on either side of the head behind the antennae: there are never more than eight to a side and often many fewer. In some Collembola they are absent as in the Onychiuridae, Neelidae and Cyphoderinae. Marlier (1941) has described additional ocelliform structures on the head of some genera. Immediately behind the antennae of some Collembola is a very characteristic structure known as the postantennal organ (Becker, 1910). This occurs in most Poduroidea and some Entomobryoidea but not in the Symphypleona. It assumes a great variety of forms among different genera, being simple and ring-like in *Isotoma*, in the form of a rosette

in *Anurida*, while in *Onychiurus* it attains considerable complexity of structure. It is evidently a sensory organ from the fact that it has a special nerve-supply, and the thinness of its cuticular investment suggests its capability for receiving external stimuli, possibly of an olfactory nature. The *mouthparts* (Folsom, 1899) are deeply withdrawn into the head and are greatly elongated, which allows of their freedom of movement when protruded. Their deeply-seated position is a secondary acquisition and has been brought about in the

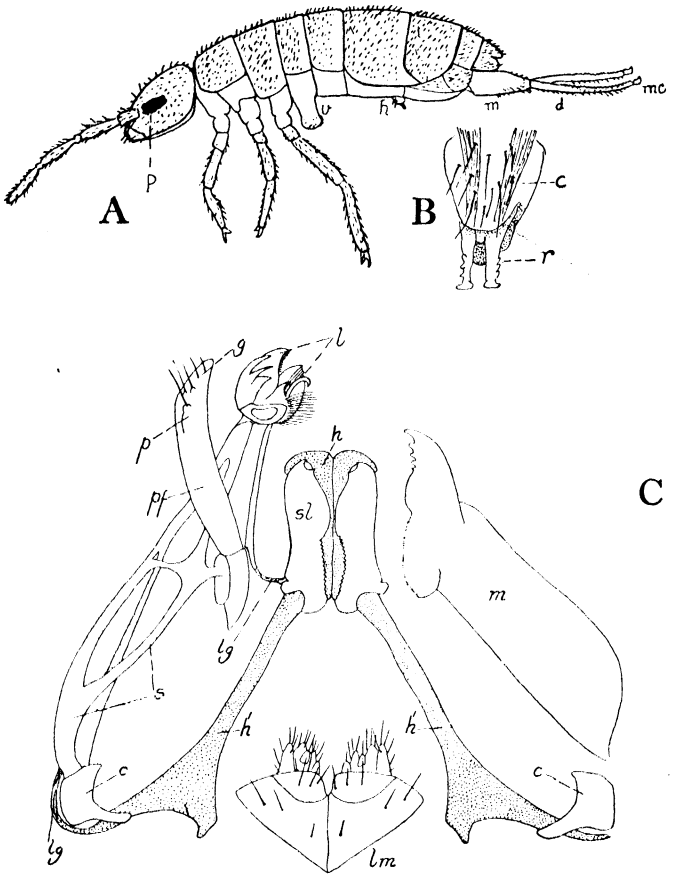


FIG. 228.—Structural details of Collembola

A, *Axelsonia*. *p*, pigment surrounding eyes; *v*, ventral tube; *h*, hamula; *m*, manubrium; *d*, left dens and mucro *mc*. (Adapted from Carpenter.)
B, *Tomocerus*, retinaculum. *h*, hamula; *c*, corpus; *r*, ramus. (*After* Willem, 1900.)
C, Mouthparts of *Orchesella*, dorsal view. *c*, cardo; *g*, galea; *h*, hypopharynx and its brachia *h'*; *l*, lacinia; *lg*, ligament; *lm*, labium; *m*, right mandible; *p*, maxillary palp; *pf*, palpifer; *s*, stipes; *sl*, superlingua. (Partly after Folsom.)

following manner. In the embryo, the sides of the head develop from a pair of lateral evaginations of the germ-band. These evaginations eventually fuse with the developing fundaments of the labrum and labium and, in this way, form a kind of enclosing box which, by further growth, comes to surround the remaining mouthparts. The mouth-cavity is roofed over by the labrum and clypeus. The mandibles (Fig. 228) are slender organs usually with toothed extremities and apparently provided with only a single articulation with the head-capsule. They are rarely absent, as in *Brachystomella*. The maxillae each

consist of a complex apical portion or 'head' which possibly represents a lacinia. In some species a digit-like palpifer is present: it carries a vestigial palp and the galea. The cardo and stipes are variable in form and sometimes rod-like. The superlinguae are well developed lamellate structures overlying the hypopharynx: as a rule they are undivided but in *Isotomurus palustris* they are bilobed. The hypopharynx is provided with a pair of elongate brachia which articulate proximally with the cardines of the maxillae. The labium is very much reduced and, although it exhibits evidences of a paired structure, neither glossa nor paraglossae are separately developed. Labial palpi have been detected in the early embryo but as a rule they subsequently atrophy. In *Neanura* and its allies the mouthparts are specialized for sucking and piercing: the labrum and labium together form a conical tube enclosing the rest of the mouthparts, the latter being modified into stylets. The thorax, in the more generalized forms, consists of three very similar segments but in the Entomobryoidea the prothorax is greatly reduced, and its tergum is fused with that of the mesothorax. In the Symphypleona the thorax becomes intimately fused with the abdomen and its segmentation is, to a large extent, obsolete. The legs have no true tarsal segments and the tibiae generally terminate in a pair of claws, an upper and a lower, but the latter, which possibly represents a modified empodium rather than a true claw, may be vestigial or wanting. A group of short setae on the trochanter forms the so-called trochanteral organ, a structure of some taxonomic importance. The abdomen is composed of six segments only: in this respect Collembola differ from all other insects and, at no stage in development, are there known to be more than that number present. In some of the Arthropleona the 4th and 5th, or 4th to 6th segments undergo fusion, while in the Symphypleona the first four segments are almost entirely undifferentiated. On the ventral aspect of the first segment, in all Collembola, there is a bilobed structure known as the *ventral tube* (Hoffmann, 1904; Ruppel, 1953). It is formed by the union of the first pair of embryonic, abdominal appendages, and consists of a basal column containing a pair of protrusible vesicles. The latter are commonly in the form of shallow sacs but in some genera they are long and tubular. The cavity of the ventral tube freely communicates with that of the body and contains blood: the vesicles are everted by means of blood-pressure, while they are withdrawn by the contraction of special muscles. Many divergent opinions have been expressed with respect to the function of the ventral tube. It has been supposed by some to be respiratory, and by others to be concerned with water absorption while many consider it as an adhesive organ, enabling the insect to walk over smooth or steep surfaces. In this connexion it is noteworthy that the surface of the vesicles is moistened by the secretion of cephalic glands which is discharged into the commencement of the *ventral groove* (Fig. 229). The latter is a cuticular channel passing down the middle ventral line of the body: it arises from a point just behind the labium and terminates on the anterior aspect of

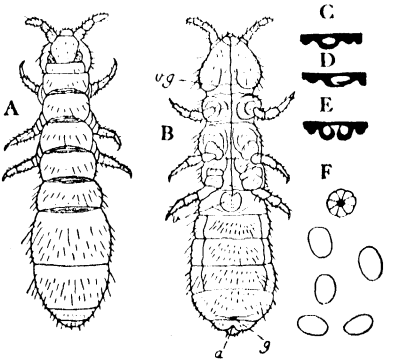


FIG. 229.—*Anurida maritima*

A, dorsal. B, ventral. *a*, anus; *g*, genital pore; *v*, ventral tube; *vg*, ventral groove. C, D, E, transverse sections of ventral groove in regions of the head, prothorax and metathorax respectively. F, eyes and postantennal organ, right side.

the ventral tube. Many Collembola retain a minute pair of appendages on the 3rd abdominal segment. They are fused proximally to form a basal piece or

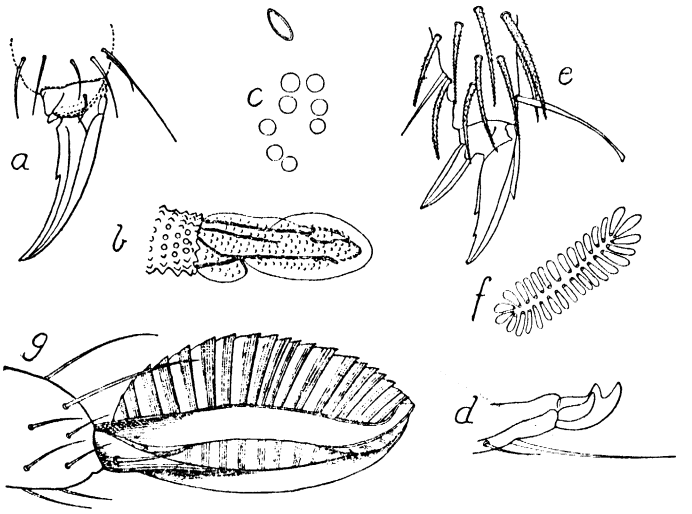


FIG. 230.—Structural details of Collembola

a, *Podura*, claw of left leg; *b*, left mucro; *c*, *Isotoma*, eyes and postantennal organ; *d*, left mucro; *e*, *Lepidocyrtus*, claws of left leg; *f*, *Onychiurus*, right postantennal organ; *g*, *Sminthurides*, left mucro. Adapted from Folsom.

corpus, while their distal portions remain free and are termed the *rami*. The organ thus formed is variously known as the *retinaculum* or *hamula*, and it serves to retain the furcula in position, when the latter is stowed away under the abdomen while not in use. The majority of Collembola carry a pair of partially fused appendages in relation with the 4th abdominal segment. They constitute the *furcula*, or springing organ, which enables the insect to take sudden leaps into the air —hence the name of 'spring-tails' which is commonly applied to the members of this order. When released from the hamula, the extensor muscles of the furcula contract, and the latter organ is forcibly pulled downwards and backwards so as to strike the ground and propel the insect a relatively long distance into the air. The common basal piece of the furcula is termed the *manubrium* which carries a pair of distal arms or *dentes*: each dens carries a very variably shaped claw-like process or *mucro*. The furcula varies greatly in development; in *Entomobrya*, for example, it extends, when at rest, to beyond the ventral tube; in *Hypogastrura* it is often very short, while in *Neanura* and *Anurida* it is wanting. The sexes are similar in Collembola, there being no external genitalia although the gonopore and the region

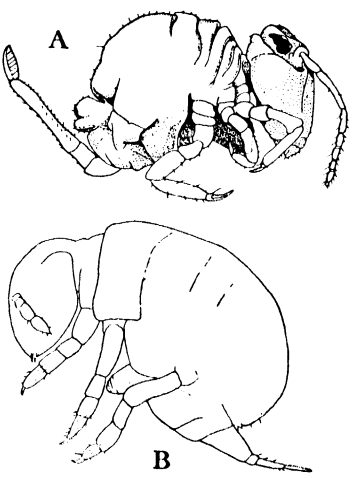


FIG. 231.—Collembola, Symphypleona (magnified)

A, *Sminthurides aquaticus*. *After* Willem. B, *Neelus folsomi*. *After* Caroli.

around it may differ slightly in the sexes (Agrell, 1937). The genital aperture is placed near the hind margin of the 5th sternum, while the anus is located on the 6th sternum.

Internal Anatomy (Fig. 232).—The *alimentary canal* (Boelitz, 1933; Tóth, 1942) is a simple straight tube, passing from the mouth to the anus

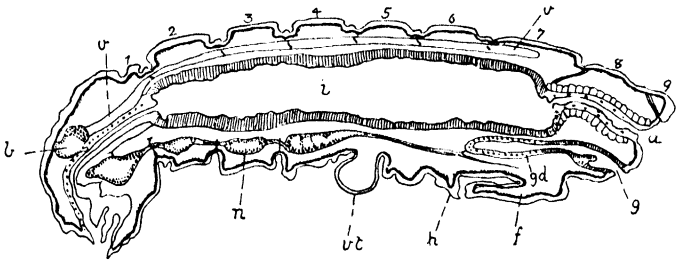


FIG. 232.—*Hypogastrura viatica*, longitudinal section

a, anus; *b*, brain; *f*, furcula; *g*, genital pore; *gd*, gonoduct; *h*, hamula; *i*, mid intestine; *n*, nerve-cord; *v*, dorsal vessel; *vt*, ventral tube. *After* Willem, 1900.

without presenting any convolutions. The greater portion is formed by the extensive mid intestine and the latter, in *Neelus*, is subdivided into four subequal chambers. With the exception of salivary glands, there are no appendages of the alimentary canal. The central *nervous system* is considerably specialized and consists of the cerebral ganglia and a ventral nerve-cord composed of four ganglionic centres—the suboesophageal and three thoracic ganglia, which are united by double connectives. There are no separate abdominal ganglia, the nerve centres of that region having fused with the metathoracic ganglion. In the Sminthuridae the ventral ganglia are closely merged together, there being no intervening connectives. The *heart*, in the more generalized forms, consists of a series of six chambers with paired lateral ostia and alary muscles at each of the constrictions. Anteriorly, the heart is prolonged into the aorta and in *Anurida* the latter vessel surrounds the fore intestine in the form of a cylinder which opens in the head beneath the cerebral ganglia. There are no Malpighian tubes and *excretion* is chiefly performed by the fat-body. The latter contains numerous concretions which, according to Willem (1900), are composed of sodium urate. These concretions increase in size with the age of the individual and are not eliminated from the insect. In addition to the fat-body, the epithelium of the mid gut performs an excretory function. Folsom and Welles (1906) have shown that the mid-gut cells contain concretions of a similar nature to those found in the fat-body. These congregate in the inner halves of the cells, which divide off from the remainder, and are periodically discharged into the lumen of the gut. They are removed from the body during each ecdysis, and a regeneration of the epithelium takes place. According to Boelitz (1933) the urate concretions of

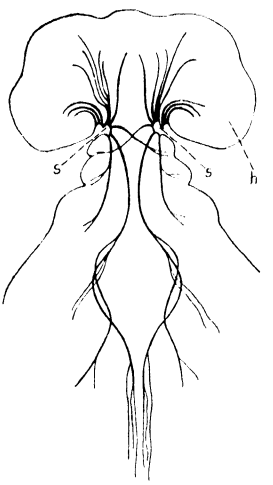


FIG. 233.—*Sminthurus fuscus*. Tracheal system

h, head; *s*, spiracle. *After* Willem, 1900.

the mid gut are actually transported to this position from the fat-body by phagocytes (see also Ichikawa, 1931).

Respiration in the majority of Collembola is cutaneous but tracheae are present in *Actaletes* and the Sminthuridae while vestiges of a tracheal system are said to occur in *Dicyrtoma fusca*. They are well developed in *Sminthurus* where there is a single pair of simple spiracular openings between the head and prothorax (Fig. 241). Tracheal branches are distributed to the head, legs and abdomen, but no anastomosis takes place between the tracheae of opposite sides of the body (Davies, 1927).

The *reproductive system* is of an extremely simple nature: the gonads consist of a pair of large sacs, their ducts are extremely short and they unite to form the vagina or ejaculatory canal as the case may be. The ovaries contain groups of vitellogenous cells and developing eggs but there is no arrangement into ovarioles, and the testes are filled with dense masses of developing spermatozoa. Unlike other insects, the germarium in both the ovaries and testes is lateral and not apical in position. Accessory organs are usually wanting in both sexes.

Postembryonic Growth and Biology.—The eggs of Collembola are smooth and spherical, usually cream-coloured, and are deposited in small groups. The newly-hatched insects are white excepting for an area of dark pigment surrounding the ocelli. Agrell (1949) finds that the number of moults which occur before the maximum size is attained is six in *Arrhopalites pygmaeus*, seven in *Hypogastrura sahlbergi* and eight in *Folsomia 4-oculata*, the external changes which accompany postembryonic development being relatively slight (e.g. secondary annulation of antennal segments and differentiation of the trochanteral organ, the teeth of the claws and the genital region). Sexual maturity is attained before maximum size—after five moults, for example, in *Folsomia 4-oculata*.

The species *Sminthurus viridis* has been more fully studied than any other (MacLagan, 1932; Davidson, 1934). It feeds on the leaves of various plants, especially Leguminosae and, according to MacLagan, the optimum conditions for growth are a humidity near saturation and soil with a *p*H of about 6·5. Under these conditions, and a temperature of about 13° C., the maximum number of eggs laid per individual is about 120: they are coated with soil voided through the anus. The incubation period is near 26 days and about 48 days elapse from eclosion to sexual maturity. There are eight instars and the last ecdysis takes place after attaining sexual maturity. As an adult the insect lives for about 15 days: the life span, from the egg onward, is approximately $2\frac{1}{2}$ months and there are five generations in the year.

A very characteristic feature of Collembola is a tendency to gregariousness or the massing together of enormous numbers of individuals comprising both adult and immature forms. This behaviour has been noted in various countries (Turk, 1932) but its significance is unknown. In some cases it may be connected with an abundance of a particular food or in others with migration.

Affinities.—The systematic position of the Collembola is uncertain. Although Tillyard (1930) regarded them as the modern representatives of a primitive group possessing few postcephalic segments and from which the other Insecta originated, other authorities such as Handlirsch (1908) emphasize their isolated position by giving them the status of a separate Arthropodan class. Certainly they differ from other insects in the possession of only six abdominal segments, gonads with a lateral germarium, a postantennal organ which resembles most closely the organ of Tömösvary in Chilopoda and Diplopoda, and eggs which undergo total cleavage during embryonic development. Their inclusion among the Insecta depends on their being opistho-

goneate hexapods with mouthparts formed on an insectan plan. On the whole it seems best to regard them as a specialized offshoot from the base of early Symphylan stock and to accept them as insects with the reservation that they represent a side development remote from the main evolutionary line of the Insecta (Imms, 1936).

Literature on the Collembola.—Useful recent systematic works are those of Gisin (1944) on the Holarctic species and Salmon (1951) on the genera of the world, both with extensive taxonomic bibliographies, while the monographs of Stach (1947–54) and Bonet (1947) give a detailed treatment of certain families. Among other taxonomic works may be mentioned Schött (1893) and Linnaniemi (1907, 1912) on Palaearctic forms and Folsom (1914–37), Mills (1934) and Maynard (1951) on N. American species; Womersley (1939) has monographed the Australian Collembola. The chief work on the anatomy of the order is that of Willem (1900) while other accounts include Sommer (1885), Fernald (1890), Prowazek (1900), Imms (1906) and Philiptschenko (1906). The biology of the group has been dealt with by Handschin (1926), Agrell (1941), Glasgow (1939), Gisin (1943; 1948), Hammer (1944), Strebel (1932) and Weis-Fogh (1948).

Classification.—The classification is due to Börner (1913), whose work is summarized by Shoebotham (1917) and forms the basis of the following key to families. There are about 1500 described species, of which over 250 are British.

1. Body more or less elongate; thoracic and abdominal segments distinctly separated except sometimes for last 2–3 abdominal segments (Suborder ARTHROPLEONA) 2
–. Body subglobose; thoracic and first four abdominal segments completely fused (Suborder SYMPHYPLEONA) 9

2. Pronotum free, similar to other terga, setose; cuticle usually granular or tuberculate (Poduroidea) 3
–. Pronotum reduced or apparently absent, not setose; cuticle smooth, setose or scaled (Entomobryoidea) 5

3. Pseudocelli present on thoracic and abdominal terga . . . ONYCHIURIDAE
–. Pseudocelli absent 4

4. Head hypognathous; furca extending beyond ventral tube, dentes annulate distally. . . . . PODURIDAE
–. Head obliquely prognathous; furca, when present, rarely reaching ventral tube, dentes not annulate distally . . . . . HYPOGASTRURIDAE

5. Abdominal tergite III much reduced; abdominal segments IV–VI fused ACTALETIDAE
–. Abdominal tergite III not much reduced; abdominal segments IV–VI free 6

6. 4th abdominal segment almost invariably longer than 3rd; trochanteral organ present . . . . . ENTOMOMOBRYIDAE
–. 4th abdominal segment not or only slightly longer than 3rd; trochanteral organ absent 7

7. Scales absent; mucro short . . . . . ISOTOMIDAE
–. Scales present; mucro long 8

8. 4th antennal segment with vesicular sense-organs . . ONCOPODURIDAE
–. 4th antennal segment without vesicular sense-organs . . . TOMOCERIDAE

9. Antennae shorter than head . . . . . NEELIDAE
–. Antennae longer than head . . . . . SMINTHURIDAE

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SUBCLASS: PTERYGOTA

Order 5. EPHEMEROPTERA (Plectoptera: Mayflies)

Soft-bodied insects with short setaceous antennae and vestigial mouthparts derived from the biting type. Wings membranous, held vertically upwards when at rest; the hind pair considerably reduced; 'intercalary' veins and numerous cross-veins present. Abdomen terminated by very long cerci either with or without a similar median caudal prolongation. Metamorphosis hemimetabolous: nymphs aquatic, campodeiform, usually with long cerci and a median caudal filament: lamellate or plumose, metameric, tracheal gills present. Adult preceded by a subimaginal winged instar.

Existing mayflies are the remnants of a former extensive order. They are familiar insects on the margins of lakes, streams and rivers, and the association of their name with the Ephemerides of Grecian mythology expresses their brief life above water which, in certain species such as *Ephoron*, *Campsurus* and *Palingenia*, lasts but a few hours. In their nymphal stages, on the other hand, they are at least as long-lived as most insects and, in some cases, this period is believed to occupy three years.

When a mayfly is about to emerge the nymph usually floats to the surface of the water: a fissure then appears in the dorsal cuticle, and a winged insect issues, and flies away in the course of a few seconds. Less frequently the nymph moults under water. In either case the resulting winged form is known as the *subimago*, and it differs from the mature imago in several features. In their general form the two stages are alike, the wings are fully expanded and spiracular respiration is established. The subimago may be recognized by its duller appearance, and by its somewhat translucent wings which are usually margined by prominent fringes of hairs. The passage from the subimago to the imago is marked by an ecdysis which is unique among insects; the subimago casts a delicate pellicle from its whole body, including the wings, and then issues as a fully formed imago. In the latter condition the insect presents a shiny appearance and has assumed its full coloration, the wings become transparent, while the eyes and legs attain their complete development. Among certain of the short-lived species the subimaginal pellicle is partially, or completely persistent in one or other sex. The males of *Oligoneuria*, for example, retain this covering on the wings, while the females of *Palingenia*, *Ephoron* and *Campsurus* do not appear to shed any part of it at all (Eaton; Spieth, 1940). The subimaginal stage is of variable duration and there is, furthermore, some correspondence between the time spent in this stage and the duration of life of the imago. Thus, the change into the imago may occur only a few minutes after the subimago has emerged from the nymphal cuticle. In such cases the life of the imago is a fugitive one, death taking place the same evening or early the following morning. In other cases the sub-

imago may exist for 24 hours, or more, leading an inactive existence resting in the shade. The resulting imago in instances of this kind may live from one to several days. The short-lived species are mostly night fliers: species of *Palingenia*, *Oligoneuria*, *Ephemera*, *Hexagenia* and *Caenis* have been observed to issue about sundown in vast swarms. Such a phenomenon is frequent on the borders of the Swiss lakes, where the mayflies sometimes appear in hundreds of thousands, and are attracted in large numbers to the arc lamps near the waterside. Certain of the more conspicuous species, especially the males, exercise familiar 'dances' in the air: when carrying out these evolutions a vertical up and down motion results, a fluttering swift ascent being followed by a passive leisurely fall many times repeated.

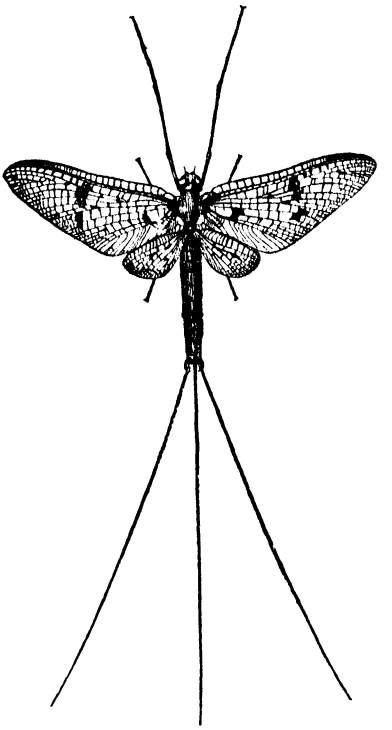


FIG. 234.—*Ephemera vulgata*
(Reproduced by permission of the Trustees of the British Museum.)

Mayflies are eagerly devoured by fishes and most of the 'duns', 'spinners' and several of the 'drakes', of the fly-fisher, are made up to represent various species of *Ephemera* (Fig. 234), and are used at times when the latter are on the wing.

A general account of the structure and biology of mayflies is given by Needham, Traver & Hsu (1935).

External Anatomy. — Anatomical accounts of a few species are given by Drenkelfort (1910), Heiner (1914) and Grandi (1940; 1947). The head (Fig. 235) is free with the antennae short, and composed of two basal segments, surmounted by a multi-articulate setaceous filament. The compound eyes are largest in the males and, in some genera, the upper portion of each has larger facets than the lower. In the Baetidae the upper divisions are mounted upon pillar-like outgrowths of the head (Verrier, 1940) and are used to recognize the female in the nuptial flight (Spieth, 1940). Between the compound eyes there are three ocelli. The mouthparts are degenerate: degeneration begins in the late nymph, it is externally complete in the subimago and complete in the imago (Sternefeld, 1907; Murphy, 1922). Individual parts do not undergo equal degrees of atrophy and the various genera differ very much in this respect. Mandibles are vestigial or wanting, and the maxillae, though greatly reduced, usually retain their palpi: in *Ephemera* the labium is represented by the postmentum and a pair of

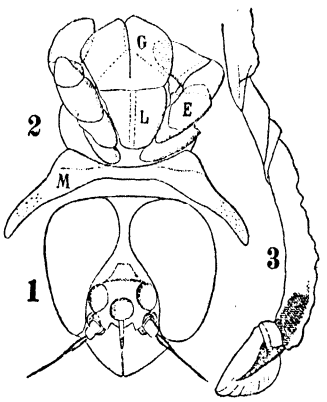


FIG. 235.—*Ephemera*. 1, head viewed from above. 2, maxillae and labium. 3, apex of tibia with tarsus
E, maxilla; *G*, ligula; *L*, prementum; *M*, postmentum. Adapted from Silvestri.

distal lobes with small palpi. In some genera the mouthparts have atrophied to the extent that they are scarcely recognizable. The often repeated statement that mayflies have no mouthparts is not literally correct for all species, but they appear always to exist in such a weak or atrophied condition as to preclude the taking of any food.

The thorax (Knox, 1935) is principally characterized by the great size and predominance of its middle segment, the pro- and metathorax both being small and comparatively insignificant. In *Hexagenia*, the form best studied, the meso- and metanota are subdivided and postnota are present. The pleural sutures are reduced or absent and the pleura of the pterothorax are fused ventrally with the sternum to form pre- and postcoxal bridges and dorsally with the postnotum to form postalar bridges. The wings are markedly triangular (Fig. 237) and fragile, durable organs not being required. As a rule they are largest in the female: the hind wings are always small or minute and, in some genera (i.e. *Caenis*, *Cloëon*), they are completely atrophied. The fore wings are longitudinally corrugated but are not folded, except when the female is ovipositing below the water surface. The corrugation is correlated with the presence of so-called 'intercalary' (accessory) veins and each vein, whether normal or intercalary, either follows the crest of a ridge, when it is termed a convex vein, or the bottom of a furrow when it is known as a concave vein. The intercalary veins are a very characteristic feature: they appear to be branches which have lost their basal connexions with the remaining veins but are united with the latter by a greatly developed system of cross-veins. The wing-venation, which is of considerable taxonomic value (Spieth, 1933), has been the subject of several conflicting interpretations (Needham *et al.*, 1935) but that of Tillyard (1932) is followed here. It shows the primitive feature of a media retaining its anterior (MA) and posterior (M) divisions in both pairs of wings. R_5 is attached basally to MA. The legs are not used for walking and are sometimes greatly reduced though in males the fore legs are usually much elongated to grip the female from below in the mating flight. In the American *Campsurus* the four posterior legs are mere stumps. There are primitively five tarsal segments but one or two of the basal segments are fused with the tibia in more specialized forms and in degenerate legs there may be only one or two tarsal segments. Two pretarsal claws are present, of which one is commonly degenerate and blunt.

The abdomen is evidently 10-segmented with an 11th segment reduced and fused to the 10th. In the female the two oviducts open by separate apertures between the 7th and 8th sterna. An appendicular ovipositor is always absent though Morrison (1919) has shown that posterior extensions of the 7th and 8th sterna form a functional ovipositor in some Leptophlebiidae. The male genitalia (Spieth, 1933; Snodgrass, 1936; Qadri, 1940) include a pair of claspers borne on the posterior margin of the 9th sternum, consisting each of a coxite (partially or completely fused with that of the opposite side) and a secondarily annulated style. Between the claspers lies a pair of penes which are more or less fused basally, bear variously shaped outgrowths and may represent appendages of the 10th abdominal segment.

Internal Anatomy.—The most characteristic feature with respect to the internal organs is the modification of the alimentary canal for aerostatic purposes (Sternefeld, 1907; Pickles, 1931). This region no longer functions as the digestive tract, but has assumed an entirely new role, and has undergone certain structural changes in consequence. In the nymph the oesophagus is wide, but in the imago it becomes an extremely narrow tube and there is a

complicated apparatus of dilator muscles which appears to regulate the air-content of the gut. Air is taken in or expelled through the mouth, and the stomach is modified into a kind of storage balloon: its epithelium is no longer secretory, but is converted into one of the pavement type, and the muscular coat has disappeared. The Malpighian tubes number up to 140, and the first portion of the hind intestine is modified to form a complex valve which precludes the escape of air from the stomach. In these short-lived insects it appears therefore to be more important that their specific gravity should be lessened, in order to facilitate the mating flight, rather than that they should take food, and live for a longer period. The sexual organs of mayflies are remarkable for their primitive nature. There are no accessory glands, and the gonoducts retain their paired nature in both sexes, each duct opening to the exterior separately. In the male the testes are ovoid sacs, and the two vasa deferentia each communicate with a separate penis of its side. Each ovary is composed of a large number of small panoistic ovarioles, disposed along a common tube which is continued posteriorly as the oviduct. The respiratory system is well developed and opens to the exterior by ten pairs of spiracles, two pairs being thoracic and eight pairs abdominal in position. The heart, which extends throughout the abdomen, comprises ten chambers and continues as the aorta into the head.

Oviposition and Postembryonic Development.—Mating swarms of mayflies (Spieth, 1940) consist normally of males. Females enter the swarm and leave with a male, copulation (which lasts only a very few minutes) occurring in flight, after which oviposition occurs. The eggs are very variable in form and structure (Morgan, 1913; Smith, 1935) and though the type of egg is quite constant within a species and sometimes within a genus it does not characterize families, nor is there any clear relation between egg-structure and the type of habitat in which they are laid. The differences involve variations in colour, and chorionic sculpturing; in the presence or absence of the micropylar apparatus; and in the form and occurrence of special anchoring filaments. A few examples in illustration of these facts may be cited. The egg of *Heptagenia interpunctata* is provided at each pole with a skein of fine yellow threads, which unravel in the water and serve to anchor it by becoming entangled with foreign objects. The egg of *Ephemerella excrucians* is white and slightly dumb-bell shaped, with a strongly sculptured chorion, but with no anchoring filaments or micropylar apparatus. That of *E. rotunda* is yellowish and oval, with a smooth chorion, and a prominent mushroom-shaped micropylar apparatus: there are four anchoring filaments each being terminated by a knob-like structure. The ovoid eggs of *Ecdyonurus* are provided with numerous short coiled filaments: after they have been in the water a little while each coil unwinds with a sudden spring, when it is seen to be terminated by a minute viscid button-like cap. The number of eggs laid by different species varies from several hundred up to about 4,000. Eaton mentions that some of the short-lived species discharge their eggs *en masse* as a pair of clusters which are laid on the water: these soon disintegrate and the eggs become scattered over the river-bed. The longer lived species lay them in smaller numbers at a time, either alighting on the surface for the purpose or descending beneath the water and depositing their eggs under stones, etc.; the insects float up again and fly away to repeat the process, or die without reappearing. According to Heymons (1896) the eggs of *Ephemera vulgata* hatch in 10–11 days at 20–25° C. In many species they require a much longer period for their development which may extend to several months. Ovoviviparity has been recorded

in *Cloëon dipterum* and some species of *Callibaetis* and seems to be correlated with a long imaginal life in the female—8 to 21 days have been recorded (Berner, 1941).

The nymphs have been described and figured in many species, notably by Vayssière (1882), Eaton (1883–88), Lestage (1917–25), Needham, Morgan and others, but detailed life-history studies are few. There is reason to believe that the number of ecdyses is very high, 23 being recorded by Lubbock (1863–66) in *Cloëon dipterum*, but the observations were not commenced from the earliest stage. Mayfly nymphs are essentially herbivorous, feeding upon fragments of the tissues of the higher plants, algae, etc.; certain forms, however, are believed to be at least partly carnivorous but are exceptional. They frequent a great variety of aquatic situations: many live in concealment in the banks, some burrow in mud, while others hide beneath stones in lakes, streams and rivers. Certain genera occur among water plants and are active swimmers, still others live in swift currents or near waterfalls, and there are some species which reside among decaying vegetation at the bottoms of ponds or ditches. This wide range of habitat is accompanied by an equal diversity of adaptive modifications and it is in the Ephemeroptera that the most complete types of the latter are met with among aquatic insects. The general shape of the body is very variable, but all are campodeiform with evident antennae, and usually elongate multi-articulate cerci. Both compound eyes and ocelli are well developed, and most species possess seven pairs of plate-like or filamentous abdominal tracheal gills. These are responsible for an appreciable proportion of the total oxygen uptake of the nymph in *Hexagenia recurvata* (Morgan & Grierson, 1932) and *Ephemera vulgata*, but they do not appear to play an important respiratory role in *Baetis* and *Cloëon* (Wingfield, 1939).

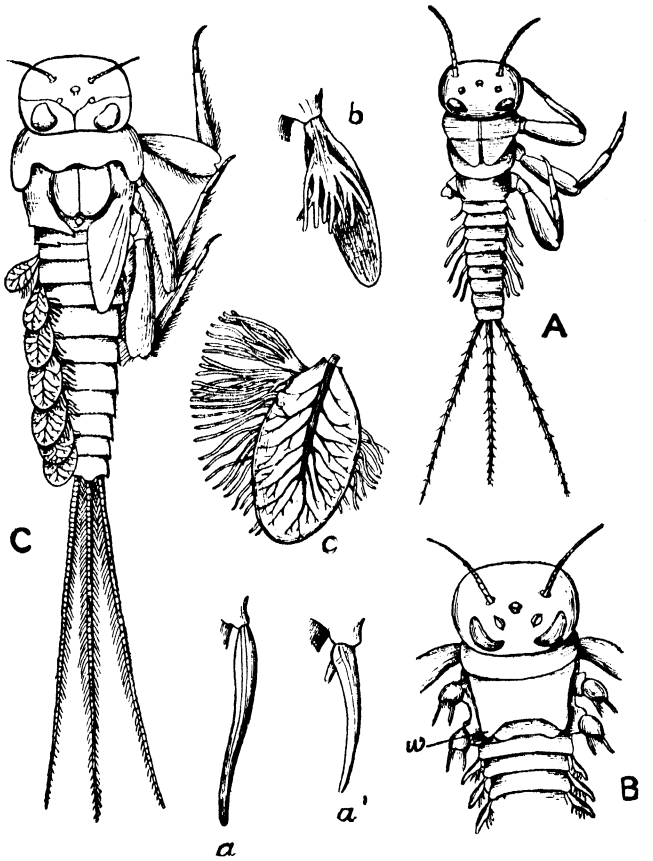


FIG. 236.—Nymphal instars of *Heptagenia*

A, 3rd instar × 16. *a*, abdominal appendage (gill-rudiment); a^1, do. of later instar × 45. B, 7th instar, anterior region with wing-rudiments *w*, × 12. *b*, abdominal gill. C, 8th instar with prominent wing-rudiments (on the right), × 4. *c*, abdominal gill. From Carpenter *after* Vayssière.

The gills are capable of co-ordinated movements by special muscles (Eastham, 1936–39) and even if they are not always true respiratory organs they may perform an accessory function in providing a flow of water over the general respiratory surface of the body. The nymphs of *Ephemera* and *Hexagenia* burrow in mud or in the banks of streams; they have elongate bodies with strong fossorial legs. The first pair of gills is vestigial, and the remainder are biramous, consisting of a pair of lamellae fringed with long filaments which are penetrated by tracheoles. When necessary the gills are carried reflexed upon the back, being protected thereby from abrasion. In *Iron*, *Epeorus*, and *Heptagenia* (Fig. 236) the body and appendages are flattened, and the nymphs of these genera are adapted for clinging to rocks in rapidly flowing water. The gills are laminate and each is provided with a basal tuft of branchial filaments. *Cloëon* and *Siphlonurus* have seven pairs of simple lamellae which project from the sides of the body: the three caudal filaments are fringed with setae and function as a kind of tail. They are active swimming nymphs living among water plants, etc. In *Caenis* and *Tricorythus* the nymphs live in an environment of mud and sand; there are six pairs of gills and the upper lamellae of the first pair form opercula concealing the gills behind. The branchial chamber thus formed is guarded by fringes of setae which preclude the entrance of mud or sand particles, held in suspension by the inhalant current. In *Oligoneuria* six pairs of dorsal gills are present on segments 2 to 7: each gill consists of small, thick, scale-like, non-respiratory lamina with a bunch of gill-filaments at its base. A pair of similar ventral gills occurs on the first segment and a tuft of gill-filaments at the base of each maxillary palpus. Similar adventitious gills occur on the thorax and mouthparts of a few other species. *Prosopistoma* (Vayssière, 1890) has a most highly modified nymph which uses its body as a kind of sucker, attaching itself by this means to stones in flowing water; it can also swim rapidly by means of its fan-like caudal filaments (Fig. 238). In this genus there are five pairs of gills located in a branchial chamber. The latter is roofed over by a carapace formed by the greatly developed pro- and mesothoracic terga, which are fused with the sheaths of the anterior wings. The side walls of the chamber are formed by the

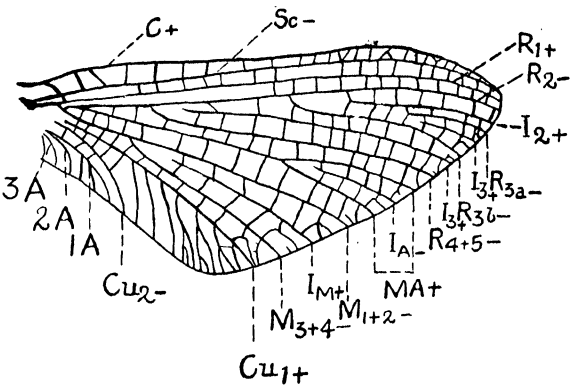


FIG. 237.—Fore wing of *Chironetes albimanicatus*

I_2, interpolated branch of R_2. I_3, I_5, interpolated branches of R_3. I_A, interpolated branch of *MA*. I_M, interpolated branch of media. *MA*, fork of anterior branch of media. (Convex veins +, concave do. −.) Venation *after* Morgan, modified.

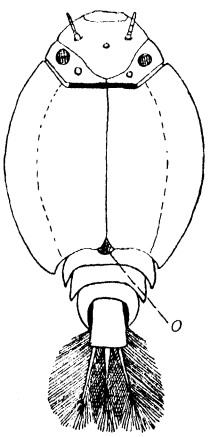


FIG. 238.—Nymph of *Prosopistoma*

o, exhalant aperture of branchial chamber. *After* Vayssière, *loc. cit.*

posterior wing-sheaths, and the floor by the combined terga of the metathorax and first six abdominal segments. Water enters this very perfect type of branchial chamber by a pair of lateral apertures and the exhalant stream passes through a median opening.

The morphology of mayfly nymphs has been studied in detail by Vayssière (1882) and certain of their more important anatomical features may be enumerated. Gills are commonly undeveloped in the newly-hatched nymphs: in *Ephemera* Heymons states that they arise as integumental outgrowths about the fourth day. Their usually flattened form, dorsal position and the fact that they are traversed by tracheae have led some observers to homologize them with wings. The researches of Heymons (1896a), Börner (1909) and Snodgrass (1931) into their development and musculature, indicate that they may be serially homologous with legs and should, therefore, be regarded as abdominal appendages which have become adapted for respiratory needs.

The mouthparts are very completely formed and the peculiar mandibles, with a single cephalic articulation, are strikingly like those of the Machilidae and of certain Crustacea; their bases are similarly elongate, and there is a median projecting molar area, which is only wanting in the few forms which are presumably predacious. Each maxilla has a single lobe, or mala, and a 2 to 4-segmented palp. The labial palpi are generally 3-segmented, and the ligula is conspicuously 4-lobed. The hypopharynx is very prominent and there is a pair of exceedingly well-developed superlinguae.

The digestive system is characterized by the great size of the stomach and the large number of Malpighian tubes: the latter organs differ greatly in character among various genera. They may either open directly into the hind intestine, or combine in groups, each group discharging into a separate pyriform sac which, in its turn, communicates with the intestine. The circulatory system is very well developed and easily observed. The dorsal vessel consists of one chamber for each abdominal segment and in the metathorax it is continued forwards as the aorta. In *Cloëon* it gives off a definite vessel into each of the caudal filaments and the terminal chamber acts as a pumping organ driving the blood into these organs: here it escapes by means of orifices in the walls of the vessels, and flows into the cavity of each filament, probably absorbing oxygen from the surrounding water.

The nervous system presents varying degrees of fusion with respect to the ganglia of the ventral chain. The brain is small but, correlated with the presence of compound eyes, the optic nerves and ganglia are well developed. In *Tricorythus* there are three thoracic and seven abdominal ganglia; in *Oniscigaster* the abdominal ganglia are reduced to six and the last two centres are closely united. In *Baetisca* and *Prosopistoma* the ganglia are fused into a common thoracico-abdominal centre; the latter genus, it may be added, is highly specialized in other directions also (Vayssière, 1890).

Classification.—Probably about 1,000 species of Ephemeroptera have been described but only the European and N. American representatives are at all adequately known. Eaton (1883–88) has monographed the order while the Nearctic species are dealt with by Needham *et al.* (1935), Berner (1950) and Burks (1953), and the European ones in works by Klapálek (1909), Ulmer (1929), Schoenemund (1930) and Kimmins (1950), the latter being a key to the 46 British species. Ulmer's (1933) classification of the order into three superfamilies and 13 families provides the basis for the following key.

Superfamily I. **Ephemeroidea.** M_{1+2} and Cu_1 of fore wing diverging strongly at base; hind tarsi with 4 movable segments or less, if a 5th segment is present it is fused with the tibia.

1. Sc of fore wing hidden in a fold and only visible at base; wings dull and translucent; legs of female short and weak; 2 caudal filaments . . PALINGENIIDAE
–. Sc of fore wing visible throughout its length. 2

2. Wings translucent in male, opaque in female; hind margin of wings without intercalary veins; legs weak, fore legs sometimes long in male, hind legs short and weak . . . . . POLYMITARCIDAE
–. Wings transparent and glistening; numerous intercalary veins at hind margin, especially of posterior wings; legs strong 3

3. Cu_1 of fore wing not forked, connected with margin by veinlets; fork of R_2 and R_4 in hind wing longer than its stem . . . . . EPHEMERIDAE
–. Cu_1 of fore wing forked, not connected with margin by veinlets; fork of R_2 and R_4 in hind wing not longer than its stem. . . . . POTAMANTHIDAE

Superfamily II. **Baetoidea.** M_{1+2} and Cu_1 of fore wing parallel at their bases; hind tarsi with 4 movable segments, if a 5th segment is present it is fused with the tibia.

1. Sc of fore wing entirely visible and separated from R 2
–. Sc of fore wing not visible, or visible at base only, fused with R or absent; wings milky or greyish with simplified venation; cross-veins limited to anterior part of fore wings . . . . . OLIGONEURIIDAE

2. MA in fore wing clearly forked 3
–. MA in fore wing not forked; wings clear; fore wings with few cross-veins; hind wings small and narrow or absent . . . . . BAETIDAE

3. Wings clear, with many cross-veins; hind wings seldom absent . . . 4
–. Wings milky, fringed on hind margin, often with but few cross-veins; hind wings absent (sometimes present in subimago); small species . . CAENIDAE

4. Cu_2 in fore wing separated from Cu_1 at base, but lying close to 1A; no free intercalary veins between M and Cu . . . . . LEPTOPHLEBIIDAE
–. Cu_2 in fore wing close to Cu_1 at base, but widely separate from 1A; usually two free intercalary veins between M and Cu . . . . . EPHEMERELLIDAE

Superfamily III. **Heptagenioidea.** M_{1+2} and Cu_1 of fore wing parallel at their bases; hind tarsi with 5 free segments.

1. Fore wing with Cu_1, Cu_2 and 1A somewhat parallel and equal in length; hind wing almost circular, with many long intercalary veins; pronotum very small BAETISCIDAE
–. Fore wings with Cu_1 and Cu_2 close at base but strongly divergent distally; Cu_2 much shorter and more strongly curved than Cu_1; hind wing oval . 2

2. Cu_1 of fore wing with more or less oblique, sinuous veinlets passing to wing-margin SIPHLONURIDAE
–. Cu_1 of fore wing without such veinlets; 2 or 4 parallel unattached intercalary veins in cubital area 3

3. With one pair of intercalary veins between Cu_1 and Cu_2; sometimes vestiges of a second pair lying near Cu_2; 2 or 3 caudal filaments . . AMETROPODIDAE
–. With 2 pairs of intercalary veins between Cu_1 and Cu_2, the larger pair near Cu_2; 2 caudal filaments . . . . . HEPTAGENIIDAE

(The imago of *Prosopistoma* does not clearly confirm the relationship to *Baetisca* which is suggested by the nymphs. Nevertheless the two genera are probably related (Gillies, 1954).)

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Order 6. **ODONATA** (Dragonflies)

Predacious insects with biting mouthparts and two equal or subequal pairs of elongate, membranous wings: each wing with a complex reticulation of small cross-veins and usually a conspicuous stigma. Eyes very large and prominent; antennae very short and filiform. Abdomen elongate, often extremely slender: male accessory genital armature developed on 2nd and 3rd abdominal sterna. Nymphs aquatic, hemimetabolous: labium modified into a prehensile organ: respiration by means of rectal or caudal gills.

Rather more than 4,500 species of these elegant insects have been described, and they are included in about 500 genera. They attain their greatest abundance in the Neotropical region and, except for Japan, no part of the Palaearctic zone contains an abundant or striking dragonfly fauna. With the exception of the Hawaiian *Megalagrion oahuense* they are aquatic in their early stages. The imagines, however, are by no means confined to the proximity of water, and the females of many groups seldom fly over such situations except for pairing or oviposition. They are essentially sun-loving insects but exceptions occur in some oriental species, which are only known to fly at night. Many are exceedingly swift on the wing and, according to Tillyard, *Austrophlebia* can fly at a speed of nearly 60 miles per hour: other species, particularly those of *Coenagrion* and *Agrion*, possess feeble powers of flight and may be caught with the greatest ease. Although no existing member of the order can compare in size with the Upper Carboniferous *Meganeura*, which has a wing expanse of over two feet, the females of *Megaloprepus coerulatus* measure about 190 mm. ($7\frac{1}{2}$ in.) across the wings.

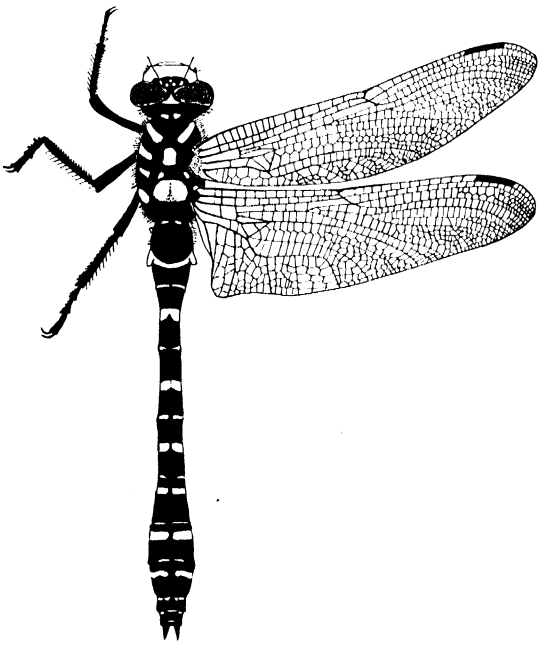


FIG. 239.—An Anisopteran dragonfly (*Cordulegaster boltonii*), male. Britain

Comparatively little information exists as to the food of different species

of these insects. It is captured on the wing and, if large, is held by the prehensile legs while being devoured. Most orders of winged insects are preyed upon, including other Odonata, Diptera, Hymenoptera and Coleoptera (Hobby, 1934). Though most species feed by day, especially in strong sun, Tillyard has recorded species preying upon Culicidae towards dusk, and Fraser states that the latter insects are captured by certain night-flying Odonata. The great majority of the order seldom travel far from their restricted haunts but certain species possess strong migratory instincts, more especially the European *Libellula quadrimaculata*. Great swarms of the latter insect have frequently been recorded and they sometimes travel many miles

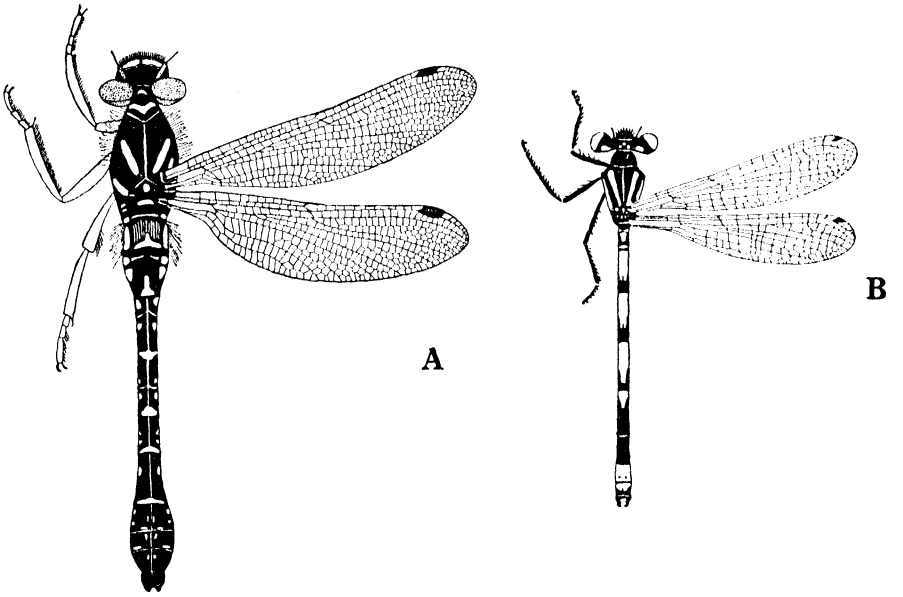


FIG. 240.—A. *Epiophlebia superstes*, female. Japan
B. Zygopteran dragonfly (*Coenagrion puella*), male. Britain
(Adapted from de Selys with wing-venation after Munz.)

out to sea. *Hemicordulia tau* has been noted by Tillyard occasionally to swarm in a like manner in Australia.

Odonata are noted for the beauty and brilliancy of their coloration and no order equals them in the wonderful development of body colours. In addition to pigmentary and structural colours, a whitish or bluish pruinescence is often present, especially in the males. It appears to be correlated with the maturation of the gonads and is exuded through fine cuticular pores, appearing as a kind of 'bloom' as on certain fruits. Since it is of the nature of an exuded supracuticular pigmentation it is easily removed by rubbing and wear. In the female it is much less frequent and develops at a later period in life.

Among dragonflies a bicolorous pattern is the most primitive, unicolorous forms being a later development. Many unicolorous males have bicolorous females, and newly emerged members of the former sex often exhibit traces of an original bicolorous marking for a shorter or longer period. Among the Coenagriidae the females are sometimes dimorphic, and one or other colour form may closely resemble the male. In the common *Ischnura elegans*, for example, the predominating or normal colour form of the female is extremely

like that of the male: the rarer or 'heteromorphic' females are conspicuously marked with orange, which is wanting in the normal form. Most Odonata possess hyaline wings but there are certain groups in which they are conspicuously coloured. Thus among species of *Agrion* the males have metallic blue or green wings. In the Australian and E. Indian *Rhinocypha* the metallic coloration reaches its maximum and consists of a combination of glistening reds, mauves, purples, bronzes and greens utterly baffling description (Tillyard). In *Rhyothemis* the wings are also exquisitely coloured with metallic green, purple or bronze.

The best general work on the order is that of Tillyard (1917) which has been invaluable in preparing the present chapter.

The Imago

External Anatomy.—The form of the head (Fig. 241) in dragonflies has become modified in correlation with the great development of the *eyes* (Lew, 1934). The latter, in many Anisoptera, meet mid-dorsally and compose by far the largest part of the cephalic region: in the Zygoptera the eyes are much smaller and button-like, but their range of vision is increased by the transversely elongated head. In the Anisoptera, occiput, vertex and frons are distinct sclerites but in the Zygoptera the sutures of the head-capsule in these regions are less distinct or absent. The clypeus is often divided transversely into two plates and a characteristic π-shaped tentorium is present (Hudson, 1948).

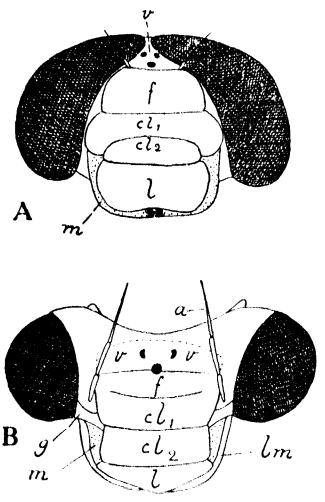


FIG. 241.—Head of A, Anisoptera: B, Zygoptera

a, antenna; cl_1, post-clypeus; cl_2, anteclypeus; *f*, frons; *g*, gena; *l*, labrum; *lm*, labium; *m*, mandible; *v*, vertex.

The *antennae* are always very short and inconspicuous: they are composed of three to seven segments, the latter number being usual, and have poorly developed sense organs. Experiments in amputating one or both antennae have been made by Tillyard who finds that the insects suffer no inconvenience by their removal, and fly with the usual facility. The reduction in the development of these organs is correlated with the increased power of the compound eyes. The *mouthparts* (Fig. 242) are entirely of the biting and masticatory type. The *mandibles* are stout with exceedingly powerful teeth, and the *maxillae* each carry a lobe-like unsegmented palpus and a dentate mala, the latter probably representing the fused lacinia and galea. The morphology of the *labium* has given rise to considerable controversy. On referring to Fig. 242 it will be seen that the prementum is expanded by the development of sidepieces or *squamae* and each squama carries the *lateral lobe* of its side. The inner border of each lobe terminates in an *end-hook* and slightly external to the latter is a small *movable hook*. The lateral lobes and hooks are probably modified labial palps. The prementum carries a single distal lobe or *ligula* which is often medianly cleft. In the Libelluloidea the movable hook is wanting, the end hook and median lobe are vestigial, while the two lateral lobes are greatly developed.

The head is exceptionally mobile and attached to an exceedingly small slender neck region which is supported on either side by four cervical sclerites.

The prothorax, though greatly reduced, remains a distinct segment, while the meso- and metathorax are intimately fused together. The two latter segments are peculiarly modified in conformity with the requirements of the legs and wings (Fig. 243). The legs have shifted their attachments anteriorly and the sterna have migrated along with them. The wings, on the other hand, have moved posteriorly and the terga have shifted likewise. Although the sterna and terga of these segments are reduced their pleura are very greatly developed. The mesepisterna extend forwards and dorsalwards so as to meet in front of the mesotergum to form the dorsal carina: by this means the terga are pushed backwards and lie between the wing bases. The metepimera on the contrary have grown downwards and backwards, usually fusing ventrally behind the metasternum. In this way the sterna become pushed forwards and the legs come to lie close behind the mouth, being enabled thereby readily to hold the prey. The legs are unfitted for walking but are of some value for climbing, and the tarsi are 3-segmented.

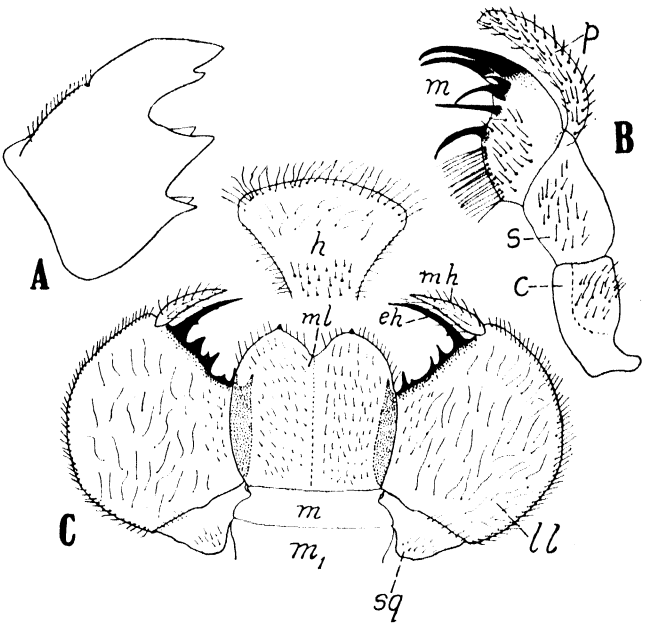


FIG. 242.—Mouthparts of *Cordulegaster boltonii*

A,l eft mandible. B, left maxilla (ventral); *c*, cardo; *s*, stipes; *m*, mala; *p*, palp. C, labium and *h*, hypopharynx; *m*, prementum; m_1, postmentum; *ml*, median lobe (ligula); *ll*, lateral lobe (palp) with *eh*, end-hook and *mh*, movable hook; *sq*, squama (palpiger).

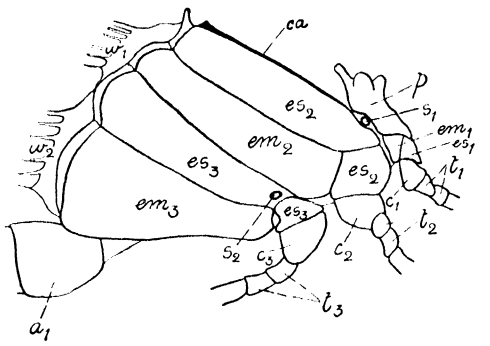


FIG. 243.—Lateral view of thorax of *Agrion virgo*

a_1, 1st abdominal segment; *c*, coxa; *ca*, dorsal carina; *em*, epimeron; *es*, episternum (es_2 and es_3 are divided into an- and kat-episternum); *p*, pronotum; *s*, spiracle; *t*, trochanter (double); *w*, wing.

The two pairs of wings (Figs. 244 and 245) are almost identical in the Zygoptera, but in Anisoptera the hind wings are broader basally and there are minor venational differences. The veinlets are developed to a remarkable degree and form a complex reticulum, giving rise to a large number of often minute cells. In a single wing of *Neurothemis* according to

Tillyard there are over 3,000 cells. The stigma, a thickening of the wing-membrane between C and R, is a very characteristic feature. In the Petaluridae it is very elongate while in the Pseudostigmatidae it may be absent or abnormal.

The homologies of the main veins have not been unequivocally decided, Needham (1951, etc.) and others relying much on the pattern of nymphal

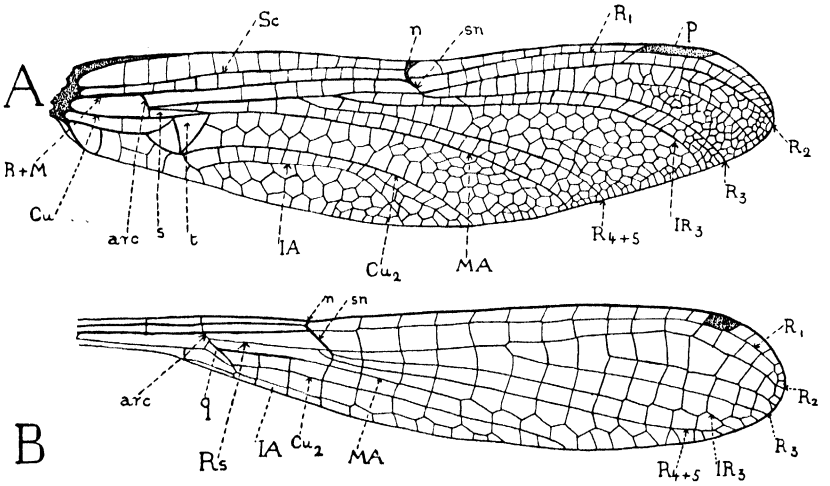


FIG. 244.—A, venation of an Anisopteran dragonfly (chief features only). B, of a Zygopteran dragonfly

arc, arculus; IR_3, intercalated vein; *n*, nodus; *p*, pterostigma; *q*, quadrilateral; *s*, supratriangle; *sn*, subnodus; *t*, triangle.

tracheation while Tillyard (1928) and Tillyard & Fraser (1938–40)—who are followed here—base their interpretation on fossil forms. Sc lies a little behind the costal margin and appears to end at the thickened cross-vein which constitutes the joint-like *nodus*. The radius and media arise basally as a single vein from which R_1 is soon given off as an unbranched vein running to the wing

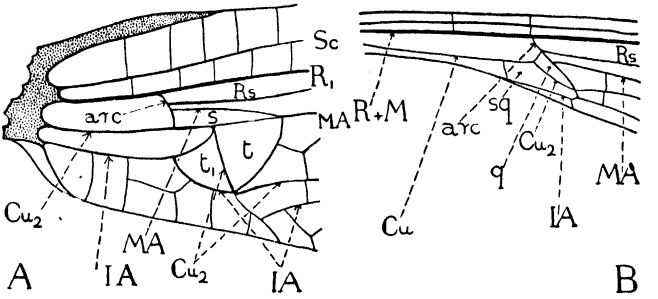


FIG. 245.—Basal area of fore wing of A, an Anisopteran, and B, a Zygopteran

sq, subquadrilateral; t_1, subtriangle. Other lettering as in Fig. 244.

apex and joined to the costal margin by a series of *ante-* and *postnodal* cross-veins. The backwardly bent stalk of R_s + M, together with the cross-vein behind it, forms the *arculus*, just distal to which is a conspicuous *discoidal cell*. The latter, in the Zygoptera, is known from its shape as the *quadrilateral*, but in the Anisoptera it is divided by a cross-vein into the *triangle* and *supratriangle*, both of which may be further subdivided by thin cross-veins. R_s is

divided into three branches between which secondary intercalary or supplementary veins may occur. The media is represented only by the anterior media (MA) and the cubitus only by its posterior branch (Cu_2), though basal traces of the missing MP and Cu are found in the fossil Meganeuridae. The anal vein (1A) arises independently and runs almost parallel to Cu_2 (Fraser, 1938) but is coincident with the hind margin of the wing basally in many Zygoptera. 1A and Cu_2 are connected basally by a cross-vein, the *anal crossing* (Ac). The venation provides many important taxonomic characters, an indication of some being given in the key to families (p. 307).

The abdomen (Fig. 246) is always greatly elongate in proportion to its breadth, and in extreme cases it is so attenuated as to be scarcely thicker than a stout bristle. Ten complete segments are evident, while according to Heymons vestiges of the 11th segment and the telson are also recognizable. In males of the Corduliidae a pair of lateral outgrowths or *auricles* are present on the 2nd tergum (Fig. 246, C): in some cases they occur in the females also but are reduced in size. The interpretation of the terminal abdominal structures is controversial (Handlirsch, 1903; Heymons, 1904; Snodgrass, 1935) but Heymons' views are given here. The 10th segment bears posteriorly a pair of *superior anal appendages*, apparently secondary structures, which are well-developed in the male but reduced or vestigial in females. The 11th segment comprises a tergite and a small divided sternite. The tergite is produced into the *median inferior anal appendage* in Anisopteran males but is otherwise rudimentary. The cerci form the *paired inferior anal appendages* of male Zygoptera but are absent or vestigial in other members of the order. The telson is probably represented by three small processes immediately surrounding the anus: a median dorsal *lamina supra-analis* and paired lateroventral *laminae infra-anales*. During pairing, in all Odonata, the female is grasped by means of the anal appendages of the male, the superior pair establishing a firm grip in the region of the neck (among Anisoptera) or prothorax (among Zygoptera) while the inferior appendage of the Anisopteran male is pressed down upon the occiput. In the Zygoptera the inferior pair is usually too short to reach the head.

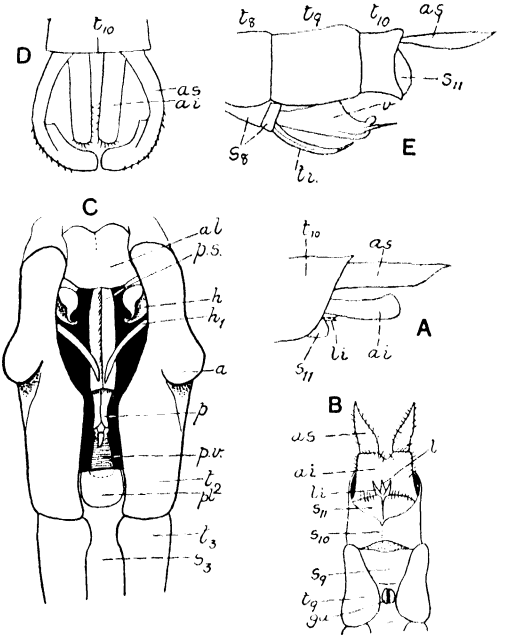


FIG. 246.—*Cordulegaster*. A, lateral view of male genitalia. B, ventral view of terminal abdominal segments of male. C, ventral view of male copulatory apparatus. D, *Agrion*, dorsal view of male genitalia. E, *Aeshna*, lateral view of terminal abdominal segments of female with left parts of ovipositor slightly separated

a, auricle; *ai*, inferior, and *as*, superior anal appendages; *al*, *pl*, anterior and posterior sternal laminae; *ga*, genital aperture; *h*, h_1, hamulae; *l*, lamina supra-analis; *li*, lamina infra-analis; *p*, penis with *ps*, its sheath; *pv*, penis vesicle; *s*, sternum; *t*, tergum; *tr*, terebra; *v*, valve.

The copulatory organs of the male (Fig. 246, C) are unique among insects,

being developed from the 2nd and 3rd abdominal sterna, though the true genital aperture opens on the 9th segment. On the 2nd sternum is a depression or *genital fossa* in which the copulatory organs are lodged and its walls are supported by a complex sclerotized framework. The fossa communicates posteriorly with a small sac—the *penis vesicle* which is developed from the anterior portion of the 3rd sternum. The *penis* arises from this vesicle and, in the Anisoptera, it forms a complex jointed organ provided with an orifice on its convex surface. In the Zygoptera its only communication is with the body cavity and there is no distal aperture. One or two pairs of claspers or *hamuli* are associated with the penis and serve to guide and retain the ovipositor in position during copulation. The posterior pair of hamuli is universal but the anterior pair is only met with in the Aeshnoidea. Great variation of structure is exhibited by the genitalia in various genera and for detailed information reference should be made to the work of Schmidt (1916). Owing to the wide separation of the copulatory organs from the genital aperture, the spermatozoa have to be transferred to the penis vesicle prior to copulation. In the female the external genitalia consist typically, as in the Zygoptera, of three pairs of appendages which make up the ovipositor (Fig. 246, E). An anterior pair, developed from the 8th abdominal segment, and an inner pair from the 9th segment are slender structures adapted for cutting and, together, constitute the terebra. A lateral pair of valves, also arising from the 9th segment, are broad, lamellate organs each terminating in a hard, pointed style which may be tactile in function. A similar type of ovipositor is found among the Anisoptera in the Aeshnidae and Petaluridae, but among the other Anisopteran families either the lateral valves alone are vestigial (Cordulegasteridae) or all three pairs are vestigial or absent. The different types of ovipositor are correlated with different modes of oviposition.

Internal Anatomy.—Most of the internal organs are greatly elongated in conformity with the length of the body in these insects. The *alimentary canal* is an unconvoluted tube throughout its course. The oesophagus is long and slender, expanding into a crop at the commencement of the abdomen. A rudimentary gizzard is present but its armature of denticles is either very weak or absent. The mid intestine is the largest division of the gut and extends through the greater part of the abdomen: it is devoid of enteric caeca and is followed by a very short hind intestine. Attached to the latter are from 50 to 70 Malpighian tubes which unite in groups of five or six, each group discharging into the gut by means of a common conduit of extremely small calibre. Six longitudinal rectal papillae are usually present. The *nervous system* is well developed and exhibits comparatively little concentration. The brain is transversely elongated and is characterized by the great development of the optic ganglia, which is in correlation with the large size of the eyes. The ventral nerve-cord consists of three thoracic ganglia and seven evident ganglia (2nd to 8th) in the abdomen, the 1st abdominal ganglion being amalgamated with that of the metathorax. A well-developed sympathetic system is present (Cazal, 1948). The circulatory system has not been studied in any detail but appears to be very similar to that of the nymph, with the exception that a ventral blood sinus is present in the imago in close relation with the main nerve-cord. The tracheal system (Wolf, 1935) consists of three pairs of principal longitudinal trunks which give off segmental branches. It communicates with the exterior by means of ten pairs of spiracles situated on the last two thoracic and the first eight abdominal segments. The *male reproductive organs* consist of a pair of very elongate *testes* extending, in *Aeshna*, from the 4th to

the 8th abdominal segments: each organ is composed of a large number of spherical lobules in which the spermatozoa are developed. The vasa deferentia are rather short narrow tubes which enter a common duct just above the genital aperture. The common passage is dilated dorsally to form a conspicuous sperm-sac. The spermatozoa adhere in a radiating fashion forming rounded masses or sperm-capsules, each of the latter being apparently derived from a single lobule of the testis. These capsules are somewhat mucilaginous externally and are adapted for transference from the 9th to the 2nd segment, prior to copulation. The *female reproductive organs* are characterized by the great size and length of the ovaries which extend from the base of the abdomen down to the 7th segment. Each ovary is composed of a large number of longitudinally arranged panoistic ovarioles. The two oviducts are very short and open into a large pouch-like spermatheca in the 8th segment. A pair of accessory glands communicate by means of a common duct with the dorsal side of the spermatheca.

Structure and Biology of the Developmental Instars

Oviposition in dragonflies may be either endophytic or exophytic. In the latter case the eggs are rounded and are either dropped freely into the water or attached superficially to aquatic plants. This method is the rule among the Anisoptera, with the exceptions mentioned below. In *Sympetrum* and *Tetragoneuria* the eggs are laid in gelatinous strings attached to submerged twigs. Endophytic oviposition is characteristic of the Zygoptera and the Anisopteran families Aeshnidae and Petaluridae (Tillyard). Dragonflies adopting this method have elongate eggs which they insert into slits cut by the ovipositor in the stems and leaves of plants or other objects, near or beneath the water. In some cases the female (alone, or accompanied by the male) descends below the water-surface for the purpose.

Before the nymph emerges from the egg it swallows amniotic fluid, the associated contractions of stomodaeal musculature being visible through the shell (Grieve, 1937). Pressure of the head of the embryo against the chorion is the immediate cause of hatching, since it forces open the lid-like anterior extremity of the egg. The newly-hatched insect is known as the pronymph: at this stage it exhibits a more or less embryonic appearance, the whole body and appendages being invested by a delicate cuticular sheath. The pronymph is of extremely brief duration, lasting but a few seconds in *Anax* (Tillyard), for two or three minutes in *Coenagrion* (Balfour Browne, 1909), but up to 30 minutes in *Sympetrum striolatum* (Gardner, 1951). At this stage the pulsations of the stomodaeum increase in frequency and the pronymphal sheath is ruptured. The insect which emerges is in its second instar: it is now a free nymph fully equipped for its future life. The nymphs of the Odonata are campodeiform and may be divided into two main types—the Anisopteran and the Zygopteran. In the former the body is terminated by three usually small processes, viz.—a median appendix dorsalis and a pair of lateral cerci: when closed they form a pyramid which conceals the anus (Fig. 247). Respiration takes place by means of concealed rectal tracheal gills. In the Zygopteran type the three terminal processes are greatly developed to form caudal gills, and rectal tracheal gills are wanting (Fig. 248). *Megalagrion oahuense* nymphs are terrestrial, living among moist debris on the floor of Hawaiian forests and some other species of *Megalagrion* spend much time crawling out of streams in a water-film on rocks (Williams, 1936) but all other Odonate nymphs are

exclusively aquatic, living in various situations in fresh water. Many live hidden in sand or mud, etc., and are homogeneously coloured without any pattern. Those which live on the river-bottom or among weed exhibit a cryptic pattern which tends to conceal them from enemies and prey. A few live in the water which accumulates at the leaf-bases of Bromeliads and other tropical plants. Certain species cling to rocks and tend to simulate the colour of the surface which they frequent. Dragonfly nymphs are also able to change their general coloration in accordance with differences in their environment. Without exception all the species are predacious, feeding upon various forms of aquatic life, the nature of the food depending upon the age of the nymphs. When advanced in life they are particularly addicted to Ephemeropteran nymphs and Culicid larvae as well as nymphs of their own and other species of Odonata. The larger Aeshnid nymphs will also attack tadpoles and occasionally small fish. The number of instars that intervene between the egg and the imago varies in different species and also among individuals of the same species. It ranges between about ten and fifteen (Munchberg, 1938; Gardner, 1951) and the whole nymphal period may be passed through within a year as in most Zygoptera, or occupy two years as in *Aeshna*, or may even last from three to five years. The principal external changes involved during metamorphosis (see, for example, Snodgrass, 1954, and Calvert, 1934) include an increase in the size of the compound eyes, and during the last few instars ocelli become evident: the antennal segments increase in number, and the wing-rudiments undergo certain changes with the result that the developing hind wings overlap the anterior pair: the wing-bearing segments increase in size, and changes are evident in the caudal gills among the Zygoptera. The internal changes which occur in the fully grown nymph just before metamorphosis is complete have been less fully studied, but they include changes in the histological structure of the gut (Straub, 1943) and the disintegration of the musculature of the nymphal labium with its replacement by a newly developed set of imaginal muscles (Munscheid, 1933).

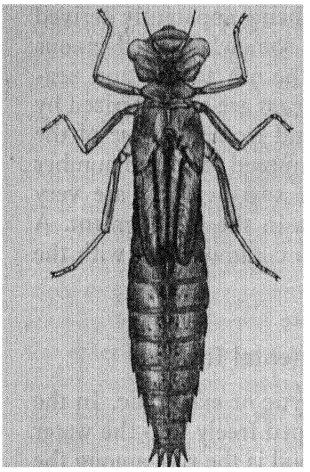


FIG. 247.—Nymph of *Brachytron pratense*. × 1·6
From a drawing by W. J. Lucas.

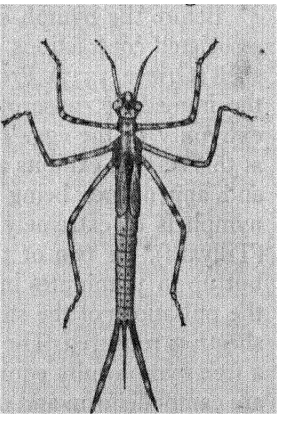


FIG. 248.—Nymph of *Agrion splendens*. × 1·25
From a drawing by W. J. Lucas.

When the imago is approaching the time for emergence the nymph ceases to feed and appears tense and swollen. The thorax in particular becomes noticeably inflated and the wing-sheaths become sub-erect. The gills are no longer functional and at the same time the thoracic spiracles are brought into use, the nymph partially protruding itself from the water in order to breathe the atmosphere. When the internal changes are complete the nymph climbs up some suitable object out of the water and fixes its claws so firmly in position that the exuviae remains tightly adherent to the support long after the imago

has flown away. The nymph remains stationary and sooner or later the cuticle splits along the mid-dorsal line of the thorax, the fracture extending forwards to the head. The imago then withdraws its head and thorax through the opening, the legs and wings become freed, but the abdomen is not yet fully drawn out from the exuviae. The insect usually hangs head downwards until the legs attain strength and freedom of movement. The withdrawal of the abdomen forms the final act, and the insect crawls away to rest until the wings and abdomen are fully extended (Fig. 198). A variable period elapses before the imaginal colour pattern is fully acquired and teneral forms, or individuals which have not yet developed their mature coloration, are very commonly observable on the wing.

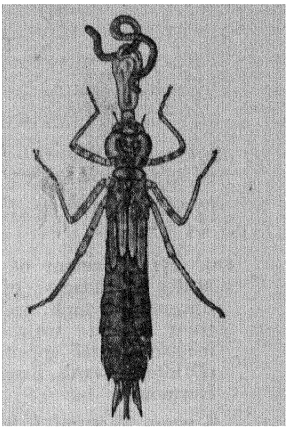


FIG. 249.—Nymph of *Anax imperator* with mask extended and seizing prey. × 0·8

From a drawing by W. J. Lucas.

The main difference between the head of the nymph and that of the imago is found in the labium. In the nymph this organ is modified for prehensile purposes and is known as the *mask* (Fig. 250) from the fact that it conceals the other mouthparts (Butler, 1904). The prementum and postmentum are markedly lengthened, and there is a great freedom of movement between the two parts. The ligula is undivided and represented by a median lobe which is fused with the prementum. The labial palpi are modified to form lateral lobes, each of which carries on its outer side a movable hook. The nymph utilizes its mask entirely for the capture of prey (Fig. 249). In a position of rest the postmentum is reflexed between the bases of the legs with the prementum hinged upon it ventrally. When about to seize a victim the mask is thrown forward and extended with lightning rapidity and the prey impaled on the movable hooks.

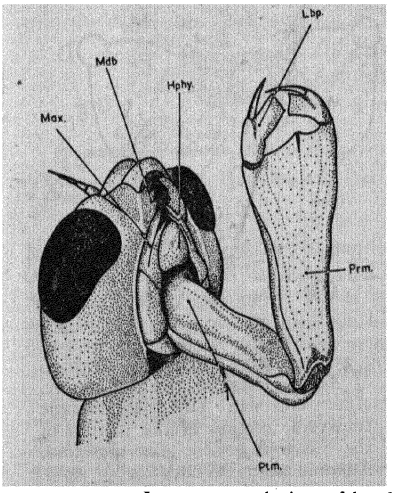


FIG. 250.—Latero-ventral view of head and mouthparts of an Odonate nymph (*after* Weber, 1933)

Hphy, hypopharynx; *Lbp*, labial palp; *Max*, maxilla; *Mdb*, mandible; *Prm*, prementum; *Ptm*, postmentum.

The prothorax in the nymph is always longer than in the imago: in advanced nymphs the meso- and metathorax are closely fused. The legs are considerably longer than those of the imago and the femoro-trochanteral articulation is modified to form a breaking joint. By a sudden contraction of the trochanteral muscles the intervening membrane can be ruptured, and the limb discarded should it be seized by a predatory insect. Ten segments are clearly recognizable in the abdomen and according to Heymons (1904) the 11th segment and telson are also present in a much reduced condition (Fig. 251). The 11th segment is represented dorsally by the base of the dorsal appendage (to be described below) and its sternum by the bases of the cerci. The telson persists as the lamina supra-analis and the laminae infra-anales. Three large appendages can be readily made out in the nymphs—a median dorsal

appendage and two lateroventral cerci: these structures form the caudal gills of the Zygoptera. From the 4th or 5th instar onwards a second set of appendages appears and gives rise to the imaginal terminalia. They consist, in both sexes, of a pair of small pointed structures (the cercoids of Heymons) lying above the cerci: the superior appendages of the male imago and the anal

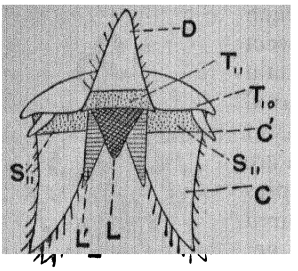


FIG. 251.—Diagram of the anal appendages of a dragonfly nymph viewed from behind with the median dorsal appendage (*D*) lifted upwards. Based on Heymons

C, cercus; *C'*, cercoid; *L*, lamina supra-analis; *L'*, lamina infra-analis; S_{11}, 11th sternum; T_{10}, T_{11}, 10th and 11th terga.

appendages of the female are derived from these organs. At the final metamorphosis the median dorsal appendage is cast off, but in male Anisoptera a small basal process persists as the inferior appendage of the adult. The cerci disappear except in males of the Zygoptera whose inferior appendages are developed within their bases.

The alimentary canal of the nymph (Sadones, 1896; Straub, 1943) differs from that of the imago in several features. The gizzard, for example, is a very highly specialized organ provided with internal denticle-bearing longitudinal ridges: the latter are either four or some multiple of four in number among different groups of the order. The mid intestine is considerably shorter than in the imago, and the Malpighian tubes at first number only three but gradually increase at each instar until the full complement is acquired. The nervous system is more especially characterized by the presence of eight abdominal ganglia, the first centre in that series being quite distinct from the metathoracic ganglion although becoming fused with the latter in the imago. The circulatory system has been studied by Zawarsin (1911) in *Aeshna*. The heart consists of eight chambers corresponding with the 2nd to 9th abdominal segments in which they lie: alary muscles are only present in relation with the two hindmost chambers.

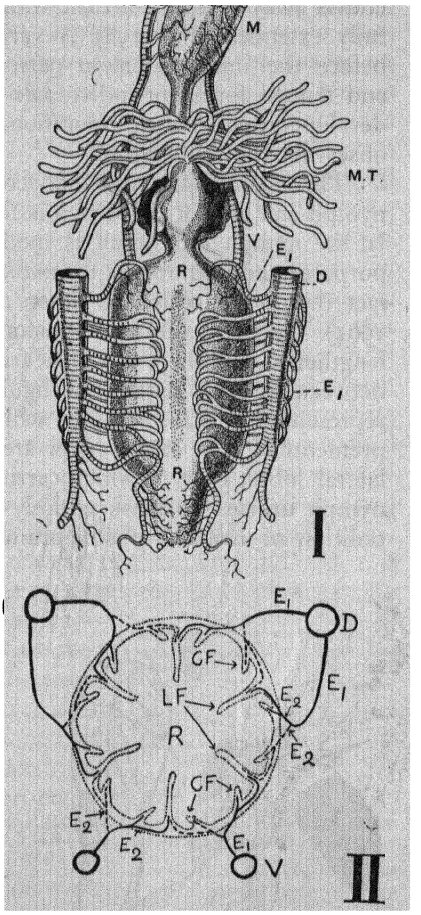


FIG. 252.—I. Hind intestine of a nymph of *Aeshna* showing tracheal supply. *After* Oustalet. II. Diagrammatic transverse section of the rectum of the nymph of *Austrogomphus*. Adapted from Tillyard

CF, cross-fold; D_1 dorsal tracheal trunk; E_1, primary efferent trachea; E_2, secondary do.; *LF*, longitudinal fold; *M*, mid intestine; *MT*, Malpighian tubes; *R*, rectum; *V*, visceral tracheal trunk.

The respiratory system presents features of exceptional interest and has been investigated more particularly by Sadones (1896), Tillyard (1916) and Wolf (1935). Spiracles are present on the meso- and metathorax, but only the mesothoracic pair is well developed and is functional when the larva has occasion to leave the water. The metathoracic and abdominal spiracles are small and usually non-functional. Special respiratory organs in the form of tracheal gills are present in the nymphs of all dragonflies. In the Anisoptera they take the form of rectal gills which form an elaborate and beautiful apparatus known as the branchial basket. In most Zygoptera the respiratory organs are caudal gills, while in a few rare cases (e.g. the Indomalaysian *Pseudophaea*) lateral abdominal gills are also present. These three types are treated separately below.

(1) **The Branchial Basket.**—This structure is formed by the expanded anterior two-thirds of the rectum, which assumes the form of a barrel-like chamber (Fig. 252). The gills are primarily developed as six longitudinal folds of the rectal wall and are

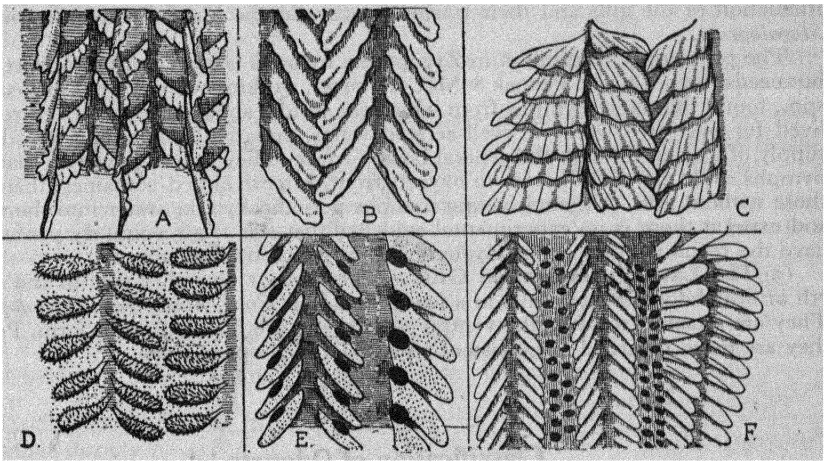


FIG. 253.—Portions of the freshly-opened branchial basket, to show form of gills

A, undulate simplex; B, implicate; C, foliate; D, papillo-foliate; E, F, lamellate. *After* Tillyard, *Biology of Dragonflies.*

homologous with the six rectal papillae. They are covered with an extremely delicate cuticle and the underlying epithelial layer is modified to form a syncytial core which is penetrated by tracheoles. Water is alternately taken into the rectum and expelled and, in this manner, the gills are kept aerated. The expulsion of the water, when forcible, also enables the nymph to propel itself forward by a series of jerks, which is its usual mode of progression. Six series of primary efferent tracheae convey the oxygen, taken up by the gills from the water, to the main longitudinal trunks of the body. Each primary efferent trachea divides into two secondary efferents which give off a very large number of tracheoles to the gills. Each tracheole forms a complete loop within the gill, returning to the same secondary efferent from which it arose. The gill system may be either simplex or duplex in character (Fig. 253). In the *simplex system* there are six principal longitudinal gill folds supported right and left by a double series of cross-folds. The simplex system is divisible into two types, the undulate and the papillate. In the undulate type the free edge of each gill-fold is undulated or wavy in character. This is the primary type of gill which persists throughout life in the more archaic groups (Cordulegasteridae, Petaluridae and in *Austrogomphus*). In most of the Gomphidae all the gill-folds are broken up into elongate filaments forming what is termed the papillate type. This specialization brings about greater respiratory efficiency since each filament is bathed on all sides by the water. The *duplex system* is a secondary development and differs in that the main longitudinal folds are either

non-functional or wanting, the gills being entirely formed from the double series of cross-folds. Three main types in this system are recognizable and depend upon the form assumed by the gills. The implicate type occurs in the tribe Brachytronini of the family Aeshnidae. The gills resemble a series of obliquely placed concave tiles slightly overlapping one another. In the foliate type, which is found in the Aeshnini, each gill is basally constricted and leaf-like in form. The lamellate type occurs in the family Libellulidae: the gills appear as flat plates projecting into the cavity of the rectum and are attached by broad bases. For full details concerning the types of rectal gills and the differences in their tracheal supply reference should be made to papers by Tillyard (1916) and Rich (1918).

(2) **The Caudal Gills.**—Nearly all Zygopteran nymphs possess three external tracheal gills at the hinder extremity (Fig. 248) and a full account is given by Tillyard (1917a). The median gill is dorsal and is developed from the appendix dorsalis, while the two lateral gills are derived from the cerci. In the young nymph the caudal gills are filamentous and hairy, but they soon acquire a triquetral form (i.e. triangular in cross-section). The triquetral gill is retained throughout life in a few cases, as for example in the lateral gills of *Agrion*. In most instances it either becomes swollen (saccoid gill) or flattened (lamellate gill). Internally the gills contain one or more large tracheal branches ending in an anastomosing tracheolar system, nerves and definite blood channels while the remaining space is filled by a peculiar alveolar tissue. Reduction of the gills and their tracheae occurs in the less fully aquatic species of *Megalagrion*.

The problem of respiration in Zygopteran nymphs is reviewed by Calvert (1915) but needs further study. Pennak & McColl (1944), working with nymphs of *Enallagma* spp., found that large nymphs from which the caudal appendages had been removed lived for over two weeks in well-aerated water, apparently obtaining an adequate supply of oxygen through the general body-surface. They found, however, that intact nymphs could extract rather more oxygen from water in closed containers than could those without gills. Although young nymphs periodically take water into the rectum and expel it there is no experimental evidence that this is a respiratory process, nor have the rectal papillae of the Zygoptera any special tracheal supply.

(3) **The Lateral Abdominal Gills.**—These occur on either side of the 2nd to 7th or 8th abdominal segments in a few genera (e.g. *Cora*, *Anisopleura*, *Pseudophaea*). They are attached towards the ventral surface and are filamentous in form. Possibly they are to be regarded as persistent true abdominal appendages.

Classification of Odonata

The general classification of the order is discussed by Tillyard (1917) and Tillyard & Fraser (1938–40). There is a good monograph of the German species by May (1933) while the 45 British representatives are dealt with by Longfield (1949), Fraser (1949) and older authors. For the N. American species see Needham & Heywood (1929) and Walker (1953). The keys to families given below are based on Tillyard & Fraser and those found in the British Isles are denoted by an asterisk.

Suborder I. ZYGOPTERA

Fore and hind wings closely similar in form and venation, more or less petiolate basally, in repose usually held vertically above the abdomen; nodus usually before middle of wing; discoidal cell similar in fore and hind wings, very rarely open basally, never divided into triangle and supratriangle though sometimes crossed by veins. Eyes projecting laterally and separated by a space greater than their dorsal diameter. Labium with middle lobe deeply cleft. Male with two superior and two inferior anal appendages; penis not distinctly jointed. Female with superior appendages only and complete ovipositor. Nymphs with 3 caudal gills and slender, elongate abdomen; gizzard with 8–16 radially symmetrical folds.

Key to Zygopteran families

1. Less than 5 (usually 2) antenodals complete (i.e. running in straight line from C to R_1); arculus usually further from base of wing than from nodus . . 2
–. 5 or more complete antenodals; arculus nearer to wing-base than to nodus (AGRIOIDEA) 11

2. Postnodals not at all in line with cross-veins behind them; 1A visible as a separate vein from wing-base, contiguous with hind margin of wing as far as Ac (HEMIPHLEBIOIDEA) . . . . . HEMIPHLEBIIDAE
–. Postnodals more or less completely in line with cross-veins behind them; 1A not visible as a separate vein from base of wing to Ac (COENAGRIOIDEA) . 3

3. Cu_2 arching strongly forwards on leaving discoidal cell . . SYNLESTIDAE
–. Cu_2 not arched at this point 4

4. R_{4+5} and IR_3 both arising nearer arculus than subnodus or, if midway, then supplementary veins between R_2, IR_2 and R_3 running from wing-margin to main stem of R_2 5
–. R_{4+5} and IR_3 arising nearer subnodus than arculus or, if midway, without such supplementary veins. 6

5. Cu_1 and 1A complete; supplementary veins present between IR_3, R_{4+5} and MA . . . . . LESTIDAE *
–. Cu_1 reduced, 1A absent; supplementary veins present between R_2, IR_2 and R_3 . . . . . LESTOIDEIDAE

6. Nodus not more than $\frac{1}{4}$ of wing-length from base; pterostigma absent or not fully sclerotized or made up of several cells. . . . PSEUDOSTIGMATIDAE
–. Nodus usually more than $\frac{1}{4}$ of wing-length from base; if not, stigma normal . 7

7. Supplementary veins extending inwards from apical part of hind margin of wing as far as level of pterostigma or further . . . MEGAPODAGRIIDAE
–. Supplementary veins absent or not extending inwards as far as level of pterostigma 8

8. 1A and Cu_2 normal 9
–. Cu_2 normal or reduced, 1A reduced or absent 10

9. Discoidal cell subrectangular; course of main veins practically straight PLATYCNEMIDIDAE*
–. Discoidal cell with acute distal angle; veins IR_3, MA and 1A running a zigzag course distally . . . . . COENAGRIIDAE*

10. A basal cross-vein traversing the cell bounded by Cu_2, Ac and the hind margin of the wing; many postnodals . . . . . PLATYSTICTIDAE
—. No such basal cross-vein; fewer postnodals . . . . PROTONEURIDAE

11. Arculus absent . . . . . POLYTHORIDAE
—. Arculus present 12

12. Two thickened (primary) antenodals present 13
—. Primary antenodals absent 15

13. R_{2+3} more or less arched towards R_1 shortly after its origin; numerous secondary antenodals 14
—. R_{2+3} not arched towards R_1; few secondary antenodals . AMPHIPTERYGIDAE

14. Clypeus produced into a prominent snout . . . CHLOROCYPHIDAE
—. Clypeus not produced . . . . . HELIOCHARITIDAE

15. R_{2+3} usually not fused with R_1 shortly after its origin; discoidal cell shorter and traversed by very few cross-veins or none . . . . EPALLAGIDAE
—. R_{2+3} almost always fused with R_1 shortly after its origin; discoidal cell longer and traversed by numerous cross-veins . . . . AGRIIDAE*

Suborder II. ANISOZYGOPTERA

It is not easy to frame a definition of this suborder to embrace its many extinct Mesozoic forms, but the recent fauna includes only two species of *Epiophlebia* from

Japan and India (Fig. 240, A). Like the fossil forms these combine the characteristics of the two other suborders: the imago has a Zygopteran venation and the general body form of an Anisopteran while the nymph resembles the Anisoptera in general facies, labium and anal appendages (Tillyard, 1921).

Suborder III. ANISOPTERA

Fore and hind wings not petiolate, dissimilar in form and venation, the hind wings broadened basally; held horizontally or depressed in repose (except *Cordulephya*); discoidal cell differentiated into triangle and supratriangle. Eyes large, never separated by more than their dorsal diameter and often contiguous dorsally. Labium variable. Male with 2 superior and 1 inferior anal appendages; penis jointed. Female with superior appendages only and ovipositor normal or atrophied.

Larvae with rectal gills and anus closed by a pyramid made up of a median dorsal appendage and the two cerci. Gizzard with 4–8 folds.

Key to Anisopteran families

1. Antenodals incomplete (i.e. not running in a straight line from C to R_1); 2 thickened primary antenodals present; triangles of fore and hind wings not markedly different in shape and position (AESHNOIDEA) 2
–. Antenodals complete; no thickened primary antenodals; triangles differing markedly in shape and position, placed nearer arculus in hind wing than in fore wing (LIBELLULOIDEA) 5

2. Eyes broadly contiguous dorsally; female with complete ovipositor AESHNIDAE*
–. Eyes distinctly separated or just touching dorsally 3

3. Middle lobe of labium entire; eyes widely separated dorsally; ovipositor reduced to one small pair of valves on 8th sternum (vulvar scale). GOMPHIDAE*
–. Middle lobe of labium with deep fissure; eyes only moderately separated above. 4

4. Pterostigma moderately long and narrow; superior anal appendages of male narrow and acute apically; female with lateral valves of ovipositor vestigial, remaining ones hypertrophied . . . . . CORDULEGASTERIDAE*
–. Pterostigma very long and very narrow; superior anal appendages of male broadly triangular and blunt apically; female with complete ovipositor . PETALURIDAE

5. Triangle of fore wing with anterior side much more than half as long as basal side; tibiae keeled in male; usually metallic green or coppery . . CORDULIIDAE*
–. Triangle of fore wing with anterior side shorter, usually less than half as long as basal side; tibiae not keeled in male; rarely metallic . . LIBELLULIDAE*

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Order 7. **PLECOPTERA** (**Perlaria:** Stoneflies)

Soft-bodied insects of moderate to rather large size with elongate, setaceous antennae. Mouthparts weak, of the biting type: mandibles normal or vestigial, ligula 4-lobed. Wings membranous, held flat over the back in repose, hind pair usually the larger, with well-developed anal lobes. Venation variable, often considerably specialized: vein M 2-branched. Tarsi 3-segmented. Abdomen usually terminated by long multi-articulate cerci: ovipositor wanting. Metamorphosis hemimetabolous: nymphs aquatic, campodeiform, with the antennae and usually the cerci elongate: tracheal gills, which are variable in position, commonly present.

The Plecoptera are a small order, whose members are of considerable interest on account of the many archaic features in their structure, and the aquatic habits of their nymphs. The imagines have the same general characters as those of the Orthoptera, but the mouthparts are weaker, there is never more than a slight difference in texture between the fore and hind wings, and the coxae are small. They are poor fliers, and do not wander far from water. Their habitation is the margins of streams and lakes, particularly in hilly districts: they are commonly found resting upon stones, tree-trunks or palings near the water's edge, while the green forms frequent herbage. The larger species are well known to anglers as a bait for trout. The nymphs are exclusively aquatic, living beneath stones in clear water, particularly in streams with stony beds, and places where there are waterfalls, or where the water is otherwise well aerated. They do not live in polluted streams and few species occur in standing water. The imagines of many of the species with well-developed mandibles have been shown (Frison, 1935; Hynes, 1942; Brinck, 1949) to feed on lichens and unicellular algae.

External Anatomy.—There is no detailed account of the anatomy of the order as a whole, but the works of Schoenemund (1912), Wu (1923), Clark (1934) and Hanson (1946) are useful. The head-capsule (Hoke, 1924) resembles that of the Orthoptera but is prognathous, the epicranial suture may be reduced or even absent and the frontoclypeal suture is wanting in many species. The antennae are long and setaceous, with a large number of small segments. Compound eyes are well developed, and there are three (more rarely two) ocelli. The mouthparts (Fig. 254), although completely formed, are usually weak structures: the mandibles are normally developed in most families, but in the Pteronarcidae and Perlidae they are in the form of vestigial flexible lamellae. The maxillae consist of the typical sclerites and their palpi are 5-segmented. In the labium, the submentum is large, the prementum is sometimes divided, and both glossae and paraglossae are evident: the labial palpi are 3-segmented. The whole of the after-body is somewhat flattened, none of the parts are strongly sclerotized, and much shrivelling takes place in dried specimens. The thorax exhibits many primitive features. The prothorax

is large and mobile with an undivided notum and the pleuron is not differentiated into episternum and epimeron though Snodgrass (1935) recognizes in it the anapleurite and coxopleurite of more primitive forms. The meso- and metathorax are subequal segments, each composed dorsally of prescutum, scutum, scutellum and postnotum while the pleura show the usual division into episternum and epimeron. The sterna exhibit the full complement of sternites except that the spinasternum is missing from the metathorax while in the Capniidae the pro- and mesosternum have an additional sclerite lying between sternum and sternellum. On each sternum a pair of furcal arms arises from pits lying between the legs.

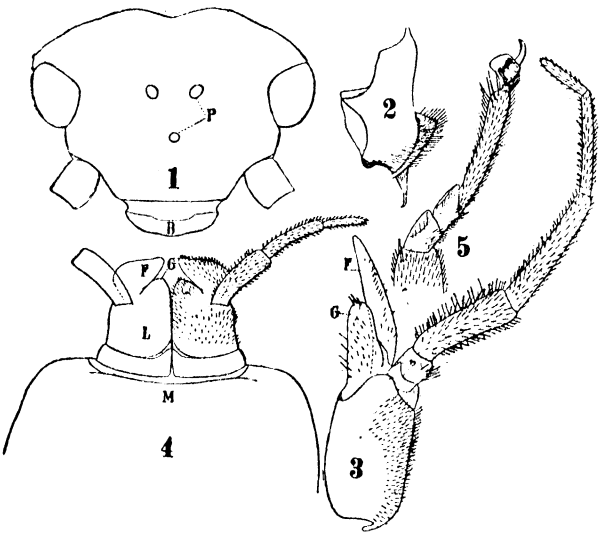


FIG. 254.—*Perla maxima*

1, frontal view of head; *P*, ocelli, *B*, labrum. 2, mandible. 3, maxilla; *F*, galea, *G*, lacinia. 4, labium; *F*, paraglossa, *G*, glossa, *L*, prementum. 5, tarsus. *After* Silvestri.

The wings are membranous: the hind wings are almost always considerably larger than the anterior pair, and a coupling-apparatus is not developed. The anal lobe is folded fanwise against the body when in repose. The tracheation in the nymphs has been studied in several genera: it closely resembles the hypothetical type in the absence of the transverse basal trachea (Fig. 33), The fully developed wings exhibit great instability of the subordinate veins, and individuals are frequently unlike with respect to the wing-venation of the two sides of the body. Apterous forms are few but several species exhibit a brachypterous condition. These include sexually dimorphic species with short-winged males (e.g. *Perla cephalotes*) and other species in which one or both sexes may be dimorphic, the brachypterous forms tending to occur at higher altitudes or latitudes (Aubert, 1946; Brinck, 1949). The most archaic type of venation is found in the Eustheniidae (Fig. 256): in this family the archedictyon is present over all parts of the wings, Rs exhibits three or more branches, and there is a large fan-like anal lobe to the hind wings carrying a number of anal veins. M is 2-branched and Tillyard (1928), on palaeontological grounds, claims that this vein corresponds to the anterior media of primitive fossil insects, the posterior media having been lost. Various transitional genera (Fig. 257) lead to more specialized types such as *Capnopsis*. In the latter genus the archedictyon has dis-

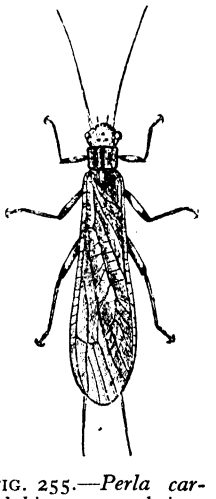


FIG. 255.—*Perla carlukiana*, natural size *After* Pictet.

appeared, Rs is 2-branched in the fore wing, and unbranched in the hind wing, while the latter has lost the anal lobe and vein 1A.

The abdomen is composed of ten evident segments, together with vestiges of an 11th segment. There is no ovipositor, the female gonopore opening on,

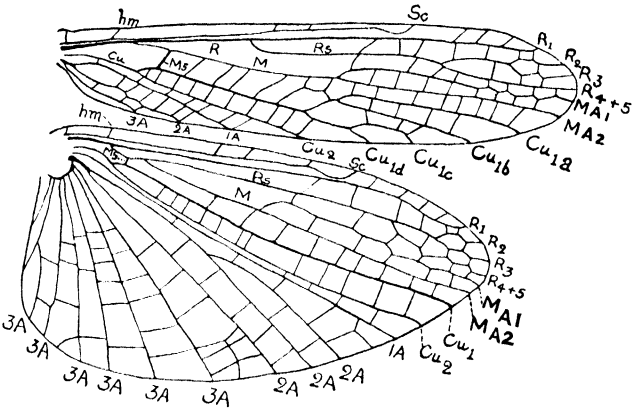


FIG. 256.—*Stenoperla prasina*, New Zealand, wings
After Tillyard, 1923 (modified).

or, much more frequently, behind the 8th abdominal sternum while the 7th, 8th or 9th sternite is usually modified to form a subgenital plate. The male, in which the gonopore opens behind the 9th sternum, lacks an appendicular copulatory organ. The 10th segment is usually a complete annulus in females

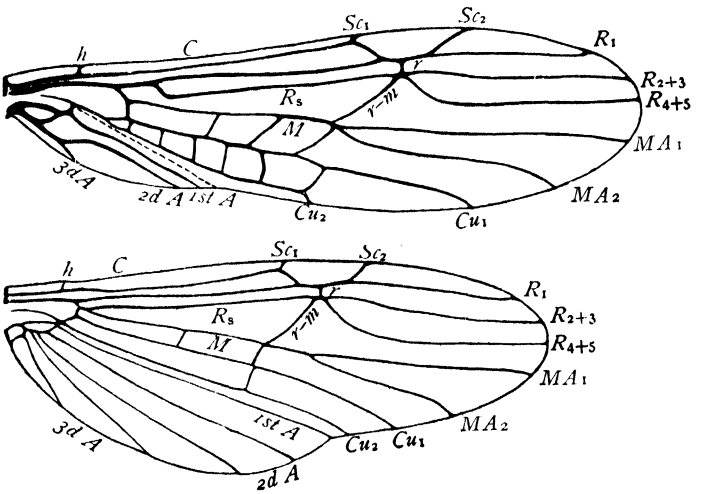


FIG. 257.—*Nemoura*, wings
After Comstock, *Wings of Insects* (modified).

but in males the sternum is generally reduced and membranous. The 11th segment is represented by a tergum (supra-anal lobe) and a divided sternum (subanal lobes), all of which may be modified in males to subserve a copulatory function. Cerci are characteristic of the order and are usually long multi-articulate structures of a primitive type: in the Nemouridae, however,

where they are sometimes used in copulation, they are small and composed of a single segment with, in some, a rudimentary 2nd segment.

Internal Anatomy.—The internal anatomy has been investigated by Pictet (1841–42), Newport (1851), Imhof (1881), Schoenemund (1912) and others. The oesophagus is exceedingly long and, in *Pteronarcys*, extends into the 4th abdominal segment: the gizzard is wanting or rudimentary, and the mid gut is small. In *Perla* there are ten anterior enteric caeca, the lateral pair being the largest. The hind intestine is short and the Malpighian tubes vary between about twenty and sixty. A pair of salivary glands is present. Both the supra- and suboesophageal ganglia are small: in *Pteronarcys* there are three thoracic and eight abdominal ganglia, but in *Perla* certain of the latter have undergone coalescence, with the result that there are only six evident ganglia in the abdomen. There are some variations in the structure of the reproductive system (Klapálek, 1896). In the male, *Leuctra* has a pair of testes, each composed of several follicles but in the majority of stoneflies the testis of each side is joined to its fellow, the two forming an arch-like structure. The paired vasa deferentia communicate with a pair of seminal vesicles (one in *Leuctra*) and in *Taeniopteryx* an accessory gland is also found. The reproductive system opens to the exterior by a median ejaculatory duct or, in some cases, by ducts from the seminal vesicles which remain paired up to the gonopore. The ovaries are composed of many panoistic ovarioles and are either separate (*Leuctra*, *Capnia*) or, more often, the ovarioles come off from a common duct joining the oviducts of each side. There is a spermatheca of variable form (absent in *Capnia*) and, in *Nemoura*, a bursa copulatrix. The rudimentary, non-functional hermaphroditism of *Perla marginata* is discussed on p. 194. The tracheal system opens to the exterior by two pairs of thoracic and eight pairs of abdominal spiracles.

Oviposition and Postembryonic Development.—Claassen (1931), Frison (1935), Kuhtreiber (1934), Hynes (1941) and Brinck (1949) give much valuable information on the nymphal stages and on the biology of the order. Mating does not occur in flight, the male mounting the back of the female on the ground and curving his abdomen down at one side of hers. In the Perlidae the eggs are fully developed when mating occurs and are laid soon after, but in other families maturation of the eggs in the adult takes several weeks. Very many eggs are laid, probably in several masses (e.g. Miller (1939) found that *Pteronarcys proteus* lays 500–1,000 eggs in batches of about 150 over a period of three weeks), the eggs of each mass being held together by a sticky slime which dissolves in water so that the eggs separate. Brachypterous females and some of the larger Perlidae crawl on stones etc. near the water's edge or move over its surface to lay their eggs, but the remainder oviposit while flying over the water, occasionally dipping the abdomen beneath its surface. According to Frison (1935) the females of some species of *Allocapnia* crawl into the water to lay their eggs and McLachlan (1864) says that females of *Leuctra* carry the eggs on their back before depositing them. The eggs of several species are described by Brinck (1949) and others. Those of the Perlidae are ovoidal or tetrahedral with a gelatinous outer membrane bearing adhesive structures which attach the egg to a substratum while the eggs of the other families are spherical and though they have a gelatinous coat they lack the adhesive bodies. *Allocapnia vivipara* and *Capnia nigra* are ovoviviparous.

The nymphs (Claassen, 1931; Hynes, 1941) resemble the adults very closely in their general form. Apart from the absence of fully developed wings, the characters which differentiate the nymphs from the adults are adaptive in

nature, fitting them for an exclusively aquatic existence. Plecopterous nymphs are characterized by their long multi-articulate antennae, and their similar elongate cerci (Fig. 258). The head may carry both ocelli and compound eyes: the legs are long, laterally fringed with natatory hairs, and terminated by paired claws. The tracheal system is apneustic, and respiration is either cutaneous or branchial. The most primitive type of nymph is found in the Eustheniidae: here there are five or six pairs of lateral abdominal appendages which function as gills (Tillyard, 1923). In other families the nymphs may breathe by means of secondary tracheal gills which, according to the species, occur on various parts of the body—submentum, neck, thorax, coxae, anterior 2–3 abdominal segments or the anal region. The gills may either be few and finger-like or in copious tufts. Nymphs of several Plecoptera such as *Isoperla*, *Leuctra* and *Capnia* are without gills. Plecoptera are also remarkable for the fact that the branchiae may persist in a somewhat shrivelled, non-functional condition in the imagines (Eggert, 1937). Perlid nymphs are largely carnivorous, preying chiefly on Ephemeropteran nymphs and Chironomid larvae, but those of the other families are mainly herbivorous, feeding on diatoms, algae and mosses. Correlated with this dietary distinction there are differences in the structure of the mouthparts. The herbivorous nymphs have large mandibles with a well-developed prostheca, stout maxillae and long glossae, while in carnivorous forms the mandibles are slender and sharp without a prostheca, the maxillae are weaker and the glossae reduced.

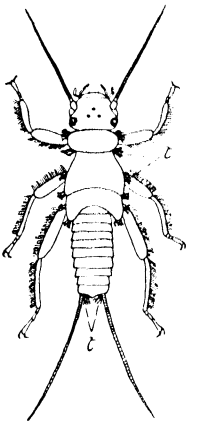


FIG. 258.—*Perla* sp., nymph
t, tracheal gills.

The time occupied in development appears to range from about a year in the smaller forms up to $3\frac{1}{2}$ or 4 years in the larger species. According to Wu (1923) a species of *Nemoura* passed through 22 instars and the same number was observed by Samal (1923) in *Perla burmeisteriana*. In *P. cephalotes* Schoenemund (1912) recorded 33 ecdyses during a period of three years and in *Pteronarcys proteus* there are 12 nymphal instars occupying two years (Holdsworth, 1941). Last-stage nymphs move to the water's edge and may crawl some distance on land before the adult emerges.

Classification.—Over 1,300 species are listed by Claassen (1940), of which the 34 which occur in the British Isles may be identified with the keys of Kimmins (1950), while most of the species from N.W. Europe are considered by Schoenemund (1927) and Despax (1951). The classification of the order has been dealt with by Enderlein (1909), Klapálek (1909), Tillyard (1921) and Ricker (1950; 1952). Monographs by Needham & Claassen (1925), Frison (1935; 1942) and Ricker (1943) also discuss the subdivision of the order. Though Klapálek and Frison, for example, have tended to recognize a large number of families and have been followed by many workers on the N. American and European fauna, the simpler arrangement of Tillyard is adopted in the key given below. Those families marked with an asterisk are represented in the British Isles.

Key to the families of Plecoptera after Tillyard (1921; 1923)

1. Anal lobe with archedictyon, margin entire (*Eusthenia*, *Stenoperla*) EUSTHENIIDAE
–. Anal lobe of hind wing without archedictyon, margin incised at apex of Cu_2 . 2

2. Anterior coxae closely approximated; mandibles vestigial; archedictyon present except on anal lobe (*Pteronarcys*) . . . . . PTERONARCIDAE
–. Anterior coxae widely separated 3

3. Mandibles vestigial; clypeus and labrum hidden beneath a frontal shelf; 3rd tarsal segment longer than 1st and 2nd together. (*Perla, Chloroperla*) PERLIDAE*
–. Mandibles, clypeus and labrum normal; 3rd tarsal segment not longer than 1st and 2nd together 4

4. More than 6 anal veins in hind wing (*Austroperla, Tasmanoperla*) AUSTROPERLIDAE
–. 6 or fewer anal veins in hind wing 5

5. No true anastomosis joining main veins from R to Cu_1 near middle of wings; distal cross-veins present (*Leptoperla, Gripopteryx*) . . . . . LEPTOPERLIDAE
–. A true anastomosis joining main veins from R to Cu_1 near middle of wings; distal cross-veins usually absent 6

6. Cerci 1-segmented, vestigial (*Taeniopteryx, Nemoura, Leuctra*) . NEMOURIDAE*
–. Cerci long, multi-articulate (*Capnia*) . . . . . CAPNIIDAE*

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Order 8. GRYLLOBLATTODEA

Apterous, with eyes reduced or absent and no ocelli. Antennae moderately long and filiform. Mouthparts mandibulate. Legs approximately similar to each other; tarsi 5-segmented. Female with well-developed ovipositor; neither 7th nor 8th abdominal sternum enlarged to form subgenital plate. Male genitalia asymmetrical. Cerci long, 8-segmented.

This order, the first representative of which (*Grylloblatta campodeiformis*) was discovered by Walker (1914) in the Canadian Rockies, contains only six species. Its members exhibit many primitive features and are therefore of considerable phylogenetic interest.

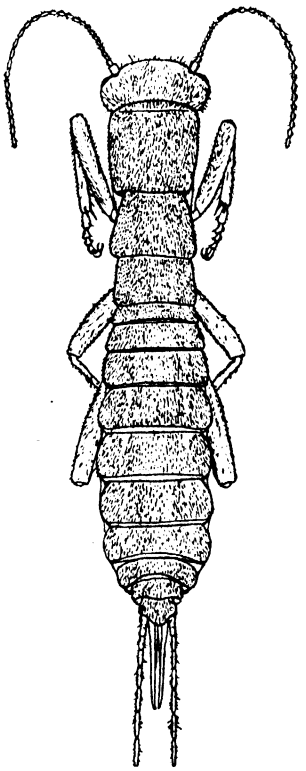


FIG. 259.—*Grylloblatta*, female
After Walker, *Canad. Ent.*, 1914.

External Anatomy.—Walker (1931) describes the *head-capsule* of *Grylloblatta campodeiformis* as flattened and prognathous. The epicranial, frontoclypeal, subgenal, occipital and postoccipital sutures are present, together with a 'parietal' suture which runs from the antennal socket to the foramen. Of the head sclerites the labrum is well developed, the clypeus large and subdivided into ante- and post-clypeus while the gena and postocciput are small. There is a complete tentorium and the eyes are either absent (as in *Galloisiana notabilis*) or reduced to about 60 ommatidia on each side. There are no ocelli.

The *antennae* in this order are moderately long and filiform, comprising about 28 to over 40 segments according to the species. The *mandibles* are well developed, toothed apically and near the base but without a molar region. The *maxillae* are composed of the typical parts, the lacinia being provided with two teeth and the subdivided galea less heavily sclerotized. The palp consists of five segments and there is no palpifer. In the *labium* a prementum, mentum and submentum are readily distinguished. The prementum bears a pair of 3-segmented palps, a pair of paraglossae and a pair of slightly smaller glossae. The *hypopharynx* is a flattened, broadly oval lobe, beneath which the salivary duct opens.

The three *thoracic terga* are subequal, undivided and carry no internal phragmata (Walker, 1938). This simple condition may well be related to the loss of the wings. The *pleura* are well-developed, each being divided into

episternum and epimeron while the propleuron also reveals traces of a subdivision into the anapleural and coxopleural arcs of the primitive insect (see p. 32). A pair of large trochantins occurs in each segment and broad precoxal bridges are found in both meso- and metathorax. The *sternal region* is partly membranous, the basisternum being most heavily sclerotized. A pair of apophyseal pits is found on each segment and an unusually primitive condition is seen in the retention of a spina in each of the three thoracic segments. The legs are cursorial, differing little in size and with large coxae but no mera. The 5-segmented tarsi are provided with ventral pads and end in a pair of claws, the pretarsus lacking an arolium and pulvilli.

Ten abdominal segments are clearly evident while the epiproct and paired paraprocts presumably represent the 11th segment (Crampton, 1927; Walker, 1943). The pregenital segments are all fully developed but the posterior ones differ in the two sexes. In the female the 8th sternite is somewhat reduced and bears the anterior pair of ovipositor valves. The 9th sternite is greatly reduced but bears the remaining two pairs of ovipositor valves. In the male (Walker, 1919; 1943), the 9th sternite is large and bears an asymmetrical pair of coxites, each with a small terminal style. Immediately behind the coxites is the male copulatory organ, composed of a pair of lobes; the right one bears irregular sclerotizations while the left is membranous and carries an eversible sac of unknown function. The gonopore lies on the inner side of the right lobe. Both sexes of all species carry flexible, 8-segmented cerci.

Internal Anatomy.—The alimentary canal (Walker, 1949) begins with the pharynx, oesophagus and thin-walled capacious crop. This leads into a muscular proventriculus which opens into the short wide mid gut, the latter being produced anteriorly into two ill-defined gastric caeca. The hind gut is partly looped, receives 12–24 Malpighian tubules and the rectum bears six rectal pads. The compact salivary glands surround the oesophagus and lack a reservoir. The ventral nerve-cord includes seven free abdominal ganglia, the one supplying the 1st abdominal segment having fused with the metathoracic ganglion. The tracheae are very delicate and open by ten pairs of spiracles—two are thoracic and eight abdominal.

Biology.—Ford (1926), Walker (1937) and Mills & Pepper (1937) have contributed short accounts of the biology of *Grylloblatta campodeiformis*. The insects are found beneath stones etc., at altitudes of 1,500–6,500 ft. They are apparently omnivorous and nocturnal, with a low temperature preference (*c.* 4° C.). The black eggs are deposited singly in the soil or among moss when the adult female is about a year old. There is an incubation period of about a year and eight nymphal instars which together occupy about five years.

Affinities.—The affinities of this group have been the subject of much discussion (see Walker, 1933; 1937; 1943; Crampton, 1937; Zeuner, 1938). On the one hand, the 5-segmented tarsi, multi-articulate cerci, large coxae and asymmetrical male genitalia suggest Blattoid affinities, while on the other the absence of a meron, the well-developed ovipositor and the structure of the tentorium indicate connexions with the Orthoptera (*s. str.*). Probably the Grylloblattodea are to be regarded as the only living remnants of a primitive stock from which both Blattoids and Orthoptera evolved, Zeuner going so far as to call them recent Protorthoptera. The reduced eyes, absence of ocelli and wings and the simplified hypopharynx are probably specializations which preclude their being directly ancestral to any of the other Orthopteroid orders.

Taxonomy.—Gurney (1937, 1948) distinguishes five species in two genera: *Grylloblatta* occurs in the mountains of western North America and

Galloisiana in Japan. *Grylloblattina djakonovi* has since been described from Russia (Beĭ-Bienko, 1951).

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Order 9. **ORTHOPTERA** (Grasshoppers, Locusts, Crickets, etc.)

Usually medium- or large-sized insects; winged, brachypterous or apterous. Mouthparts mandibulate. Prothorax large. Hind legs usually enlarged and modified for jumping; coxae small and somewhat widely separated; tarsi 3- *or* 4-*segmented, rarely with* 5 *or fewer than* 3 *segments. Fore wings forming more or less thickened tegmina with submarginal costal vein. Wing-pads of nymph undergo reversal during development. Female generally with well-developed ovipositor, not concealed by 7th or 8th abdominal sterna. Male external genitalia symmetrical, concealed at rest by enlarged 9th abdominal sternum which may or may not bear a pair of styles. Cerci usually short and almost invariably unsegmented. Specialized auditory and stridulatory organs frequently developed. Metamorphosis slight.*

This large order, with over 10,000 described species, was formerly held to include the groups here treated as the separate orders Grylloblattodea, Dictyoptera and Phasmida. As restricted by the above definition, the Orthoptera includes not only such familiar forms as the grasshoppers, locusts and crickets but also the mole-crickets and grouse-locusts together with the wetas and king-crickets of Australasia and many others. The order is best represented in the tropics though members occur in all but the coldest zones. They are almost all terrestrial and, though usually capable of jumping actively, relatively few strong fliers are known, all belonging to the Acrididae.

The large literature on the order is best approached through the general accounts of Handlirsch (1930) and Chopard (1938; 1949).

External Anatomy.—Among other anatomical works may be mentioned those of Albrecht (1953), Ander (1939), Davis (1927), Jannone (1939a, b), Kramer (1944), Maskell (1927) and Snodgrass (1929; 1935; 1937).

The head-capsule (Yuasa, 1920; Strenger, 1942) is hypognathous or occasionally prognathous and exhibits most of the sutures and sclerites in a relatively primitive condition though the epicranial suture is not always fully developed. The frontoclypeal suture is distinct and a trans-clypeal suture is usually present. The tentorium is well-developed, X-shaped and without a central aperture (Hudson, 1945). The compound eyes are usually large, but are reduced in some Stenopelmatids and the Cylindrachetidae. Ocelli are absent in apterous species but in winged forms there are usually three, though some Tettigoniidae have only two.

The antennae of the suborder Ensifera are elongate, filiform structures, often greatly exceeding the length of the body and composed of a large number of small segments. In the Caelifera they are shorter, with fewer than 30 segments and though generally filiform are sometimes ensiform, clavate, serrate or pectinate. The mouthparts are mandibulate and relatively primitive. The mandibles are well developed and bear a series of strong grinding ridges

in the phytophagous Acridoidea but are more elongate and apically pointed in omnivorous or carnivorous species. The males of some Stenopelmatidae have greatly enlarged, tusk-like mandibles. The maxillae are typically developed with a pair of 5-segmented palps and the laciniae apically bidentate. The labium (Fig. 260) is divided into submentum, mentum and prementum, the latter bearing 3-segmented palps, large paraglossae and more or less reduced glossae.

The thoracic structures are most fully developed in alate species and are best known in the Acrididae (Snodgrass, 1929). The prothorax is large and its notum is extended laterally so as to conceal a great deal of the small propleuron (Ander, 1939) while the meso- and metathorax are closely associated to form the pterothorax. The pterothoracic nota are usually divided into prescutum, scutum and scutellum, while the intersegmental sclerites are represented by an acrotergite (precosta) on the mesothorax and both acrotergite and postnotum on the metathorax. The pterothoracic pleura are clearly divided into episternum and epimeron. Ventrally, the broad sternum of each pterothoracic segment is made up largely of the basisternum; widely separated apophyseal pits are present and sternellar regions may usually be discerned. Spinasterna occur only on the pro- and mesothorax. In apterous species the thoracic structure is simplified by the loss of many sutures. The legs are usually unequally developed. The hind pair is typically adapted for jumping with enlarged femora which accommodate the powerful tibial levator muscles. In the Gryllotalpidae, Pneumoridae, Cylindrachetidae and some others the hind legs are secondarily reduced to a more normal appearance. The fore legs are strongly fossorial in the Gryllotalpidae (Fig. 22, E) and Cylindrachetidae, the tibia being particularly broad and provided with large teeth. Four tarsal segments are found in the Tettigonioidea, three in the Grylloidea and Acridoidea and one or two in the Tridactyloidea. The legs may also bear structures concerned in stridulation or sound-perception (see below).

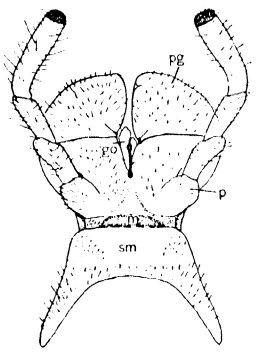


FIG. 260. — Labium of *Melanoplus differentialis*, ventral aspect

pg, paraglossa; *go*, glossa; *p*, palpiger; *m*, mentum; *sm*, submentum. *After* Yuasa, *J. Morph.*, 33.

The degree of development of the wings varies considerably; in some cases both sexes of a species may include normal and brachypterous forms while in others the short-winged condition is characteristic of the female. Certain species or larger groups are exclusively brachypterous or apterous and in the Tetrigidae the fore wings are always vestigial while the hind wings may be polymorphic. When fully developed, the wings have a relatively complete venation with numerous cross-veins (Fig. 261). In the fore wing—which is sclerotized to form a tegmen—the costa is submarginal, the radial sector, media and first cubitus possess several branches and Cu_2 is a straight vein delimiting a long, narrow anal region. Extensive modifications of the cubito-anal area occur in males of the Tettigoniidae and Gryllidae (q.v.) in connexion with the stridulatory apparatus (Zeuner, 1939). The hind wing is membranous and notable for its enlarged anal lobe supported by numerous anal veins; the costa is marginal.

Eleven segments are recognizable in the abdomen, though the first sternum is reduced and the terminal segments modified in connexion with

the genitalia. In the female (Qadri, 1940; Snodgrass, 1933; 1935) there is usually a well-developed ovipositor which, in its most complete form (Tettigonioidea), consists of three pairs of long valves held together by tongue and groove joints (Figs. 48, 49). The anterior (ventral) valves are derived from the 8th abdominal segment, the basal valvifer sclerite representing all or part of the coxite while the large valve is thought to correspond either to the gonapophysis (Snodgrass) or to the style (Qadri). The inner and posterior (dorsal) valves originate from the reduced 9th abdominal sternum, the former pair being gonapophyses while the latter, together with the valvifers, are modified coxites. In the Gryllidae the ovipositor is long and needle-like, with vestigial inner valves, but in the Gryllotalpidae it has been lost completely. The Acridoidea (Agarwala, 1952) have three pairs of valves but the inner ones are reduced and the others are short, stout structures adapted for boring into the soil where the eggs are laid (Fig. 267). In the Tridactyloidea the ovipositor of *Rhipipteryx* resembles that of the Acrididae, but the Cylindrachetidae lack one. The male genitalia (Snodgrass, 1937; Qadri, 1940) are mostly concealed by the enlarged 9th abdominal sternum which sometimes (Tettigonioidea) bears a pair of styles. The aedeagus is a complex structure without parameres and its homologies are uncertain. Qadri (*l.c.*) and Else (1934) consider it to be derived by fusion of the appendages of the 10th abdominal segment. In both sexes the 11th segment consists of a median dorsal epiproct, representing the tergum and united with the 10th tergum in Gryllidae, and a pair of lateral paraproct which correspond to the sternum. The cerci are almost invariably unsegmented (the Stenopelmatid *Lezina* being an exception) and though usually short they are elongate in the Grylloidea and some others.

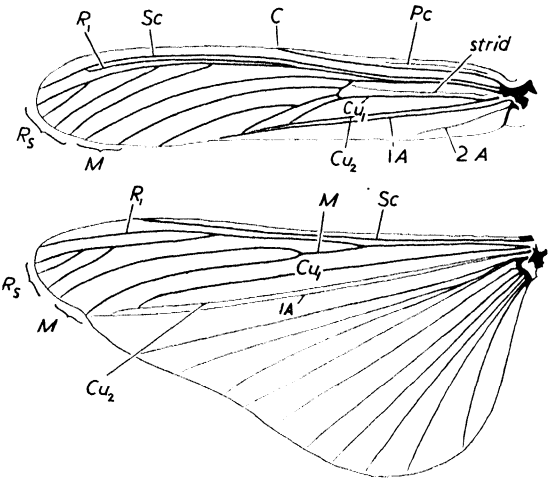


FIG. 261.—Wing-venation of *Locusta migratoria* (*after* Albrecht, 1953)

Pc, precostal vein; *strid*, stridulatory vein. N.B. Only the principal veins are figured.

Among the most characteristic features of the Orthoptera are the stridulatory organs. With some exceptions (Fulton, 1933) it is the males alone which are capable of sound-production and the organs concerned are of two main types: (*a*) alary and (*b*) femoro-alary. The first type occurs in a simple form in the Prophalangopsidae and reaches its highest development in the Tettigoniidae and Grylloidea; it is described in detail below (p. 328). The femoro-alary type is found in most Acridoidea and is discussed on p. 329. In a few groups (e.g. the Pneumoridae) there is a modified zone on each side of the 2nd or 3rd abdominal segment which, when rubbed by the inner face of the hind femur, produces a sound. A somewhat similar organ in the Pamphagine Acrididae is unlikely to be stridulatory (Uvarov, 1943). Though the significance of all aspects of stridulation is not clear, in most Orthoptera it

serves to bring the sexes together. The sound-pattern which they produce is relatively complex (Pierce, 1948) and characteristic sounds are produced by each species in many cases (Faber, 1929; 1932; Jacobs, 1950). In addition to the normal sounds, special songs are said to be associated with epigamic behaviour in some European Acridids. Correlated with the presence of stridulatory organs is the occurrence of auditory organs (see p. 89) which occur in both sexes. Whatever the type may be, each organ consists of a thin cuticular membrane or tympanum whose vibrations are transmitted to the sensory centres by means of scolopidia which are connected with the nerve-endings. In the Acridoidea the auditory organs are highly specialized and their tympanal portions are seen one on either side of the first abdominal segment. In Tettigoniidae and Gryllidae these organs are different in type and consist of a pair of tympana situated near the proximal end of each fore tibia. In many genera these tympana are freely exposed, but in some cases they are largely concealed. In the latter event each is covered by an integumental fold, so that it comes to lie in a cavity which only communicates with the exterior by means of an elongate slit-like opening (see also p. 90).

Internal Anatomy.—The *alimentary canal* (Bordas, 1897) is almost straight in the Acridoidea but a little convoluted in the Ensifera (Fig. 102). The narrow oesophagus opens into a capacious crop which is followed by the gizzard (Judd, 1948). This is not very strongly developed in the Acridoidea but is provided with a strong, sclerotized armature in the Ensifera. The mid gut is produced anteriorly into a number of gastric caeca—two simple outgrowths occur in the Tettigonioidea and Grylloidea, but the Acridoidea possess six caeca, each composed of a forwardly directed part and a shorter posterior diverticulum. The Malpighian tubules are numerous and enter the gut separately (Acridoidea) or in groups at the end of small ampullae (Tettigoniidae) or by uniting to form a common ureter (Grylloidea, Fig. 102). The hind gut ends in the rectum which bears six rectal papillae. Salivary glands are not very strongly developed in the Acridoidea, where they lack a reservoir, but they are large and provided with one in the Ensifera.

The *central nervous system* (Nesbitt, 1941; Hanström, 1928; 1940) is of a generalized character and in addition to the cephalic centres there are three thoracic and usually five or six free abdominal ganglia. The ganglia supplying the anteriormost one or two abdominal segments are fused with the metathoracic centre while fusion of the ganglia of segments 7–11 or 8–11 always occurs and there may also be fusion of the ganglia supplying segments two and three. *Gryllotalpa* is exceptional in having only four free abdominal ganglia. The *stomatogastric nervous system* is well developed (Cazal, 1948) with a frontal ganglion, a pair of partially fused corpora cardiaca, a hypocerebral ganglion and a pair of oesophageal nerves; the paired spherical corpora allata are each connected to the corpora cardiaca by a short nerve. The *tracheal system* (Vinal, 1919; Carpentier, 1927) communicates with the exterior by two pairs of thoracic spiracles and eight abdominal pairs. In many Acridoidea there is a highly developed system of segmentally arranged air-sacs whose main function is probably to increase the efficiency of tracheal ventilation. In the *circulatory* system (Nutting, 1951), the heart extends throughout the abdomen into the mesothorax and is flanked by 10–12 pairs of alary muscles. Nine pairs of abdominal incurrent ostioles are present and two or three pairs of thoracic ones. In addition there may be up to two pairs of excurrent ostia in the thorax and up to five pairs in the abdomen.

The male *reproductive organs* of several species have been described by

Snodgrass (1937). The testes are a pair of compact bodies composed of a variable, usually large, number of follicles enclosed in a peritoneal sheath. In the Acridoidea the testes are closely pressed together in the mid-line (Laird, 1943) while in the Gryllacrididae they are united in a common sheath. The vasa deferentia maybe simple (Acridoidea) or much convoluted near the testis to form an epididymis-like organ, especially conspicuous in the Gryllotalpidae. After looping round the cercal nerves the vasa join the mesodermal part of the ductus ejaculatorius from which arise the numerous tubular accessory glands and, when they are present, the paired seminal vesicles. Finally the ectodermal part of the ductus runs into the aedeagus after giving off, in the Ensifera, a pair of globular vesicles (prostate glands) of unknown function. The female gonads consist of a pair of ovaries made up of a more or less large number of panoistic ovarioles (Voy, 1949) which may be arranged pectinately along the lateral oviducts or arise from them in a cluster. A spermatheca is always present, opening independently of and behind the gonopore while accessory glands of variable form also occur. In the Acridoidea the latter consist of a tubular structure arising from the anterior end of each lateral oviduct and their secretion makes up the pod in which the eggs are laid. Some Acridids also possess a pair of small Comstock-Kellogg glands at the sides of the vagina. In some Ensifera accessory glands open at the base of the ovipositor independently of the gonopore and spermatheca.

Postembryonic Development.—Parthenogenesis is rare in the Orthoptera and viviparity is unknown. The epigamic behaviour is not very striking though the males of a few species have special glands on the dorsum of the thorax (Oecanthine crickets) or abdomen (*Troglophilus* etc.), the secretion of which is attractive to the female. Copulation takes place in different ways in the various species (Boldyrev, 1915; 1929) and a spermatophore (Khalifa, 1949) is always found. Oviposition usually takes place either in or on the ground (most Gryllidae, some Stenopelmatidae, almost all Acridoidea, Fig. 267) or in plant tissues (e.g. the Oecanthine crickets; many Tettigoniidae, notably the Phaneropterinae). The eggs of the Ensifera are almost always laid separately (either in clusters or widely spaced), but those of most Acridoids are enclosed in a cylindrical 'pod' (Zimin, 1938; Waloff, 1950) made of the hardened secretion of the accessory glands sometimes mixed with particles of soil or debris. The eggs of Orthoptera are usually somewhat elongate and ovoidal or are flattened (Phaneropterinae) with one or a few micropyles on the ventral side near the anterior end. The first instar in most, if not all, Orthoptera, is the so-called 'vermiform larva' (pronymph) with a loose cuticle which envelops the appendages in such a way that they are pressed to the sides of the body and their segmentation is indistinct. This stage is of very short duration and is succeeded by instars of more normal appearance; these are usually 4–6 in number, but up to ten moults have been recorded in *Gryllus campestris*. In many Orthoptera the soft cervical membrane plays an important part during ecdysis: it is capable of being distended, by the influx of blood, into a swollen dorsal ampulla which protrudes immediately behind the head. According to Herculais (1890) in *Dociostaurus* a turgid condition is maintained by the accumulation of air in the crop which lies beneath the ampulla and, by means of the pressure thus exerted, the insect is able to rupture the old cuticle. This observer also mentions that the cervical ampulla plays an important part in the escape of the insects from the capsule which encloses the eggs. Six or seven young insects combine their efforts and force open the lid of the capsule by means of their ampullae, thereby effecting their exit.

In the apterous members of the order postembryonic growth consists mainly of an increase in size, and in the further differentiation of the appendages and genital segments: in other words metamorphosis is slight and the young closely resemble their parents. In the winged forms a slight but gradual metamorphosis is also evident, and the wing-pads usually appear in the third instar. In *Melanoplus* and *Oecanthus*, which pass through six nymphal instars, the wing-rudiments arise as slight extensions of the meso- and metanota in the second instar, becoming clearly evident after the subsequent ecdysis. The position assumed by the wings in the saltatorial Orthoptera during their later nymphal instars is different from that found in the adults. In the immature forms the wings have undergone torsion with the result that their surfaces and margins are inverted; the costal margin thus assumes a dorsal position and the hind wings are placed outside the fore wings. At the last moult the wings are untwisted into the normal positions of the adult. This type of wing development appears to occur elsewhere only in the Odonata.

Classification.—General works on this large order include those of Brunner von Wattenwyl (1893) and the catalogue of Kirby (1904–10). The North American species are dealt with by Blatchley (1920) and the European ones by Brunner von Wattenwyl (1882), Burr (1910), Lucas (1920), Hincks (1949) and Chopard (1951). See also Beĭ-Bienko & Mishchenko (1951). Phylogenetic aspects of classification are considered by Ander (1939) and Zeuner (1939). There is some disagreement on the details of the subdivision of the order but the following key, which owes much to Handlirsch (1930), distinguishes the commonly recognized families.

1. Antennae about as long or longer than body, many segmented; tympanal organs, when present, on fore tibiae (suborder **Ensifera**) 2
–. Antennae shorter, with less than 30 segments; tympanal organs, when present, at base of abdomen (suborder **Caelifera**) 9

2. Tarsi 4-segmented, at least on middle and hind legs (superfamily **Tettigonioidea**) 3
–. Tarsi 3-segmented (superfamily **Grylloidea**) 8

3. 2nd and 3rd tarsal segments with large, mobile lateral lobes; wings, when present, coiled spirally in repose . . . . . SCHIZODACTYLIDAE (p. 327)
–. Tarsi and wings otherwise 4

4. Body elongate, apterous, rod-like; hind femora not thickened PHASMODIDAE (p. 328)
–. Body more thickset; hind femora enlarged 5

5. Tarsi depressed 6
–. Tarsi compressed or cylindrical 7

6. Fore wings without stridulatory apparatus; fore tibiae without tympanal organs; middle and fore tibiae armed beneath with mobile spines GRYLLACRIDIDAE (p. 327)
–. Fore wings of male usually with stridulatory apparatus; fore tibiae almost always with tympanal organs; tibiae without mobile spines beneath TETTIGONIIDAE (p. 327)

7. Fore wings of male with stridulatory apparatus; tibial tympanal organ present PROPHALANGOPSIDAE (p. 327)
–. Fore wings of male without stridulatory apparatus or apterous; tibial tympanal organ usually absent. . . . . STENOPELMATIDAE (p. 327)

8. Fore legs strongly fossorial, with tibiae expanded and digitate; ovipositor vestigial GRYLLOTALPIDAE (p. 329)
–. Fore legs not markedly fossorial, tibiae simple; ovipositor elongate GRYLLIDAE (p. 328)

9. Tarsi almost always 3-segmented; antennae usually longer (superfamily **Acridoidea**) 10
–. Tarsi 1- or 2-segmented; antennae short, with 12 or fewer segments (superfamily **Tridactyloidea**) 14

10. Pronotum extended backwards to cover abdomen; empodium absent; antennae longer than fore femur . . . . . TETRIGIDAE (p. 332)
—. Pronotum normal or if, rarely, extended behind, then empodium present or antennae shorter than fore femora 11

11. Body elongate and rod-like, usually apterous, with long, thin legs PROSCOPIIDAE (p. 332)
—. Not thus 12

12. Hind legs not markedly different from two anterior pairs, femora not greatly enlarged; male with inflated abdomen and stridulatory ridges on 2nd abdominal tergite . . . . . PNEUMORIDAE (p. 332)
—. Hind legs markedly saltatorial with enlarged femora 13

13. Prosternum unarmed; antennae shorter than fore femora; pronotum not compressed, usually flattened dorsally . . . . EUMASTACIDAE (p. 332)
—. Without this combination of characters . . . . ACRIDIDAE (p. 329)

14. Elongate, cylindrical, apterous forms; fore legs fossorial, hind legs not enlarged CYLINDRACHETIDAE (p. 333)
—. Small forms of more normal facies; fore legs normal, hind legs saltatorial with enlarged femora . . . . . TRIDACTYLIDAE (p. 332)

FAM. STENOPELMATIDAE.—As defined in the key on p. 326 this family includes the Rhaphidophorinae, Henicinae and other groups sometimes given the status of separate families; to it belong the Australasian wetas and king-crickets and other less well-known forms. Karny (1937) has provided a generic revision and anatomical works include those of Davis (1927), Maskell (1927) and Jannone (1939b). Representatives of the family are found in all regions in a number of different habitats and though omnivorous they seem to prefer animal food. Some (e.g. *Troglophilus*) are cavernicolous, being apterous, often with long appendages and probably feeding on dead insects (Chopard, 1933). Others burrow in decaying wood (e.g. a common weta, *Hemideina*) and many are subterranean. The latter forms may have fossorial fore legs and *Oryctopus* females even have vestigial eyes and antennae. A further peculiarity of some male Stenopelmatids is the presence of very large mandibles (e.g. *Anostostoma*, the Australian king-cricket). *Tachycines asynamorus* has become established in glasshouses in Britain and elsewhere and though partly carnivorous also injures plants (Tetry, 1936); *Daihinia brevipes* is also a minor agricultural pest in Oklahoma (Whitehead & Miner, 1944). For the development of the cave-dwelling *Dolichopoda palpata* see Varrichio (1936).

FAM. GRYLLACRIDIDAE.—Like the Stenopelmatidae, this is another relatively primitive family of saltatorial Orthoptera. It is a predominantly tropical group of over 500 species (Karny, 1937), its members being usually dark brown in colour and mostly living in trees where some construct shelters of rolled leaves with the aid of an oral secretion. They appear to be mainly predacious.

FAM. SCHIZODACTYLIDAE.—This group has a discontinuous old-world distribution and includes only three genera (Ramme, 1931; Karny, 1937). *Schizodactylus*, the only alate genus, has long wings whose apices are coiled spirally at rest. These insects are able to burrow into the soil, spending the daylight hours in the holes they have dug and seeking their prey at night.

FAM. PROPHALANGOPSIDAE.—Only three recent species are placed here—the Indian *Prophalangopsis obscura*, which is unusual in having only three tarsal segments, and two N. American species of *Cyphoderris*. Zeuner (1939), however, has referred a number of fossils to the family and considers it of great phylogenetic importance, being ancestral to the Tettigoniidae and Grylloidea. A simple stridulatory apparatus is present in the male, similar on both fore wings.

FAM. TETTIGONIIDAE (Locustidae: Long-horned Grasshoppers, Katydids).—The Tettigoniidae (Fig. 262) are a predominantly tropical group of over 4,000 species,

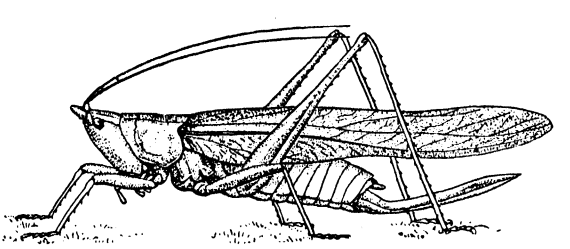


FIG. 262.—A long-horned grasshopper *Neoconocephalus palustris*
After Blatchley

divided into many subfamilies (Caudell, 1908–16; Karny, 1912–13; Zeuner, 1936). Apterous forms are common and include some of the largest species. When winged, the left tegmen usually overlaps the right one and in males the cubito-anal regions of the tegmina are modified asymmetrically for stridulation. Typically, each such tegmen has a specialized, approximately circular area delimited by Cu_2 and a branch of Cu_1 and behind this lies the stridulatory vein, 1A. The circular area is best developed on the right tegmen, where it is known as the 'mirror', while the stridulatory vein on the left tegmen bears a row of teeth and is known as the 'file'. Stridulation occurs through the file being scraped by the edge of the right tegmen, the mirror acting as a resonator. In some groups the hind wings are absent and the tegmina reduced to the stridulating areas only; this is seen, for example, in the Ephippigerinae and Bradyporinae where, it may be added, the females are also able to stridulate, though they apparently only do so infrequently. Winged Tettigoniidae are predominantly green and live amidst herbage, particularly bushes and trees, where some (Pseudophyllinae) simulate leaves. The wingless forms live nearer the ground but some are agile climbers and reach the tree-tops. The eggs of Tettigoniidae are not enclosed in pods, and the ovipositor frequently attains a great length, even exceeding that of the body (Fig. 48). In some cases it is used for depositing the eggs in the earth, but usually they are laid in plant-tissues of various kinds, often in neat longitudinal rows. Five or six ecdyses are prevalent and the members of this family are less predominantly herbivorous than the Acrididae: some forms (Saginae) are notably carnivorous while others appear to be omnivorous.

The Tettigoniidae are divided into as many as eighteen subfamilies and five, including eleven species, extend into the British Isles. The largest of the latter species is *Tettigonia viridissima* which occurs in the southern half of England where it attracts attention from its strident notes. *Pholidoptera griseoaptera* has vestigial wings, and its range in England is very similar to that of the former insect. The biology of several N. American species is described by Iseley (1941).

Allied to the Tettigoniidae are the **Phasmodidae,** with two Australian genera superficially resembling elongate Phasmids.

FAM. GRYLLIDAE (Crickets).—Like the Tettigoniidae, the members of this large family (over 900 species) stridulate by friction of the tegmina and possess tibial auditory organs (Fig. 78). The stridulatory apparatus of the male tegmen occupies a larger area than in the Tettigoniidae and the two tegmina are similarly modified. The mirror, bounded by Cu_2 and a branch of Cu_1, is displaced distally in comparison with the long-horned grasshoppers and a large space between Cu_2 and 1A is traversed by cross-veins and forms the harp. 1A is the stridulatory vein or file and is provided with a row of teeth while a small zone on the hind margin of each tegmen forms the scraper. During stridulation the tegmina are elevated at an angle of about 45° to the abdomen and moved backwards and forwards laterally. Although the right and left tegmina are similar to each other it is said that the sound is always produced by the scraper of the left tegmen rubbing against the file of the right one, so throwing the mirrors into vibration. The sound-producing powers of the Gryllidae are well exemplified in the house cricket; *Brachytrypes megacephalus* is stated to make a noise so penetrating that it can be heard at the distance of a mile. The auditory organs differ from those of the Tettigoniidae in that those of the pair on each fore leg differ from one another, the outer organ being larger than the inner one. Many crickets are entirely devoid of tegmina and wings: in *Trigonidium* the tegmina are arched and horny, and impart to these insects the appearance of Coleoptera. The ovipositor is slender and cylindrical, being more or less acicular, and there is a pair of exceptionally long unsegmented cerci.

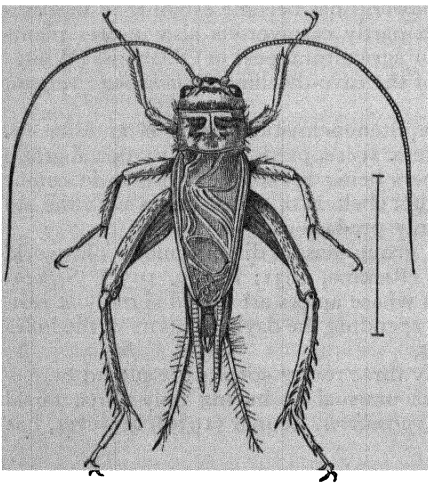


FIG. 263.—*Acheta domesticus*, male
After Sharp, *Camb. Nat. Hist.*

The eggs of most species are laid singly in the ground: a few of the subterranean

forms deposit them in masses in underground chambers, while some Oecanthinae place them in a single uniform row in the pith of twigs (Fig. 264). There are five ecdyses in the latter subfamily but among other Gryllidae the number is stated to be higher. Crickets are, for the most part, omnivorous and frequent hot dry places, or live in holes or burrows, under logs, among dead leaves, etc., while the Oecanthinae occur on trees and bushes. Out of the seven or more subfamilies into which Gryllidae are divided only one occurs in Britain. The Gryllinae include the typical crickets of which there are three indigenous British species, viz. the Ground Cricket *Nemobius sylvestris*, the Field Cricket *Gryllus campestris* and the House Cricket *Acheta domesticus* (Fig. 263). The Myrmecophilinae (Schimmer, 1909) are very small subspherical apterous crickets that live in association with ants and occur in Europe, Asia and America (Fig. 265). *Mogoplistes* and its allies are covered with minute scales and are often regarded as a separate subfamily while the Oecanthinae (Fulton, 1915) are a large group of pale-coloured tree crickets. The Eneopterinae include the larger brown bush crickets mostly found in the Old World.

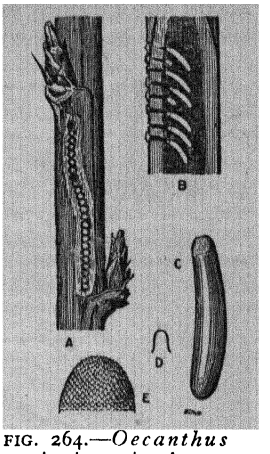


FIG. 264.—*Oecanthus nigricornis*. A, egg punctures in stem of raspberry. B, longitudinal section. C, egg, magnified. D, projection of egg-cap. E, egg-cap.

After Fulton, *N.Y. Agric. exp. Sta. Tech. Bull.*, 42.

FAM. GRYLLOTALPIDAE (Mole-crickets). — This well-defined group of about 50 species (Fig. 266) is distinguished by its adaptations to a subterranean habit, the fore legs being greatly expanded and armed with strong teeth to assist digging, the eyes reduced and the ovipositor vestigial. When fully winged, the mole-crickets are able to fly, but brachypterous and apterous species are also known. *Gryllotalpa gryllotalpa* is rare in Britain but common in continental Europe and has been introduced into N. America. Like other species, it is sometimes injurious to cultivated plants though it is said also to eat insects and worms. The eggs are laid in a sort of nest, 10–15 cm. below the surface, there are five nymphal instars and the life-cycle takes two years to

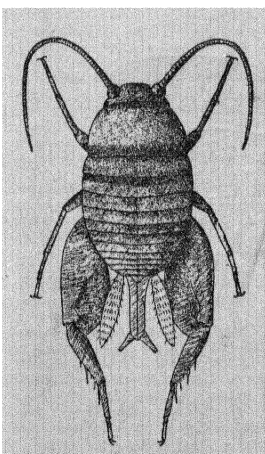


FIG. 205.—*Myrmecophila acervorum*, female × 5

After Chopard, *Faune de France*.

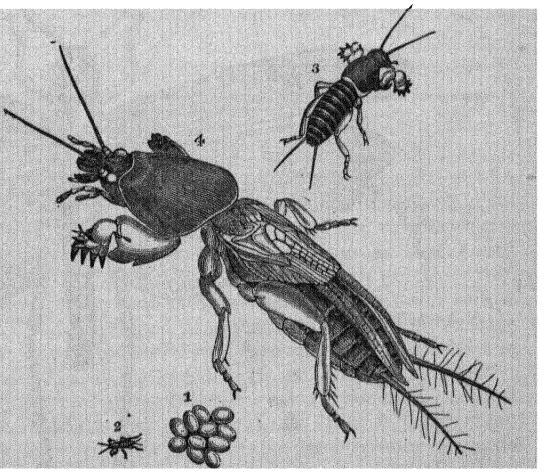


FIG. 266.—*Gryllotalpa gryllotalpa*, with eggs and nymphs

After Curtis.

complete. Hayslip (1943) describes the biology of *Scapteriscus* in Florida and Tindale (1928) that of some Australian species.

FAM. ACRIDIDAE (Short-horned Grasshoppers; Locusts).—The Acrididae, with about 5,000 species, are the largest Orthopteran family and, though found predominantly in the hotter regions, include the familiar grasshoppers of the temperate countryside as well as the notoriously destructive locusts. Stridulation takes place in several ways, only three of which will be mentioned here. The best-known method,

seen for example in the subfamily Acridinae, is by means of a ridge bearing many small peg-like projections on the inner side of each hind femur which is rubbed against the hardened radial vein of the closed tegmen, thus causing the latter to vibrate and produce a low, buzzing sound. The males stridulate by day and females of some species can also produce a sound though they possess a somewhat reduced stridulatory apparatus. In the Oedipodinae, stridulation is again femoro-alary but the row of peg-like projections lies on a secondary vein near the base of the tegmen and the femur bears a simple longitudinal ridge. Some other Acrididae, mostly Oedipodines, are also able to stridulate during flight, apparently by friction between the hind wings and the under surface of the tegmina. A crackling sound results, which has been compared to that of burning stubble. The auditory organs are located one on each side of the basal segment of the abdomen. The ovipositor is not conspicuous and its valves are short and curved. By means of the latter organs the female excavates a hole in the ground or more rarely in decaying wood. The eggs are then deposited (Federov, 1927; Snodgrass, 1935) until they form a mass of 30–100 or more and, during the process, a glutinous fluid is discharged around them which hardens to form the egg-pod (Zimin, 1938; Waloff, 1950)—a waterproof protection, corresponding to the more

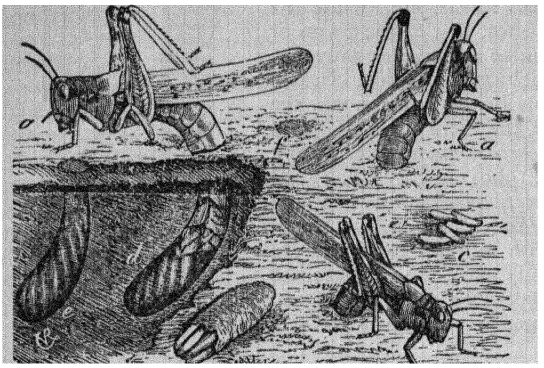


FIG. 267.—Locusts in the act of oviposition
After Riley.

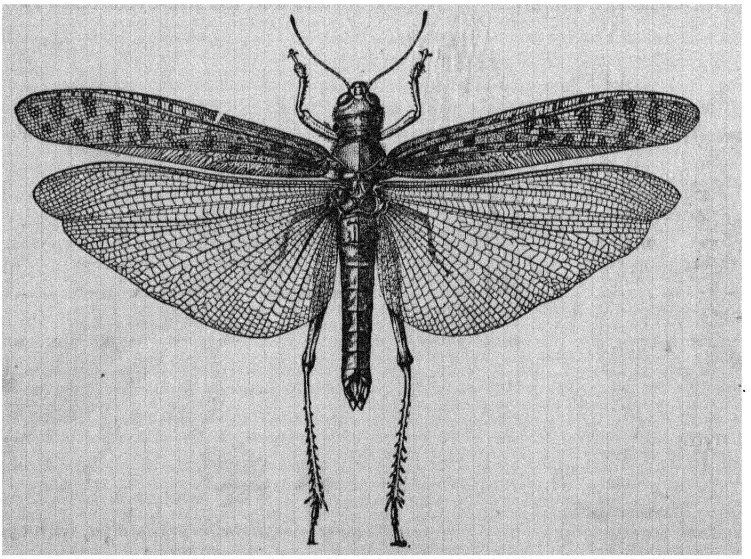


FIG. 268.—A typical migratory locust, *Schistocerca gregaria*
Reproduced by permission of the Trustees of the British Museum.

perfect oothecae of the Dictyoptera. Several of these masses are usually deposited by each female and the oviposition period in *Melanoplus* extends, according to Riley, over a period of two months. There appear to be four to eight ecdyses in the life of a species and commonly one or two generations in the year. These insects are voracious devourers of vegetation during both their young and adult stages. Iseley (1938) has

shown that the Acridinae and Oedipodinae are primarily grass-feeders while the Catantopinae eat broad-leaved plants and are more selective in their feeding habits.

The Acrididae are usually divided into about ten subfamilies (Uvarov, 1943, but cf. Roberts, 1941; Dirsh, 1956) and with the possible exception of *Mecostethus grossus*, all ten British species are referred to the Acridinae. For their biology, see Clark (1948) and Richards & Waloff (1954). The Oedipodinae or band-winged grasshoppers are more or less brightly-coloured insects, often with blue, yellow or red hind wings crossed by a characteristic black fascia. The tegmina, however, are sombrely coloured and when closed the insect harmonizes very closely with its environment.

The term 'locust' is correctly given to a few species of Acridids which are capable under certain conditions not fully understood of forming large swarms which move over wide areas causing great devastation of natural and cultivated vegetation where they feed (Fig. 268). Uvarov (1921; 1928) has proposed a theory that each species of locust can exist in two main forms ('phases') which differ structurally and biologically. These are the gregarious phase (*phasis gregaria*) and the solitary phase (*phasis solitaria*)

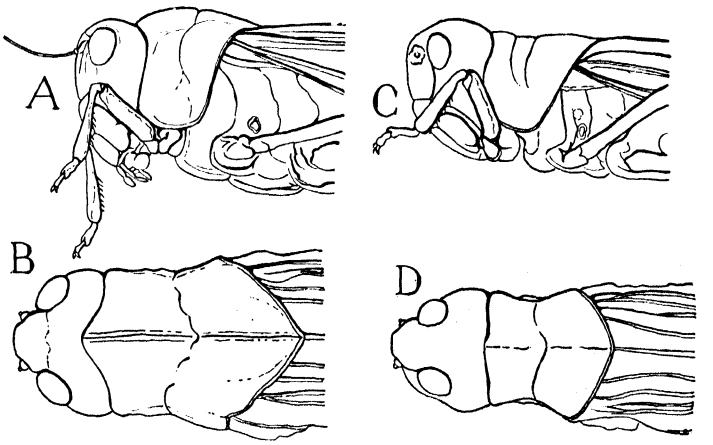


FIG. 269.—Form of thorax in phases of the locust, *Locusta migratoria migratorioides* A, B, *phasis solitaria*; C, D, *phasis gregaria*. *After* Faure. N.B. The tarsi should be represented with 3 segments.

and the two are often so distinct as to have been regarded by earlier taxonomists as separate species. Intermediates (*phasis transiens*) also occur during the transition of a population from one extreme to the other. The solitary phase is characterized in its nymphal instars by being variable in colour, green, grey or brown and similar to the colour of its normal environment; in the adult state, the pronotum is longer and crested (Fig. 269), while the hind femur is relatively long compared with the fore wing. In *gregaria* forms, the nymphal coloration is a bold pattern mainly of black and yellow or orange and the adult has a shorter, saddle-shaped pronotum and a relatively shorter hind femur. Biologically, the most important difference between the phases is the higher activity and gregarious tendencies of the *gregaria* phase. This is manifested in the nymphs by their habit of living in large bands which, during the hotter part of the day, march from place to place. In adults, the *gregaria* forms occur in large, more or less dense swarms which may fly over great distances under the influence of winds until environmental conditions (e.g. a fall of temperature) cause them to settle. Laboratory studies have shown that nymphs reared in isolation are of the *solitaria* phase while the crowding together of many young nymphs results in increased activity which, in turn, is associated with the development of black pigment and usually of other characteristic attributes of the *gregaria* form. Further, the high level of activity of the latter is promoted by the higher internal body temperature of the black *gregaria* nymphs which absorb more radiant heat than do the green or brownish *solitaria* nymphs. The natural conditions which induce crowding and therefore cause 'gregarization' and lead to locust plagues are not completely clear, but in general it appears that the process takes place in restricted regions ('outbreak areas') where, as a result of flooding or variable rainfall, the habitats favourable to breeding are liable to irregularly periodic contractions in size. Swarms originating in the outbreak areas

invade large regions and, when they breed there, may give rise to *solitaria* or *gregaria* forms according to local conditions. After a few years, however, the area affected by swarms becomes smaller and the locust plague ends. New plagues apparently originate only in the more or less permanent outbreak areas and measures designed to prevent gregarization in these places are therefore fundamental to locust control.

The most important locusts of the Old World are (i) *Locusta migratoria*, with several subspecies, of which the African one has an outbreak area in the flood-plains of the Middle Niger; (ii) *Nomadacris septemfasciata* (the Red Locust) with outbreak areas in N. Rhodesia and Tanganyika and (iii) *Schistocerca gregaria* (the Desert Locust), the outbreak areas of which are not established with certainty but appear to vary with the rainfall in Pakistan, Arabia and possibly also much further west in Africa. Other economically important locusts include the S. American *Schistocerca paranensis*, the Mediterranean *Dociostaurus maroccanus* and the Indomalaysian *Patanga succincta*. The history of recent attempts at investigating and controlling the more injurious locusts is summarized by Uvarov (1951) while detailed accounts of various aspects of their biology are given in the publications of the Anti-Locust Research Centre, London, and by Kennedy (1939; 1950).

There is a very large literature on Acrididae, of which important taxonomic papers are those by Bolivar (1909; 1916), Bruner (1900–09) and Uvarov (1943) while biological topics are dealt with by Chesler (1938), Isley (1937–44), Rubtzov (1935), Shotwell (1941), Uvarov (1928; 1938; 1948) and others.

Three relatively small families closely associated with the Acrididae may be mentioned here. The **Pneumoridae** (Rehn, 1941) include about 20 South African species remarkable for the inflated abdomen of the male, which bears stridulatory ridges on the sides of the 2nd abdominal tergum, and the relatively small hind legs. The **Eumastacidae** (Bolivar y Pieltain, 1930; Rehn, 1948) are a mainly tropical group of about 120 species which live among bushes; oviposition in the soil has been observed in *Erianthus* which has six nymphal instars. Finally the **Proscopiidae** (Mello-Leitão, 1939) consist of about 100 species endemic to South America. They are superficially similar to elongate Phasmids, enjoying a protective resemblance to the vegetation on which they live; almost all are apterous and they rarely jump.

FAM. TETRIGIDAE (Tettigidae, Acrydiidae: Grouse-locusts).—This well-defined group consists of over 700 species (Hancock, 1906; Günther, 1938) and its

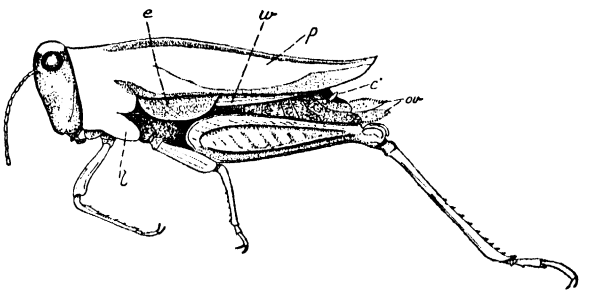


FIG. 270.—*Tetrix vittata* × 5

c, cercus; *e*, tegmen; *ov*, ovipositor; *p*, pronotum; *l*, lateral lobe; *w*, wing.

members are readily distinguished from almost all other Acridoids by the backwardly directed, sometimes grotesquely shaped, process of the pronotum (Fig. 270) which covers the abdomen and conceals the hind wings, the tegmina being reduced to small scales. Many species exhibit polymorphism in the development of the hind wings and pronotum. Though the Tetrigidae are best represented in the tropics, they are relatively numerous in cooler regions, over 50 species being Palaearctic (three British). They tend to frequent moist places and some are semi-aquatic. Their biology is not very well known but at least some of the temperate species pass the winter both as adults and partly grown nymphs. Their eggs are laid in the ground in a loosely associated mass and they feed on the algae and mosses growing in moist soil or at the sides of lakes and streams.

FAM. TRIDACTYLIDAE (Pigmy Mole-crickets).—About 50 species of these small insects are known, four occurring in the Mediterranean region. They possess short antennae and very large hind femora while each hind tibia, in addition to a

number of subapical articulated spines, bears a pair of longer apical appendages between which lies the vestigial, unsegmented hind tarsus. The anterior tarsi are 2-segmented. The Tridactylidae live near water, where they burrow into sandy ground, apparently feeding on fragments of vegetable matter in the soil. They are also capable of moving on or beneath the water-surface. For biology, see Urquhart (1937).

FAM. CYLINDRACHETIDAE.—Though formerly associated with the Gryllotalpidae, this small family is now known to be allied to the Tridactylidae (Ander, 1934; Carpentier, 1936). Its members occur in Australia, New Guinea and Patagonia and are highly adapted to a burrowing subterranean life, being apterous with an elongate, cylindrical body, fossorial fore legs, short antennae and reduced ocelliform eyes; the hind legs are not saltatorial. See Tindale (1928).

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Order 10. **PHASMIDA** (Stick- and Leaf-Insects)

Large, apterous or winged insects, frequently of elongate, cylindrical form, more rarely depressed and leaf-like. Mouthparts mandibulate. Prothorax short; meso- and metathorax usually elongate, the latter closely associated with 1st abdominal segment. Legs similar to each other; coxae small and rather widely separated; tarsi almost always 5-segmented. Fore wings, when present, usually small and with submarginal costa. Wing-pads do not undergo reversal during development. Ovipositor small and mostly concealed by enlarged 8th abdominal sternum. Male external genitalia variable and asymmetrical, concealed by 9th abdominal segment. Cerci short, unsegmented. Specialized auditory and stridulatory organs absent. Eggs deposited singly. Metamorphosis slight.

The Phasmida is a group of predominantly tropical insects (Günther, 1953) remarkable for their close protective resemblance to the foliage or, more frequently, twigs, of the vegetation on which they occur and feed. Though formerly classified with the Dictyoptera as Cursorial Orthoptera, they show some similarities to the Saltatoria and because of their uncertain affinities they are here given separate ordinal status. For general accounts, see Handlirsch (1930) and Chopard (1938; 1949).

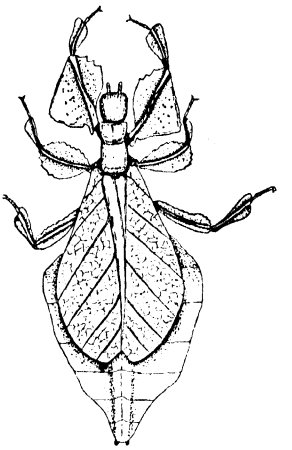


FIG. 271.—*Phyllium crurifolium*, half natural size Oriental region.

External Anatomy.—In addition to the references cited below, the following papers deal with the anatomy of various members of this order: Heymons (1897), de Sinety (1901), Marshall & Severin (1906), Leuzinger *et al.* (1926) and Littig (1942). Two main types of bodily structure occur in the Phasmida: elongate, often apterous, cylindrical, rod-like forms which closely resemble twigs in colour and appearance (Fig. 272) and the less frequent depressed, leaf-like, winged species (Phylliidae) with lamellate expansions of the legs (Fig. 271). A few more thick-set forms, superficially similar to saltatorial Orthoptera, are also known and are probably more primitive than the plant-simulating species.

The cuticle of the Phasmids is frequently beset with spines and other cuticular prominences. The head is prognathous with a well-developed frontoclypeal suture, but the epicranial and occipital sutures are not evident and the transverse division of the clypeus is indistinct. The labrum is large and cleft apically and the tentorium (Hudson, 1945) is imperforate, with long anterior arms and a small body. Compound eyes are always present, but ocelli are found only in some of the winged species. The antennae vary considerably in length, being filiform or moniliform, with from 8 to over 100 segments.

The biting mouthparts have strong mandibles and each maxilla possesses a 5-segmented palp, a 2-segmented galea and a lacinia which is spinose on its inner face. The labium is subdivided into prementum, mentum and submentum; the labial palps are 3-segmented, the paraglossae are well developed and the glossae narrower. A hypopharynx is also present.

The prothorax is always short, while the meso- and metathorax are longer, the latter being closely attached to the 1st abdominal segment (median segment), the suture between them sometimes being obliterated. In the elongate, cylindrical, apterous forms, the terga and sterna form a tube-like structure, the pleura being greatly reduced. The ventral side of the thorax is dominated by the large basisterna, but a sternellum is also found on each segment and a spinasternum occurs in the meso- and metathorax. The prothoracic pleura are typical in appearance, but the epimera of the other two segments are very small. Many Phasmids are completely apterous and many others show varying degrees of brachyptery. When wings are well developed, the fore wings are rather strongly sclerotized to form tegmina and are commonly reduced in size. The hind wings possess an anterior sclerotized region, correlated with the presence of small tegmina, and a membranous posterior part made up largely of the anal lobe. The venation has not been adequately studied and, in the leaf-like forms, that of the fore wing is considerably modified to imitate the veins of a leaf. The costa of the fore wing is set back from the front margin and the other veins run longitudinally with little or no branching. The hind wing also has a simple venation with a large number of straight anal veins supporting the large anal lobe, which can be folded at rest in a fan-like fashion. The legs are similar to each other, the coxae rather small and widely separated and, in the Phylliidae, the femora and tibiae are provided with lamellate expansions. There are five tarsal segments, except in *Timema*, which has three, and in regenerated legs where four are present.

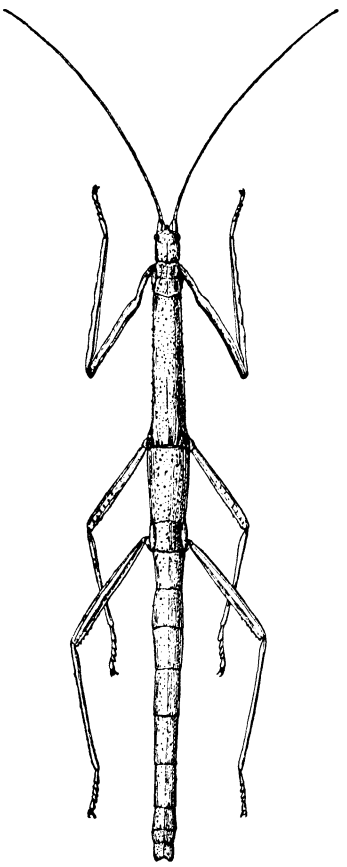


FIG. 272.—*Carausius morosus*, natural size
After Ling Roth.

Eleven segments may be recognized in the abdomen. The 1st segment is closely associated with the metathorax (though the tergum is free in *Timema*) and the first sternum is reduced. The genital segments differ according to the sex, but the 10th segment is always well developed and the 11th is represented by a small epiproct (tergum), a pair of paraprocts (divided sternum) and the cerci. The ovipositor (Günther, 1933; Maki, 1905) is composed of three pairs of small valves, the first pair being appendages of the 8th abdominal segment while the two posterior pairs are derived from the 9th segment. The whole structure is concealed within the enlarged 8th sternum (operculum). In the

male (Pantel, 1915; Snodgrass, 1937) the terminal abdominal segments and aedeagus are rather variable in form. The latter is asymmetrical and made up of a number of lobes, which are sometimes more or less completely united into a single structure. The 9th abdominal sternum is prolonged beneath the genitalia and is usually divided into an anterior part and a distinct subgenital plate. The 10th segment in the male may be a simple plate or is sometimes desclerotized except for a conspicuous anterior lobe, the so-called vomer. The cerci, which may have a prehensile appearance in some males, are always unsegmented.

Internal Anatomy.—The alimentary canal (Bordas, 1897) is without convolutions and the crop is normal but the gizzard is atrophied and there are no gastric caeca. The anterior part of the mid gut is provided with thick bands of circular muscles while the posterior part bears numerous glandular papillae on its outer surface, each produced into a terminal filament. There are numerous Malpighian tubules and a pair of large, bilobed salivary glands. In the central nervous system there are three thoracic ganglia and the first 1–3 of the abdominal ganglia are united with the metathoracic nerve-centre so that 5–7 free abdominal ganglia occur. The stomatogastric nervous system (Pflugfelder, 1937; Hanström, 1940) is well developed with a frontal ganglion, recurrent nerve, hypocerebral ganglion, partially fused corpora cardiaca and a single oesophageal nerve. A pair of asymmetrically arranged corpora allata is also found. The dorsal vessel (Nutting, 1951) extends forwards from the 9th abdominal segment into the metathorax as the heart and is then continued into the head in the form of the aorta. There are 9–11 pairs of alary muscles and 9 abdominally situated pairs of incurrent ostia while one pair of excurrent ostia is found in the metathorax and another pair in each of the first two abdominal segments. In the male reproductive system (Snodgrass, 1937), the testes of *Timema* are each composed of a longitudinally arranged series of ovoidal follicles, but in other Phasmids the testes are a pair of elongate, tubular structures not divided into follicles. The short vasa deferentia are not convoluted and open into the ductus ejaculatorius at the point where a variable number of tubular accessory glands arise. Distinct seminal vesicles have not usually been reported but de Sinety (1901) claims that two tubular structures very similar to the accessory glands act as sperm reservoirs in *Leptyniella*. In the female, each ovary comprises a variable number of panoistic ovarioles widely spaced along the median side of the lateral oviduct. The common oviduct opens behind the 8th sternite and dorsal to it there lies a large bursa copulatrix which opens near the gonopore. The single or paired spermatheca opens into or just behind the bursa and a pair of accessory glands is also present (Heberdey, 1931; Günther, 1933).

In many Phasmids, a pair of long tubular glands—apparently repugnatorial in function—is found in the prothorax and open in front of each fore coxa.

Postembryonic Development and Biology.—Mating (Stockard, 1908) occurs by the male mounting the back of the female and curving his abdomen down at the side of, or behind (*Phyllium*), that of the female. Copulation sometimes lasts several hours and a spermatophore is probably formed in most species. The eggs are laid singly, usually falling to the ground, and they often resemble seeds very closely—those of *Aplopus mayeri*, for example, being similar to the seeds of *Suriana maritima*, the plant on which it feeds (Stockard, *l.c.*). Each egg has a rather complex structure, with a distinct operculum and a thick shell which, in *Bacillus libanicus* (Moscona, 1950),

for instance, comprises a many-layered, hard, brittle exochorion whose organic framework is partly impregnated with calcium salts, a double-layered, membranous endochorion and a thin vitelline membrane (Fig. 273). The egg is often retained in the genital chamber of the female for some time before laying and many months may elapse before it hatches. The postembryonic

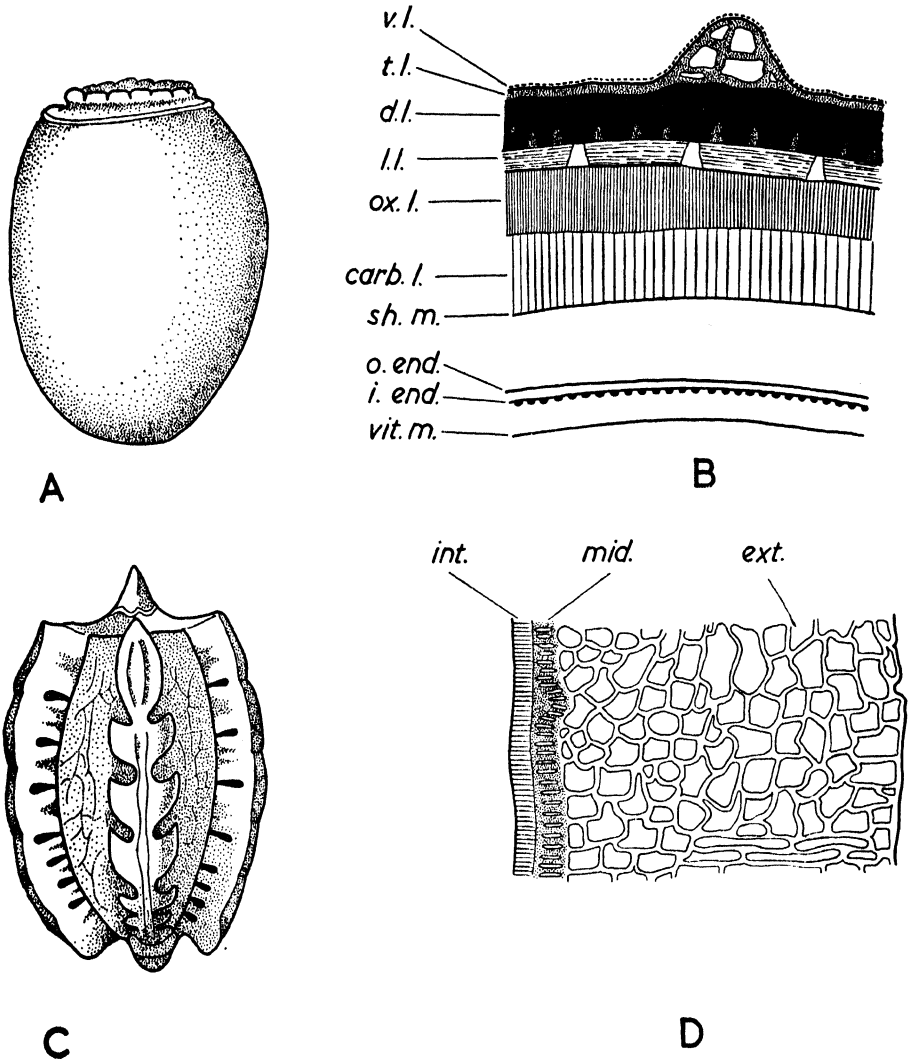


FIG. 273.—Eggs of Phasmida. A, B. *Bacillus*. C, D. *Phyllium* (B *after* Moscona, 1950; C & D *after* Henneguy, 1904)

carb.l, carbonate layer; *d.l*, dark layer; *ext*, external layer; *i.end*, inner endochorion; *int*, internal layer; *l.l*, lamellar layer; *mid*, intermediate layer; *o.end*, outer endochorion; *ox.l*, oxalate layer; *sh.m*, shell membrane; *t.l*, tubercular layer; *vit.m*, vitelline membrane; *v.l*, varnish layer.

development has been studied in only a few species. Grimpe (1921) found that in *Phyllium bioculatum* females there are usually six nymphal instars which are completed in about 125 days at 20–24° C. Males develop more rapidly and have one or two less instars. They also have a shorter adult life than the females which live for about 90 days and start oviposition 14–20 days after

copulation, producing over 100 eggs before they die. See also Favrelle (1938), Ling Roth (1917) and Talbot (1920).

Many other interesting aspects of the biology of these insects are reviewed by Chopard (1938). Thus, some species of the genera *Bacillus*, *Clonopsis* and *Carausius* are almost exclusively parthenogenetic, while in other Phasmids the males are uncommon and facultative parthenogenesis probably occurs, only females developing from unfertilized eggs. Another peculiarity is the occurrence, on stimulation or injury, of autotomy of the nymphal legs, the affected limb breaking off at a specialized point between trochanter and femur and being capable of rapid regeneration (though with only four tarsal segments) in subsequent instars. Finally, one may mention the rapid 'physiological' colour changes which have been studied in a few Phasmids, notably *Carausius morosus*. Various colour-forms of this species are known, varying from brown to green and in all except the green variety a change in the intensity of the colour can be produced quite rapidly by the migration of pigment-granules within the hypodermal cells, probably under the influence of a hormone. High humidity, low temperature and low light intensities cause darkening, while pallor is induced by the opposite conditions. Under normal influences a rhythmical colour-change occurs diurnally (dark at night, light in the day) and this rhythm persists for some time if the insects are subjected to continuous darkness.

Classification.—About 2,000 species of Phasmida are known, the greatest number occurring in the Oriental region. Only a small number of species are found outside the tropics though it is interesting to note that two New Zealand species (*Acanthoxyla prasina* and *Clitarchus laeviusculus*) have now established themselves as members of the British fauna in the Scilly Isles (Uvarov, 1950). Taxonomic works include those of Brunner von Wattenwyl & Redtenbacher (1906–08), Kirby (1910), Karny (1923), Günther (1928) as well as papers by Hebard and J. A. G. Rehn. There is still disagreement about the subdivision of the order, but the following key will serve to identify the three families recognized by Handlirsch (1930).

1. Middle and hind tibiae with apical triangular area formed by division of median inferior carina 2
–. Carina of middle and hind tibia continued to apex . . . BACTERIIDAE

2. Body depressed and leaf-like . . . . . PHYLLIIDAE
–. Body of various forms but never depressed and leaf-like . . PHASMIDAE

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Order 11. **DERMAPTERA** (Earwigs)

Elongate insects with typical biting mouthparts: superlinguae distinct: ligula 2-lobed. Fore wings modified into very short leathery tegmina devoid of veins: hind wings semicircular, membranous, with the veins highly modified and disposed radially. Apterous forms common. Tarsi 3-segmented. Cerci unjointed and almost always modified into heavily sclerotized forceps: ovipositor reduced or absent. Metamorphosis slight or wanting.

The general form and appearance of these insects is well exemplified in the common 'earwig', *Forficula auricularia* (Fig. 274), which is abundant throughout Europe: it also occurs in other parts of the Palaearctic region and has been introduced into N. America. About 900 species of the order are known and, for the most part, they exhibit no very marked variations in form or structure. In habits they are mostly nocturnal and many tropical species are attracted to a light. During the day they hide away in the soil, under bark and stones, or among herbage, etc. Excepting *Labia minor*, the European species rarely take to the wing and, notwithstanding the well-developed wings of the common earwig, the latter insect has only on very rare occasions been noted to use them. The majority of species are probably omnivorous but more especially incline to animal food. In captivity *Labidura riparia* will readily devour flies and other insects in preference to vegetable food. *Forficula auricularia* is frequently destructive to flower petals and tender foliage: it is, however, an unsettled point whether it is normally carnivorous, but the species is known to devour both living and dead insects (Brindley, 1918). The term 'earwig' possibly took its origin from the fact that these insects have been known to use the human ear for purposes of concealment: on the other hand it has been suggested that the word is a corruption of 'ear-wing' in allusion to the form of the hind wings. The function of their most characteristic organs—the forceps—is uncertain. They have been reputed to use these appendages for opening and folding up the wings: on several occasions they have been known to impale their prey with them, but in all probability they are principally brought into use as organs of offence and defence and also play a part in copulation. When alarmed, or molested, the extremity of the

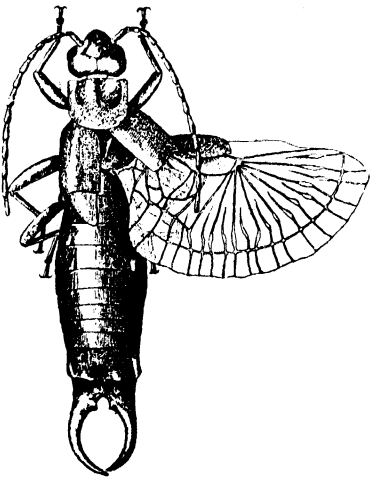


FIG. 274.—*Forficula auricularia*, male with right wing extended
After Chopard, *Faune de France.*

abdomen is often upraised and the forceps widely opened in a threatening manner. The most interesting feature in the biology of earwigs is the parental care that is exercised for the eggs and young. This trait was first observed by De Geer in 1758 and others after him (e.g. Verhoeff, 1912–13; Fulton, 1924; Weyrauch, 1929) have added to his account. The eggs are deposited in the soil in a group, and the female rests over them very much like a hen and her chickens. The newly hatched young also remain around and beneath their parent, who exhibits evident care for them until they are able to look after themselves. If the eggs be removed, and distributed among soil contained in a box, De Geer states that in a few days they are all collected together again and the female seated over them.

External Anatomy.—Among the more noteworthy structural features is the broad horizontal *head* (Henson, 1950), frequently with a distinct Y-shaped epicranial suture. The antennae consist of from 10 to about 50 segments, the eyes are circular and there are no ocelli. In *Arixenia* the eyes are vestigial, and they are absent in *Hemimerus*. The mandibles are broad and strong and almost always carry two apical teeth. The maxillae closely resemble those of the Orthoptera while the labium differs in the ligula, which consists of a single pair of lobes (Fig. 14). The homologies of the latter are uncertain but, in view of the tendency to atrophy exhibited by the glossae in the Acrididae, it is possible that these parts have totally disappeared in the Dermaptera, and the lobes that remain would therefore be interpreted as the paraglossae. The hypopharynx is well developed, and the superlinguae are represented by a pair of relatively large lobes recalling those of the Diplura. The *cervix* is supported by tergal, pleural, and sternal sclerites. According to Snodgrass (1908) the *thorax* presents features which approximate mrre closely to those found in Coleoptera than in Orthoptera though the resemblance is probably due to convergence. The pronotum is a large and more or less quadrangular shield: a postnotum is wanting from the mesonotum, but is present in the metanotum although fused with the first abdominal tergum. Tegmina and wings are absent in *Anisolabis*, the Brachylabini and in *Arixenia* and *Hemimerus*, while the wings vary greatly in development in other members of the order. The tegmina are short, truncated structures devoid of veins, and meet along the median line, thus resembling the elytra of the Staphylinidae. The large semicircular wings are almost entirely composed of the greatly extended anal area: the pre-anal portion of the wing is sclerotized and contains two reduced longitudinal veins (R and Cu). The greater part of the wing is supported by a series of secondarily developed radially disposed branches. The wings are folded longitudinally in a fan-like manner, accompanied by two folds in a transverse direction and, in this way, they are stowed beneath the small tegmina (Verhoeff, 1917). The legs do not call for special mention, and the tarsi are 3-segmented in all cases.

The *abdomen* is 11-segmented; the 1st tergum is fused with the metathorax and the 11th is represented by the small pygidium. In the females of the Forficulina and Hemimeridae the 8th and 9th terga are greatly reduced and invisible without dissection. In the Arixeniidae, on the other hand, the nymphal or ancestral condition is maintained in that both sexes have the full complement of terga, with only very slight reduction of the 8th and 9th shields in the female. The 1st sternum is always wanting, while sterna 2 to 9 in the male and 2 to 7 in the female are clearly visible. The 9th sternum in the male largely overlies the 10th, the latter being represented in both sexes by a pair of plates at the base of the cerci. In the female the 7th sternum com-

pletely conceals the 8th and 9th (Fig. 275). According to Berlese a vestigial 11th sternum is present in both sexes and takes the form of a minute divided plate close to the anus. The females of some primitive Forficulina (Pygidicraniidae) possess a reduced ovipositor composed of a pair of valves developed from the 8th abdominal segment and another pair from the 9th but the more specialized families lack an ovipositor. The male genitalia (Burr, 1915–16; Snodgrass, 1936) are of considerable taxonomic value: the Pygidicraniidae and Labiduridae have two penes but one of these is greatly reduced or absent in the other families. In all the Forficulina the cerci are modified into unjointed forceps (Lhoste, 1942). The latter present great diversity of form among different species, and are often variable within the limits of a single species as in *Forficula auricularia* (Bateson & Brindley, 1892). In the females of almost all earwigs they are shorter than in the males, being as a rule straight and unarmed. In *Hemimerus* the cerci are represented by hairy unjointed styliform appendages. The cerci of *Arixenia* resemble those of *Hemimerus*, except that they are bowed inwards in the male, and bear a closer resemblance to the forceps of true earwigs.

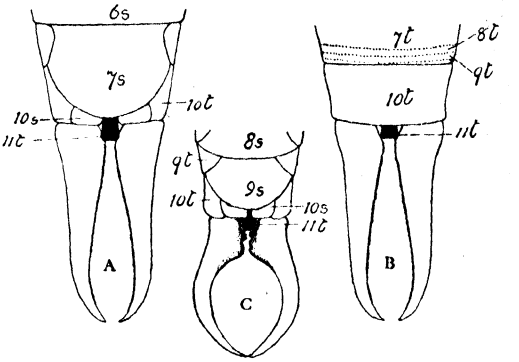


FIG. 275.—*Forficula*, terminal abdominal segments
A, female (ventral). B, female (dorsal). C, male (ventral). *s*, sterna; *t*, terga.

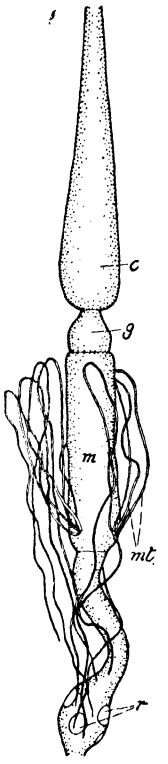


FIG. 276.—*Forficula*, alimentary canal
c, crop; *g*, gizzard; *m*, mid intestine; *mt*, Malpighian tubes; *r*, rectal papilael.

Internal Anatomy.—The *alimentary canal* (Fig. 276) is of a very uniform structure throughout the order. The oesophagus leads into the crop which is followed by a small globular gizzard. The mid intestine has no enteric caeca and is slightly coiled posteriorly, but in *Arixenia* it forms nearly two complete coils. The Malpighian tubes vary from eight or ten to about twenty, and are grouped in bundles. In *Forficula* there are four groups of five tubules (Henson, 1946). The hind intestine presents a partial or, in *Arixenia*, a complete convolution, and there are six rectal papillae. The *nervous system* (Fig. 61) appears to be very constant and, in addition to the two cephalic centres, there are three thoracic and six abdominal ganglia. The *tracheal system* communicates with the exterior by means of ten pairs of spiracles as in Orthoptera. The *female reproductive organs* (Fig. 156) are divisible into two types. In *Forficula* there are three rows of numerous, very short, polytrophic ovarioles, distributed at regular intervals along the greater part of the length of each oviduct. In *Labidura riparia*, *Arixenia* and *Hemimerus* the ovarioles are much fewer, and are disposed in a single series. In *Labidura* there are five elongate ovarioles: in *Hemimerus* there are eight (Jordan) or 10–12 (Heymons), while in *Arixenia*

there are fewer (Jordan). In the two last mentioned genera the ovarioles are very short, each containing a single egg, and viviparous reproduction occurs. According to Heymons (1912) a maternal placenta is present in *Hemimerus* and envelops the embryo. At the anterior extremity of the latter the placenta forms a large cell-mass and, lying beneath it, is a foetal placenta which is developed as a proliferation of the amnion and serosa in that region. The whole placental organ, thus formed, is in direct connexion with the body of the embryo by means of a diverticulum of the head-cavity, known as the cephalic vesicle. The embryos, to the number of about six at a time, are nourished *in situ* within their respective ovarioles, until they develop into young insects and are ready for birth. The *male reproductive organs* (Fig. 153) exhibit considerable differences among various genera. In *Forficula* and *Anisolabis* the testes each consist of a pair of elongate closely apposed follicles: in *Hemimerus* the follicles are likewise paired, but are filiform and tightly coiled: in *Arixenia* the testes are compact and globular, each consisting of sixteen short follicles. The vasa deferentia are very slender, and in *Anisolabis* and *Hemimerus* they dilate posteriorly to form vesiculae seminales: the latter open, in *Hemimerus*, into a small vesicle which communicates with the base of the penis. The ejaculatory duct is stated to be wholly mesodermal in origin and in those Dermaptera with paired penes it is double, whereas in other members of the order one ejaculatory duct atrophies, although a rudiment of it may apparently persist in a few cases.

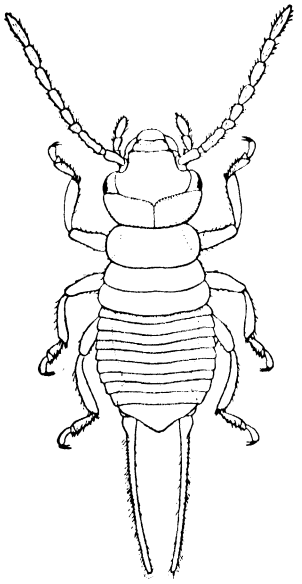


FIG. 277.—*Forficula*, newly-hatched nymph, × 15

Life-History and Postembryonic Growth.—The eggs of Dermaptera are pale coloured, being whitish in *Forficula*, and elliptical with smooth surfaces. *F. auricularia* in Europe lays, according to Weyrauch (1929) 21–80 eggs. The eggs have been found during winter or early spring and eclosion is assisted by an egg-burster. The adult condition is assumed during the summer, and there appears to be a single generation in the year. Hincks (1949) records four nymphal instars in each of five British Dermaptera. The young nymphs resemble their parents in general form, except that they have fewer antennal segments and the forceps are simple and more or less styliform (Fig. 277). In *Diplatys* and *Karschiella*, the forceps are preceded by segmented cerci in the nymphal stages. According to Green, in *D. gerstaeckeri* nymphs 2·5 mm. long bear 14-segmented cerci which are equal in length to the body. During subsequent instars the number of segments increases up to 45, and the cerci attain a length nearly double that of the body. In the preimaginal instar they become abruptly curtailed to a single segment, within which the future forceps can be made out. In almost all other earwigs the forceps are not preceded by segmented cerci, and no trace of segmentation in these organs has been detected in the few embryos that have been examined.

Classification.—The Dermaptera have been monographed by Burr (1911) and general information on the order is given in the earlier work (1910) of that authority and by Beier (1933). There are eight families as follows, and the ten British species (five introduced) may be identified from Hincks (1949).

Suborder I. **FORFICULINA** (Earwigs)

Free-living forms. Eyes well developed. Wings often present: cerci modified into sclerotized forceps.

Superfamily I. **Labiduroidea**

Body normally convex: aedeagus paired: forceps not sickle-shaped: 11th tergum and telson present as separate plates.

FAM. PYGIDICRANIIDAE.—Femora compressed and usually keeled. *Pygidicrania, Diplatys.*

* **FAM. LABIDURIDAE.**—Femora not compressed or keeled. *Anisolabis, Labidura.*

Superfamily II. **Apachyoidea**

Body usually much flattened: aedeagus paired: forceps sickle-shaped: 11th tergum and telson fused together with 10th segment.

FAM. APACHYIDAE.—*Apachyus.*

Superfamily III. **Forficuloidea**

Aedeagus unpaired: 10th tergum well developed: 11th tergum and telson vestigial or absent.

* **FAM. FORFICULIDAE.**—2nd tarsal segment bilobed. *Forficula, Apterygida.*

FAM. CHELISOCHIDAE.—2nd tarsal segment produced into a narrow lobe beneath 3rd segment. *Chelisoches.*

* **FAM. LABIIDAE.**—2nd tarsal segment unmodified. *Labia, Prolabia, Spongiphora.*

Families marked * occur in Britain.

Suborder II. **ARIXENIINA**

Ectoparasitic. Eyes vestigial. Apterous: cerci not horny but arched and hairy.

FAM. ARIXENIIDAE.—This small group is constituted by the genus *Arixenia* with two species, viz. *A. esau* from Sarawak and *A. jacobsoni* from Java (Fig. 278)

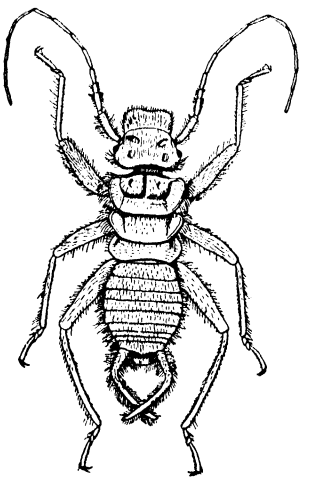


FIG. 278.—*Arixenia jacobsoni*, male
After Burr, *Ent. Month. Mag.*, 1912.

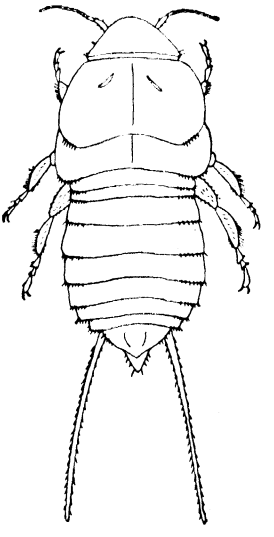


FIG. 279.—*Hemimerus talpoides*
Adapted from Hansen.

The first mentioned species was found in the breast-pouch of the bat *Cheiromeles torquatus*; the second species has been met with in large numbers on guano in a cave much resorted to by bats. *Arixenia* is apterous and viviparous, the eyes are greatly reduced, and the mandibles are strongly flattened with their inner edges rounded and clothed with bristles. The cerci are feebly sclerotized and hairy: they are unjointed and somewhat bowed, which gives them the appearance of incipient forceps. For further information on the genus vide Jordan (1909a), Burr and Jordan (1913).

Suborder III. HEMIMERINA

Ectoparasitic. Eyes absent. Apterous: cerci long, straight and unsegmented.

FAM. HEMIMERIDAE.—This family is composed of the single genus *Hemimerus* which is considered by Rehn & Rehn (1936) to comprise eight species. These are ectoparasitic on different species or subspecies of rats of the genus *Cricetomys* from Africa between about 10° N. and 20° S. and are believed to feed upon the epidermal products of their hosts. *Hemimerus* is apterous and viviparous, devoid of eyes, and the cerci are feebly sclerotized, unjointed, hairy appendages which resemble those of the Gryllidae. The structure of these remarkable insects has been investigated by Hansen (1894), Jordan (1909), Heymons (1912) and Deoras (1941; 1941a): they may be annectant forms connecting the Dermaptera with the Orthoptera.

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See also Blatchley (1920), Chopard (1938; 1951), Hincks (1949) and Lucas (1920) under Orthoptera.

Order 12. **EMBIOPTERA**

Gregarious insects living in silken tunnels. Mouthparts adapted for biting, ligula 4-lobed. Tarsi 3-segmented; 1st segment of anterior pair greatly inflated. Both pairs of wings alike: veins but little pronounced, R greatly thickened, remaining veins often reduced or vestigial. Cerci 2-segmented, generally asymmetrical in the male. Females apterous and larviform. Metamorphosis gradual in the male, absent in the female.

The Embioptera are a small group of fragile insects with a soft thin cuticle and weak powers of flight. All are sombre coloured, being either brown or yellowish brown, with smoky wings. In their habits these insects generally avoid daylight, living beneath stones, or under bark, etc. The females are much more rarely met with than males, the latter not infrequently being attracted to a light. Sexual dimorphism is a marked characteristic of the order, the males being winged and the females apterous (Figs. 280, 281). In several species, notably *Anisembia texana* (Melander, 1903), both winged and wingless males are present.

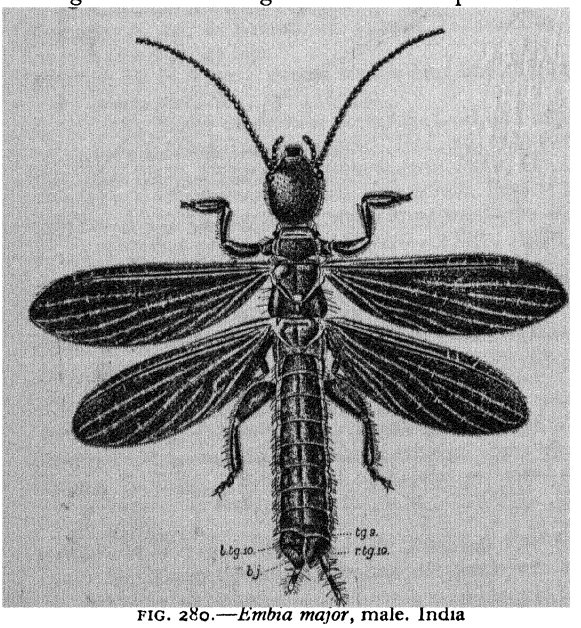


FIG. 280.—*Embia major*, male. India
*Tg*9, 9th tergum; *tg*10, right and left plates of 10th tergum; *bj*, basal segment of left cercus. From Imms, 1913.

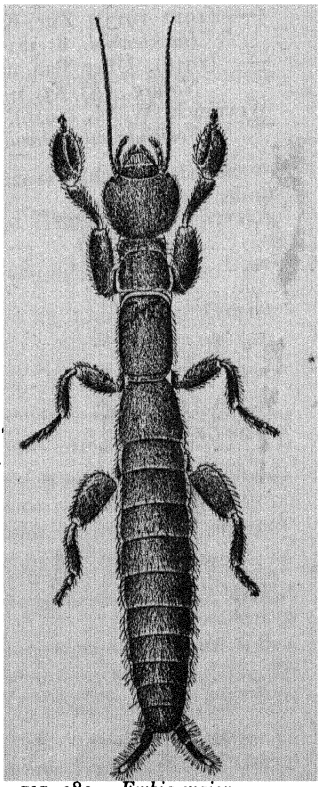


FIG. 281.—*Embia major*, Female
From Imms, 1913.

The most striking feature in the biology of the Embioptera is their habit of constructing silken tunnels in which they live (Imms, 1913). When disturbed in these retreats they are able to run backwards or forwards with equal agility and upwards of twenty individuals may be found associated together. *Embia major* constructs a nest composed of a series of superimposed silken tunnels communicating usually with one or two subterranean chambers. In addition to forming a retreat, it is probable that these tunnels subserve other functions—they appear to be adapted for protection against predacious insects which would become entangled in the threads should they attempt to enter them. Grassi and Sandias consider that they serve to protect the body from an excessive loss of moisture and to retain about the occupants an atmosphere not too dry. During the construction of the tunnels the fore legs are in constant activity, crossing and recrossing one another repeatedly. The faculty of weaving the tunnels is possessed equally by both sexes and also by the nymphs. Newly hatched nymphs, when removed from the proximity of the

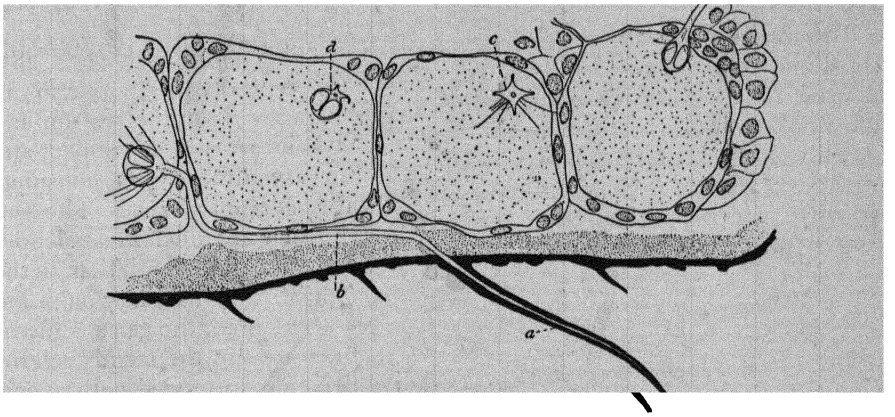


FIG. 282.—*Anisembia texana*, section of portion of 1st tarsal segment, showing silk glands *a*, spinning bristle; *b*, duct of silk gland; *c*, *d*, ampullae at bases of ducts. *After* Melander, *Biol. Bull.*, 1902.

parent female, were observed to weave fine tunnels on their own account. The silk glands are situated in the fore tarsi. On the plantar surface of the 1st and 2nd tarsal segments of the fore legs are a number of hollow bristles which communicate, each by means of a fine duct, with a small glandular chamber. The chambers are situated on the lower area of the enlarged 1st tarsal segment; each is bounded by a single layer of epithelium which encloses a central space filled with a viscid secretion (Fig. 282). In *Anisembia texana* Melander estimates that about 75–80 chambers are present in the whole segment. Since a fine thread is emitted from each bristle a number are available simultaneously, which accounts for the rapidity with which these insects weave their tunnels (Melander, 1903: Rimsky-Korsakov, 1914).

Little information exists with reference to the feeding habits of these insects. Both sexes of *Embia* have been reared from the egg upon vegetable food, but it is likely that the males are normally more or less carnivorous, and their mandibles differ markedly in form from those of the opposite sex.

The eggs are elongate-cylindrical with a conspicuous operculum at one pole. They are laid in small groups along the course of the silken tunnels of the nests, and the females exhibit parental care for their offspring after the manner so well known in Dermaptera. Parthenogenesis occurs in *Gynembia tarsalis*.

Embioptera are tropicopolitan but extend their range into the warmer temperate zones. They occur in all zoogeographical regions including Australia, and species are also found in Madagascar, New Zealand, Ceylon and various smaller islands. Three species, comprised in as many genera, are European and are found in countries bordering on the southern littoral of that continent. It is noteworthy that *Oligotoma michaeli* has been found in a London orchid house where it had become temporarily established. *O. saundersii* is stated to be so abundant on Ascension I. as to become injurious.

External Anatomy.—The head in the Embioptera is always rather small and projects in a line with the body: the epicranial suture is wanting and there are no ocelli. The compound eyes are reniform in the males and rather smaller in the females. The antennae are filiform, shorter than the body, and composed of 15–32 segments.

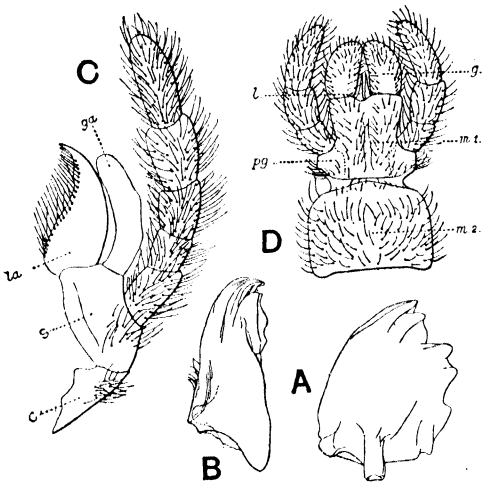


FIG. 283.—*Embia major*

A, left mandible of female. B, do. of male. C, right maxilla, *c*, cardo; *s*, stipes; *la*, lacinia; *ga*, galea. D, labium (ventral), *g*, paraglossa; *l*, glossa; *pg*, palpiger; *m*1, prementum; *m*2, postmentum.

The mouthparts (Fig. 283) are typically Orthopteran in character: both the labrum and clypeus are well developed, and the mandibles differ considerably in the two sexes. Those of the male are much more slender and have fewer teeth than in the female. The maxillary palpi are 5-segmented, the galea is membranous and the lacinia sclerotized and provided with a pair of apical teeth. Both cardines and stipites are well developed. In the labium the ligula consists of a pair of rather fleshy paraglossae and, between the latter, lie the very small pointed glossae: the labial palpi are 3-segmented. The hypopharynx is large and its dorsal surface is covered with minute pectinate scales.

The prothorax is narrower than the head, and a deep transverse sulcus cuts off the anterior portion of the pronotum from the remainder. The meso- and metathorax are subequal in size and broader than long in the male, but elongate and narrower in the female. The fore legs are stout, the middle pair is reduced in size, and the hind pair has swollen femora accommodating the large tibial depressor muscles. The tarsi are always three-segmented: the first segment of the anterior pair is inflated at all stages of life and in both sexes.

The two pairs of wings (Fig. 284) are almost identical in size and shape and only differ in unimportant details with regard to the venation—a similarity which finds a parallel among the Isoptera. The wing-membrane is smoky in colour, with narrow hyaline areas running in a longitudinal manner between the principal veins, giving the wings a very characteristic appearance. After the last ecdysis the newly expanded wings are clear and subsequently assume the fuscous coloration, the hyaline areas remaining unmodified. The surface of the wings is clothed with microtrichia, together with macrotrichia distributed along and between the veins. The radial vein is always greatly thickened, thus serving to strengthen the anterior portion of the wing; the

remaining veins are for the most part weakly defined, exhibiting reduction and degeneration (Fig. 284). The venation is seen in a generalized condition in *Donaconethis*, but even in this genus reduction is evident, as R_s is only 3-branched and M is represented by a single fork. In the Oligotomidae and some other families the venation is greatly reduced and markedly degenerate: R_{4+5} is represented by a mere spur, M has practically disappeared and Cu is unbranched. Traces of a former more complete venation are evident as slight thickenings of the wing-membrane.

The abdomen is composed of 10 evident terga: in the females, and the immature forms of both sexes, the 10th tergum is entire but in the adult males it is divided into a pair of asymmetrical plates (hemitergites). One or both of these plates is drawn out into a sclerotized process of variable form. In *Clothoda* (S. America) the 10th tergum of the male is entire and symmetrical as in the female (Fig. 285). A pair of 2-segmented cerci is present at the apex of the abdomen and, as a general rule, the left cercus in the male is modified basally and the pair is asymmetrical in consequence (Fig. 285). In *Clothoda*, however, the cerci are unmodified, and these organs exhibit also only slight asymmetry in the Oligotomidae. Each cercus is borne upon a basal plate, and these plates are universally present in the females and immature forms of both sexes. Among the males they have disappeared in certain of the more specialized forms. Morphologically they may represent vestiges of an 11th segment. Ten sterna are present, although this number is not always evident and, in some, the 1st sternum in the female is largely aborted. In the immature forms of both sexes, and the females, the 10th sternum is divided into two symmetrical plates. In the males the 9th sternum is usually asymmetrical in form and the 10th sternum is possibly represented by a pair of minute sclerites sometimes fused with the 9th sternum. The female genital aperture is placed on the hind border of the 8th sternum, the latter functioning as the subgenital plate. In the male the 9th sternum is the subgenital plate and a true phallic organ is absent or little developed.

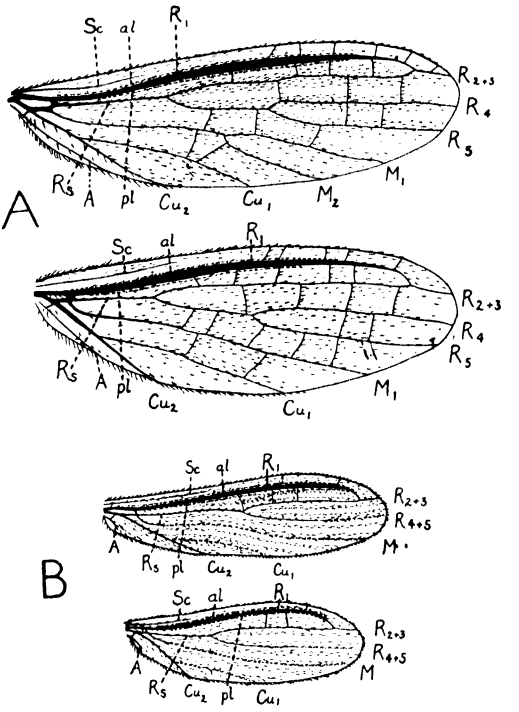


FIG. 284.—Right wings of A, *Embia major*; B, *Oligotoma saundersii*
al, *pl*, anterior and posterior radial lines.

Internal Anatomy.—The internal organization of the Embioptera needs fuller investigation as its general features are mainly known from incomplete accounts by Grassi & Sandias (1896–97), Melander (1903) and Mukerji (1927). It is evident, however, from the descriptions of these observers that it is

a generalized type. The *alimentary canal* is an almost straight tube from the mouth to the anus. The mouth leads into a small buccal cavity which is lined with backwardly directed denticles. This is succeeded by a narrow pharynx, and the remainder of the fore intestine consists of a large dilated oesophagus and crop. The mid intestine is a long tubular chamber which narrows somewhat posteriorly. The hind intestine consists of a slightly coiled ileum, a very short colon and a dilated rectum, the latter being provided with six cushion-like rectal papillae. *Malpighian tubes* are variable in number: in adult individuals there are about 20–30 of these organs. A pair of large *salivary glands*

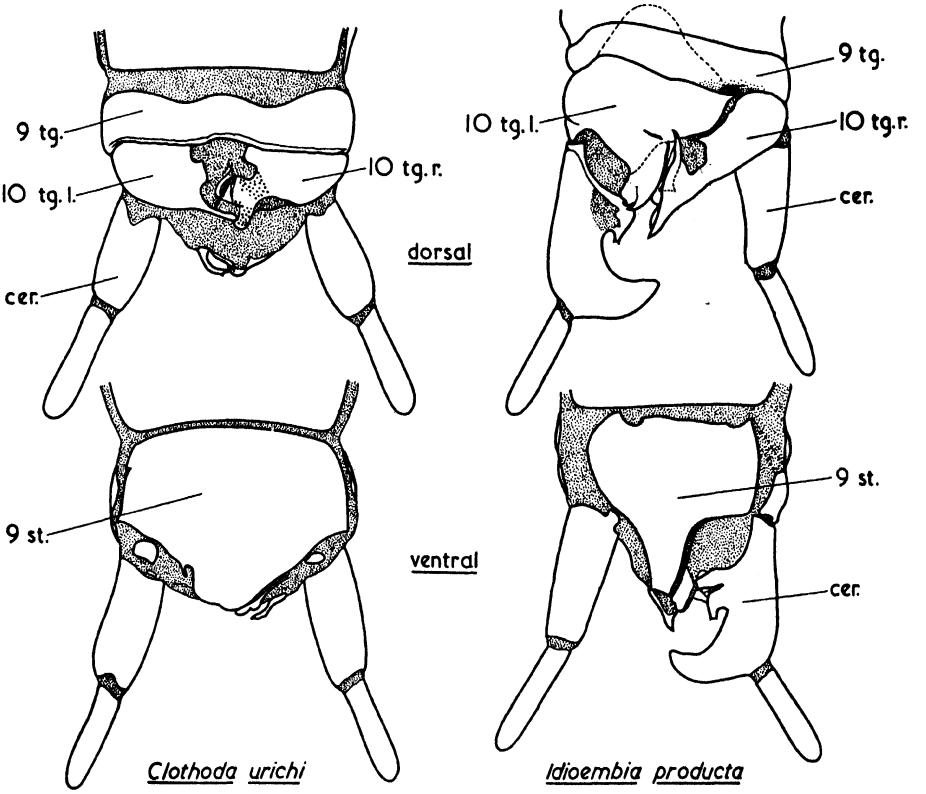


FIG. 285.—Abdominal terminalia of male Embioptera (*after* Ross, 1944)

cer, cercus; 9 *st*, 9th abdominal sternite; 9 *tg*, 9th abdominal tergite; 10 *tg.l*, 10 *tg.r*, left and right hemitergites of 10th abdominal segment.

and reservoirs are present in the thorax, and their ducts unite anteriorly to form a common canal which opens on the floor of the mouth. The *nervous system* consists of a rather small supra-oesophageal ganglion, a suboesophageal ganglion, and a chain of three thoracic and seven abdominal ganglia, which are united throughout by double connectives: the visceral system is also well developed. The *tracheal system* communicates with the exterior by means of ten pairs of spiracles which belong to the meso- and metathorax, and first eight abdominal segments respectively. The tracheae anastomose by longitudinal and transverse branches. The *reproductive organs* exhibit indications of a primitive segmental arrangement recalling that found in certain of the Thysanura. Each ovary consists of five panoistic ovarioles which open at intervals along the course of the oviduct: there is a short vagina which receives

the aperture of a large spermatheca. There are similarly five testes on either side, which are disposed successively along the course of the vas deferens. The latter tube dilates posteriorly to form a vesicula seminalis and ultimately unites with its fellow to form a common ejaculatory duct: two pairs of accessory glands are also present.

Postembryonic Growth.—Metamorphosis is wanting in the females and comparatively slight in the case of the males. The newly hatched young of both sexes do not differ in any important characters from the female parent and, in individuals of the latter sex, the whole postembryonic development is one of simple growth, unaccompanied by structural change. In the males, the nymphs do not differ from the newly hatched young until the appearance of the wing-buds, when the thorax also undergoes correlated changes (Mills, 1932). The characteristic asymmetry of the terminal abdominal segments is only assumed with the final ecdysis.

Classification.—Krauss (1911) and Enderlein (1912) have monographed the order but the work of Davis (1939–40, etc.) and Ross (1944) has extended considerably our knowledge of the Embioptera. About 140 species are to be recognized and Davis (1940) gives a key to the genera of the world. Classification is based to a large extent on characters of the male terminalia and wing-venation and no satisfactory classification of females has yet been established. The following key to families is taken from Davis (1940a), the Embiidae being the largest family.

1. Ventral structures of male terminalia markedly asymmetrical 2
–. Ventral structures of male terminalia not markedly asymmetrical CLOTHODIDAE

2. Fission of 10th abdominal tergite of male incomplete; hemitergites of this segment not separated by a membranous area extending forwards to the 9th abdominal tergite 3
–. Fission complete; hemitergites separated by membranous area extending forwards to 9th abdominal tergite 5

3. R_s three-branched; New World genera 4
–. R_s two-branched or wingless; not indigenous in New World . OLIGOTOMIDAE

4. R_{2+3} bifid, R_{4+5} simple . . . . . TERATEMBIIDAE
–. R_{2+3} simple, R_{4+5} bifid . . . . . OLIGEMBIIDAE

5. Central or N. American genera with R_{4+5} simple or wingless . ANISEMBIIDAE
–. Otherwise 6

6. Indo-Malayan or Australian genera with left cercus 1-segmented in male NOTOLIGOTOMIDAE
–. Indian, African, Mediterranean and Neotropical genera with left cercus 2-segmented in male . . . . . EMBIIDAE

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Order 13. **DICTYOPTERA** (Cockroaches and Mantids)

Antennae almost invariably filiform, with numerous segments. Mouthparts mandibulate. Legs similar to each other or fore legs raptorial; coxae large and rather closely approximated; tarsi 5-segmented. Fore wings modified into more or less thickened tegmina and with marginal costal vein. Wing-pads of nymph do not undergo reversal during development. Female with reduced ovipositor concealed by enlarged 7th abdominal sternum. Male genitalia complex, asymmetrical and largely concealed by 9th abdominal sternum which bears a pair of styles. Cerci many-segmented. Specialized stridulatory and auditory organs absent. Eggs contained in ootheca.

Though formerly associated with the Stick-Insects, Saltatorial Orthoptera and *Grylloblatta* in the Orthoptera, the Dictyoptera are probably best regarded as a separate order, with the distinctive characters enumerated above. They are medium or large-sized insects and include two distinct, homogeneous groups: the Cockroaches (suborder Blattaria) and the Mantids (suborder Mantodea). Though a very few semi-aquatic cockroaches are known (Shelford, 1909), the Dictyoptera are essentially terrestrial forms occurring predominantly in tropical and subtropical regions. They do not fly well and the wings of many species are reduced or absent, more especially in the female. For general accounts of these insects see Handlirsch (1930) and Chopard (1938; 1949).

External Anatomy.—The general structure of *Blatta* is described by Miall & Denny (1886) and that of *Stagmomantis* by Leverault (1937; 1938).

The head, which is usually hypognathous, is relatively primitive in structure with most of the typical sutures and sclerites well-defined, though the arms of the epicranial suture are not always present in the adult. The frons is well-developed, both clypeus and labrum are large and the tentorium is characterized by the presence of an aperture in its central part (Hudson, 1945). Compound eyes are usually well developed, especially in Mantids, but in a few cavernicolous or myrmecophilous cockroaches they are reduced or absent. Three ocelli occur in the Mantodea, being larger in males than in females; in a few cockroaches two ocelli are present but in most members of the latter group these structures are represented by the so-called fenestrae—a pair of pale-coloured areas, each with a nervous connexion to the brain and a histological structure reminiscent of a degenerate ocellus. The mouthparts (Mangan, 1908; Bugnion, 1920; Yuasa, 1920) are complete and adapted for biting (Fig. 10). The mandibles are strong and toothed, bearing a prostheca in *Blatta* and *Periplaneta*. In the maxilla the cardo is subdivided, the stipes elongate and partly differentiated to form a subgalea; the palp is 5-segmented and borne on a small palpifer. The galea is a relatively soft structure, but the lacinia is toothed apically and bears bristles or teeth on its inner face. The labium comprises a large submentum, a small mentum and a prementum

bearing a pair of 3-segmented labial palps, each on a palpiger. Glossae and paraglossae are both well developed. The hypopharynx is large, with lateral suspensory sclerites and a median basal depression—the sitophore (Snodgrass, 1951).

In the neck region the cervical sclerites are well developed. The prothorax bears dorsally a large pronotum, shield-like and usually overlapping the head in cockroaches, usually elongate and not covering the head in Mantids. The meso- and metaterga are similar, each subdivided into acrotergite, prescutum, scutum and scutellum, no postnota being present. The pleural region is normal, that of the prothorax not being concealed by lateral expansions of the pronotum (cf. Orthoptera). The sternal region of the Blattaria has undergone extensive desclerotization, especially in the pterothorax where the basisternum is reduced to a small pair of plates and the sternellum is even more reduced. In the Mantids, the sterna are more fully sclerotized and are dominated by the large basisterna. In all Dictyoptera there are well-developed furcal arms and a spina is present in the pro- and mesothorax.

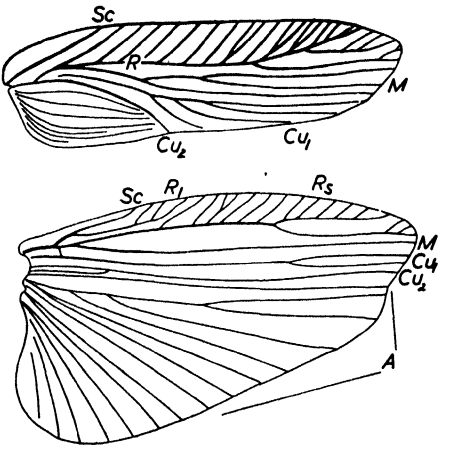


FIG. 285A.—Wings of *Blattella* (*after* Comstock, 1918, and Rehn, 1951)

The legs of the Blattaria are unmodified with large, closely approximated coxae and 5-segmented tarsi. The middle and hind legs of the Mantids are similarly unmodified but the fore legs are highly adapted for catching the small insects on which they prey. The coxae are elongate and mobile while the femora are thickly spinose and grooved along their lower side. The tibiae, which are also spinose, can fit into the groove along the femur and just before their apex—which is usually produced into a hook—there is inserted a reduced 5-segmented tarsus. When present, the two pairs of wings differ markedly. The front pair, known as tegmina, is rather strongly sclerotized and serves mainly to protect the membranous hind wings. The wing-venation of the cockroaches has been studied in detail by Tillyard (1937) and Rehn (1951). The costa of the fore wing is marginal, its subcosta short and Rs possesses numerous anterior pectinate branches. M and Cu_1 occupy a large part of the tegmen and the short, curved Cu_2 cuts off a distinctively shaped clavus. The hind wings possess a large anal lobe which at rest is folded beneath the anterior part between Cu_2 and 1A and is then usually further folded in a fan-like manner (Fig. 285A). The tegmina of a few cockroaches (e.g. *Diploptera*) are greatly thickened and resemble the elytra of beetles. The venation of the Mantodea has not been adequately studied.

The abdomen consists of 10 evident segments represented by their terga, and a reduced 11th segment. The first sternum is small and the 7th (females) or 9th (males) sterna are enlarged to form the subgenital plate which conceals most of the terminal abdominal structures. The ovipositor (Snodgrass, 1933; Qadri, 1940) consists of three pairs of small valves which are probably homologous with those of the Orthoptera (q.v.) and are covered by the 7th sternum. The 8th, 9th and 10th sterna of the female are reduced and partly mem-

branous. In the male, the external genitalia comprise a group of complex, asymmetrical sclerites or membranous lobes (Snodgrass, 1937) with the gonopore opening between them. Khalifa (1950) describes the role which these complicated structures play in copulation; at rest they are largely concealed by the 9th sternum which bears a pair of styles, one or both of which are missing in a few Blattaria. The 11th segment is represented in both sexes by its subdivided sternum (paraprocts) and its appendages—a pair of cerci, which are short and many-segmented except in the cockroach *Panesthia* where they consist of a single segment.

Internal Anatomy.—The alimentary canal (Bordas, 1897) is usually long and sinuous, but in some Mantids it is straight. The crop is well developed and the gizzard either rather poorly developed, as in the Mantids, or provided with a powerful masticatory armature in the Blattaria (Judd, 1948). The mid gut (Fig. 102) bears eight tubular enteric caeca and at its junction with the hind gut there arise about 80–100 Malpighian tubules (Henson, 1944). Large salivary glands are present and are provided with conspicuous reservoirs in the cockroaches (Fig. 143). The nervous system (Nesbitt, 1941) is relatively generalized. The circumoesophageal connectives pass through the aperture in the tentorium and 1–3 of the anterior abdominal ganglia are fused with the metathoracic ganglion, so resulting in the presence of only 4–6 separate abdominal ganglia. The stomatogastric nervous system is well developed (Cazal, 1949) with a recurrent nerve, hypocerebral ganglion, paired corpora cardiaca and a single oesophageal nerve. The tracheal system (Fig. 121) communicates with the exterior by ten pairs of spiracles—two thoracic and eight abdominal. The circulatory system has been described by Nutting (1951). The heart (Fig. 125) occupies most of the thorax and the first nine abdominal segments is flanked by twelve pairs of alary muscles and provided with three thoracic and nine abdominal pairs of incurrent ostia. Six pairs of segmental vessels (two thoracic, four abdominal) leave the heart in the Blattaria, but in the Mantids there are either only four abdominal pairs or the latter are replaced by four pairs of excurrent ostia. In the male reproductive system (Snodgrass, 1937; van Wyk, 1952) the testes each consist of four or more follicles usually enclosed in a common peritoneal sheath. The vasa deferentia run back with few or no convolutions and then loop forward round the cercal nerves to join the ductus ejaculatorius. Arising near the anterior end of the latter are one or more pairs of small ovoidal seminal vesicles and a large number of tubular accessory glands of various lengths. These glands secrete the material from which the spermatophore is constructed (Khalifa, 1950) and are apparently mesodermal in origin, developing in the nymph from an ampulla at the end of the rudiment of each vas deferens. In addition, male cockroaches possess an unpaired 'conglobate gland' (Miall & Denny) of variable form which lies beneath the accessory glands and opens separately between the lobes of the phallus. In the female reproductive system (Voy, 1949; van Wyk, 1952), each ovary comprises a number of panoistic ovarioles (6 in *Diploptera*, 15–20 in *Leucophaea*) leading by short ducts into the common oviduct which opens on the reduced 8th abdominal sternum into the large genital chamber, the floor of which is formed of the 7th sternite. Between the 8th and 9th abdominal sterna—i.e. in the dorsal wall of the genital chamber—there opens the duct of the spermatheca, which is accompanied in some cockroaches by a small spermathecal gland and in a few species (e.g. *Blattella germanica*) is paired, with separate ducts. The female accessory glands ('collaterial glands') are a pair of large structures which also open separately into

the genital chamber and secrete the materials from which the ootheca is formed in the chamber. They have been studied in detail by Brunet (1951–52) in *Periplaneta*: the left gland produces a protein which becomes shaped to form the ootheca while the right one secretes a diphenolic substance which is converted into a quinonoid tanning agent used to harden the oothecal material. An additional 'vestibular organ' of uncertain secretory function also arises from the dorsal wall of the genital chamber in *Periplaneta* (Brunet, *l.c.*). Several subcutaneous glands have been described in the cockroaches. Harrison (1906) reported a bilobed sternal gland in *Blatta orientalis*, opening between the 6th and 7th sterna and Minchin (1888; 1890) a pair of tergal glands in the same species, opening between the 5th and 6th abdominal terga. The functions of these organs are not known. In the males of several genera (*Ectobius*, *Blattella*) there are well-developed dorsal glands opening on specially modified areas of the 6th, 7th or 8th abdominal terga by fine canals and secreting a substance licked by the female before copulation (Konček, 1924).

Postembryonic Development.—Details of postembryonic development and biology are given below for the two families separately.

Classification.—The modern tendency is to divide both cockroaches and mantids into many families, but as the various authorities are not in agreement, it is convenient here to treat them as each represented by a single family.

Suborder **BLATTARIA**

Dictyoptera with head nearly or completely covered from above by large, shield-like pronotum. Two ocelli usually represented by fenestrae. Fore legs unmodified. Gizzard with powerful masticatory armature.

FAM. BLATTIDAE.—The Blattidae include about 3,500 species and are predominantly tropical forms although the few species occurring in temperate areas are sometimes numerically abundant under artificial conditions. Several species are readily distributed by human agency and have become established in all areas—e.g. such well-known domestic pests as *Blatta orientalis*, *Periplaneta americana* and *Blattella germanica*. Although usually of a testaceous or dark mahogany colour, there are tropical species which are more brightly coloured, *Panchlora*, for instance, being pale green. Apterous and brachypterous forms are not uncommon, particularly in the females. Cockroaches are usually found in or on the ground and among low vegetation and debris, but some inhabit caves (e.g. *Nocticola*) and a few, such as *Attaphila*, are myrmecophilous. Some species of *Rhicnoda* and *Epilampra* live near water and are said to be capable of withstanding short periods of submergence. On the other hand, a few species live in deserts and the females are provided with spinose fore tibiae which enable them to burrow into the ground. The domestic species are omnivorous, with a partiality for sugary and starchy foods but Brunner considered the food of most wild species to be composed largely of dead animal matter. *Panesthia* and *Cryptocercus* (Cleveland, 1934) feed on dead wood, digesting the cellulose through the assistance of symbiotic bacteria and Protozoa respectively (cf. Isoptera). *Cryptocercus*, incidentally, exhibits subsocial behaviour as does also *Polyzosteria*. Mating may be preceded

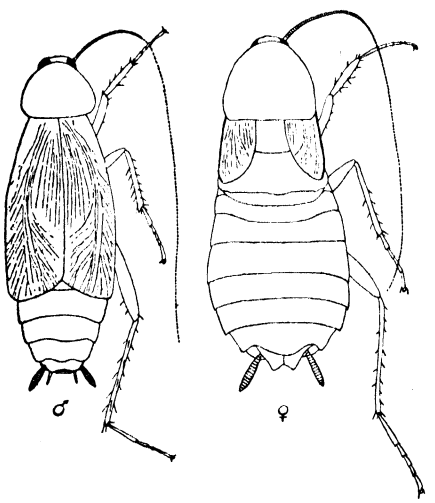


FIG. 286.—*Blatta orientalis*, slightly enlarged

by simple courtship behaviour and a spermatophore is known to be formed in a few investigated species (Khalifa, 1950). Shelford (1906) distinguished three modes of reproduction in the Cockroaches: (i) Oviparous species with the eggs enclosed in a sclerotized ootheca (Lawson, 1951; Rau, 1943) which is carried by the female for only a short time, protruding from her body (e.g. *Ectobius* and *Blatta*) (Fig. 287); (ii) Ovoviviparous species in which the eggs are carried by the female for most of the incubation period either in a sclerotized (*Blattella germanica*) or a membranous (*Temnopteryx*) ootheca and (iii) Viviparous species (Fig. 287) in which the eggs are retained until hatching in the enlarged genital chamber (brood sac) of the female enclosed in either a sclerotized ootheca (e.g. *Blaberus*) or a membranous sac, the latter being complete (*Panchlora virescens*) or incomplete (*Panchlora viridis*). Typically the

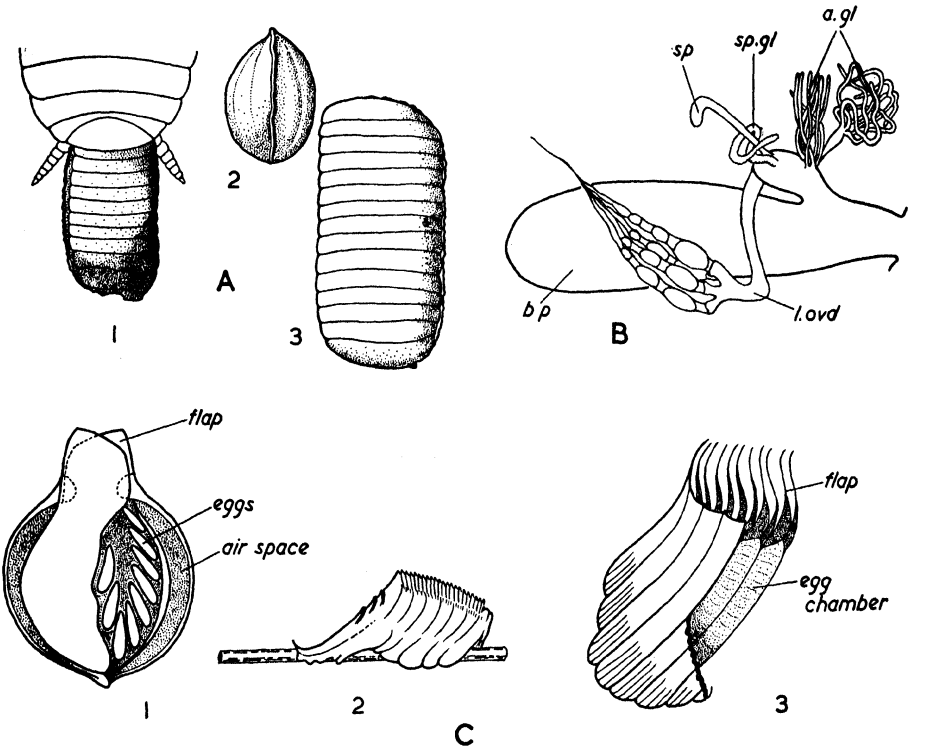


FIG. 287.—A. Ootheca of *Blattella germanica* (*after* Laing, 1938)

1, ootheca protruding from body of female; 2, 3, end and side views of ootheca.

B. Female reproductive system of *Diploptera*, showing brood pouch (*after* Hagan, 1941)

a.gl, accessory glands; *b.p*, brood pouch; *l.ovd*, lateral oviduct; *sp*, spermatheca; *sp.gl*, spermathecal gland.

C. Ootheca of *Hierodula* (Mantidae) (*after* Kershaw, 1910)

1, transverse section; 2, entire ootheca; 3, details in lateral view.

ootheca is divided into two rows of pockets by a longitudinal partition and each egg (16 in *Blatta*, 40 in *Blattella*) occupies a pocket. When the nymphs are ready to emerge, the ootheca splits along its dorsal edge, the two halves separate and the young struggle out. The first-stage nymph in *Blatta orientalis* (Qadri, 1938) is a 'pronymph' with the instar of very short duration and its appendages not fully formed and apparently soldered down so as to give it a vermiform appearance. The six subsequent nymphal instars of this species can be distinguished from one another by differences in the developing genital segments, number of cercal segments and size of wing-pads and take 279 days to complete their development at 27·5° C. *Periplaneta americana*, according to Griffiths & Tauber (1942), has 11 nymphal instars in the female and 12 in the male and takes about 250–270 days to develop at 29° C. See also Gould & Deay (1940). Taxonomic works on the Blattidae include those of Shelford (1907–10), Rehn

(1931–37), Bruijning (1948) and Rehn (1951). For the few British species (three indigenous species of *Ectobius* and four established introductions) see Lucas (1920) and Hincks (1949). Chopard (1951) deals with the French forms, and Blatchley (1920) with those of N.E. America.

Suborder **MANTODEA**

Head not covered by pronotum. Three ocelli present. Fore legs raptorial. Gizzard not powerfully armed.

FAM. MANTIDAE (Praying Mantids).—This family is composed of about 1,800 exclusively carnivorous species occurring in all the warmer parts of the world (Beier, 1939). Its members are easily recognizable by the peculiar form of their front legs and, armed in this way, the mantis often sits motionless for long periods at a time, with the head upraised upon the elongate and sub-erect prothorax. The powerful raptorial fore legs are raised together in front, their pincers being partially opened to seize any suitable prey which ventures within range. This curious attitude, which suggests one of supplication, has earned for its possessors the name of 'praying mantids'. They feed voraciously on flies, grasshoppers, caterpillars, etc., and are very pugnacious, the larger forms attacking the smaller, and females the males. Some of the larger S. American species have been recorded as even attacking small birds, lizards and frogs. Mantids are extremely variable in form and are assimilated in a remarkable manner to their surroundings, perhaps more to deceive their prey than to protect themselves.

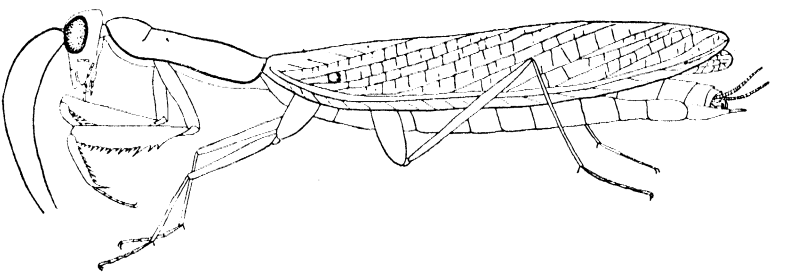


FIG. 288.—*Mantis religiosa*, male. S. Europe

The green colour of the typical mantis serves this purpose admirably while those that simulate flowers have the advantage of attracting flower-haunting insects within their reach. Certain tropical species possess foliaceous expansions on the prothorax and limbs, while *Pyrgomantis* is so attenuated as to resemble a Phasmid. Mating in the mantids has often been described in rather spectacular terms on account of a tendency for the female to attack and start eating the male before or during copulation. In an experimental study of mating in *Mantis religiosa*, Roeder (1935) suggests that this attack occurs through the failure of the female to recognize the male, which is therefore treated as legitimate prey. If the male is able to secure the correct grip on the female's body from the start of copulation he remains unmolested. Even when the male is attacked and his head eaten, this does not interfere with effective mating since the copulatory movements are under the control of the last abdominal ganglion and are even stimulated by the destruction of inhibitory centres in the suboesophageal ganglion.

The eggs of mantids are laid in oothecae (Fig. 287) which are attached to twigs, bark, walls and other objects. Each female makes a number of these cases (twenty-two have been recorded in *Miomantis* by Adair, 1913) and their type of construction varies according to the species. In the Indian *Gongylus*, for example, Williams (1904) states that the ootheca consists of a more or less frothy secretion which hardens into a firm, spongy substance. Within this envelope is a layer of about forty egg-chambers arranged four abreast: they are constructed of a viscid material which very rapidly hardens to the consistency of horn. In the Chinese *Hierodula saussurii* Kershaw (1910) mentions that the oothecae are about an inch long, and the egg-chambers number about twenty-four, arranged in two longitudinal rows. An air space is left between the layer of eggs and the outer covering, and the latter is composed of overlapping strips of extremely hard, tough material. Other types of oothecae are described by Breland &

Dobson (1948) and others. Though it would appear that the eggs of Mantids are admirably protected by these cases, the latter are ineffective in warding off the attacks of insect enemies, judging from the frequency with which parasitic Hymenoptera are bred out from them. It is possible, however, that they serve to protect the eggs from birds and lizards. As in the cockroaches, the first-stage nymph is a 'pronymph' and is rapidly succeeded by a more normal second-stage form (Williams & Buxton, 1916). The pronymph was observed by Williams & Buxton to hang suspended from the ootheca by means of silken threads secreted from a pair of papillae on the 10th abdominal sternum, but no silk is produced in later instars. The number of nymphal stages in the Mantidae is not constant and from accounts given by different observers it varies from three to twelve, the whole life-cycle taking about a year to complete. More than a dozen species occur in western Europe, of which the most familiar is *Mantis religiosa*. This insect ranges as far north as Paris and has been introduced by means of nursery stock into N. America where it has become locally established.

Among recent taxonomic works may be mentioned those of Rehn (1911), Giglio-Tos (1913–27) and Beier (1934–35). The French species are described by Chopard (1951).

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Order 14. **ISOPTERA** (Termites or White Ants)

Social and polymorphic species living in large communities composed of reproductive forms together with numerous apterous, sterile soldiers and workers. Mouthparts of the typical biting type: ligula 4-lobed. Wings very similar, elongate and membranous, superposed flat over the back when at rest and capable of being shed by means of basal fractures: anterior veins strongly sclerotized, regular cross-veins wanting and an archedictyon often present. Tarsi almost always 4-segmented. Cerci short or very short: genitalia usually wanting or rudimentary in both sexes. Metamorphosis slight or absent.

The Isoptera are usually known as termites or 'white ants'; the latter expression, however, is unfortunate since these insects are only very distantly related to the true ants or Formicoidea. Nevertheless, the two groups offer certain striking analogies of habits and structure. Their remarkable social life and the presence of specialized wingless individuals, known as soldiers and workers, are cases in point.

Termites abound throughout the tropics of the world and also occur in most warm temperate countries. Over 1,700 species have been described and, of these, the vast majority occur south of the Holarctic region. Only two species, *Kalotermes flavicollis* and *Reticulitermes lucifugus*, are common in Europe, but these do not extend their range into the British Isles.

A termite community includes several castes or types of individuals which live in habitations, or termitaria, of extremely varied kinds. The castes are four in number, and are divisible into reproductive and sterile forms consisting of individuals of both sexes. The reproductive castes comprise (*a*) completely sclerotized macropterous or fully-winged forms whose mission in life is the formation of new colonies (Fig. 289): (*b*) less sclerotized forms with reduced wings (Fig. 302). A termite colony usually contains a royal pair—the queen and king: these are commonly deälated individuals of the fully-winged caste and are the original founders of the colony (Fig. 301). The sterile castes consist of (*a*) soldiers and (*b*) workers which are apterous males and females adapted for special non-reproductive functions. Every colony also contains numerous immature individuals of different ages undergoing development into most of, or in some cases all, the above four castes. Besides the legitimate occupants of a termite habitation, there are to be found symbionts and inquilines belonging not only to other orders of insects but also to different classes of arthropods. It is evident, therefore, that the study of termite associations involves problems of the widest biological significance and, it may be added, an extensive field for research awaits those investigators who may be located in favoured countries. General reviews of the order are given by Hegh (1922), Handlirsch (1930) and Grassé (1949).

External Anatomy.—The *cuticle* in termites is thin and flexible and, in the apterous castes, only that of the head is at all hard while the covering of

the abdomen is frequently a delicate translucent membrane. The aerial winged forms are more completely sclerotized than any other caste; as a rule, the

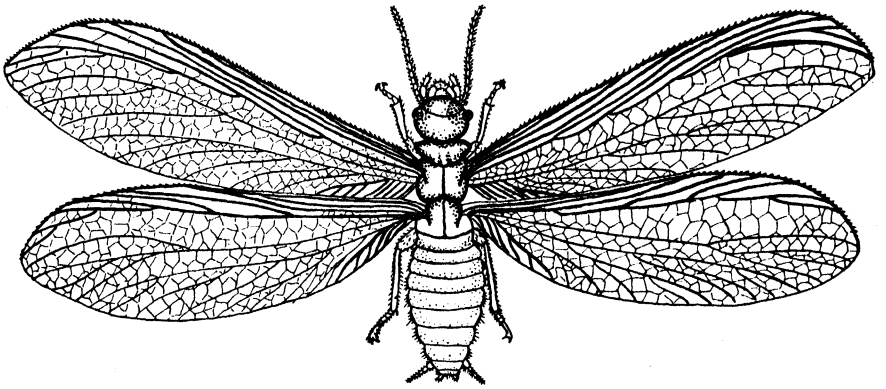


FIG. 289.—A winged termite (*Archotermopsis*), male

cuticle is more darkly coloured in species which either forage in daylight, or inhabit wood above ground than it is in subterranean forms. The *head* in the reproductive castes and workers is ovoid or rounded, while in the soldiers it is much larger and more often oblong or pyriform (Figs. 290, 291): in the latter caste it may exceed in size the whole of the rest of the body. The median and V-shaped *epicranial sutures* are frequently evident although extremely variable in their degree of development. The perforate tentorium resembles that of the Blattidae (Hudson, 1946). *Compound eyes* are universally present in the macropterous forms, but suffer reduction to a greater or lesser extent in the other reproductive forms. They may be present in all castes of species which live or forage above ground, and are hence more exposed to daylight, but when present in the soldiers and workers they almost invariably exhibit degeneration. *Ocelli* are frequently present but do not occur unless accompanied by compound eyes: the median unpaired ocellus is wanting. The *antennae* are moniliform and arise from shallow fossae situated immediately above the base of each mandible. The number of segments varies from about 9 or 10 to over 30, being greatest in some of the more primitive genera; it also varies according to the caste and age of the individual and is highest in the macropterous forms. After emergence from the egg, the antenna increases in length by means of the intercalation of new segments, through the growth and subdivision of the third segment, and those segments directly derived from it. The *labrum* is well developed and largely overlies the bases of the mandibles. It is

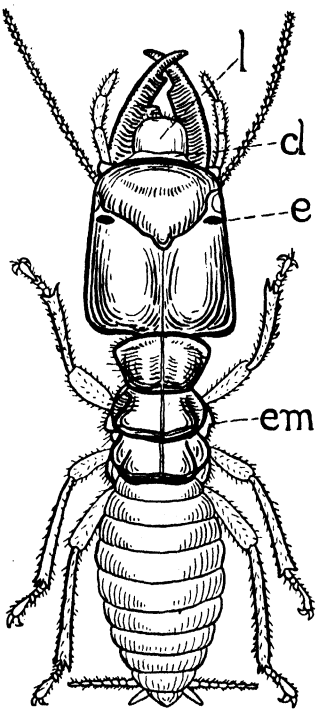


FIG. 290.—A soldier termite (*Archotermopsis*), male

cl, clypeus; *e*, eye; *em*, epimeron; *l*, labrum.

extremely variable in form (Fig. 291) and is hinged to the *clypeus*. The latter is divisible into a sclerotized *post-clypeus*, which is firmly fused with the frons, and a more membranous distal portion or *ante-clypeus*.

The mouthparts (Figs. 291, 292) closely resemble those of the Orthoptera in their general features. The *mandibles* in the reproductive forms and workers are very similar and present few striking deviations in form. In the soldiers, on the other hand, they are exceedingly variable in different genera, often attaining a great size (Fig. 291), accompanied by curious anomalies of shape: among the nasute soldiers, however, they are vestigial and minute. The *maxillae* only differ in points of detail throughout the order. The galea is hood-like and commonly 2-segmented: the lacinia is strongly sclerotized, and powerfully toothed distally, becoming more or less laminate basally, and is armed with stout setae along its inner margin: the palpi in all cases are 5-segmented. The *labium* possesses a large basal plate which has received various names and may be termed the *postmentum*, or undifferentiated mentum and submentum (Fig. 15). Anteriorly it bears the *prementum* which is of a generalized type. The latter region exhibits more or less evident traces of a paired origin and carries both glossae and paraglossae and the 3-segmented labial palps. The *hypopharynx* is always large and is very similar to that of the Orthoptera; *superlinguae* are wanting, unless a pair of minute sclerotizations are to be regarded as their counterparts.

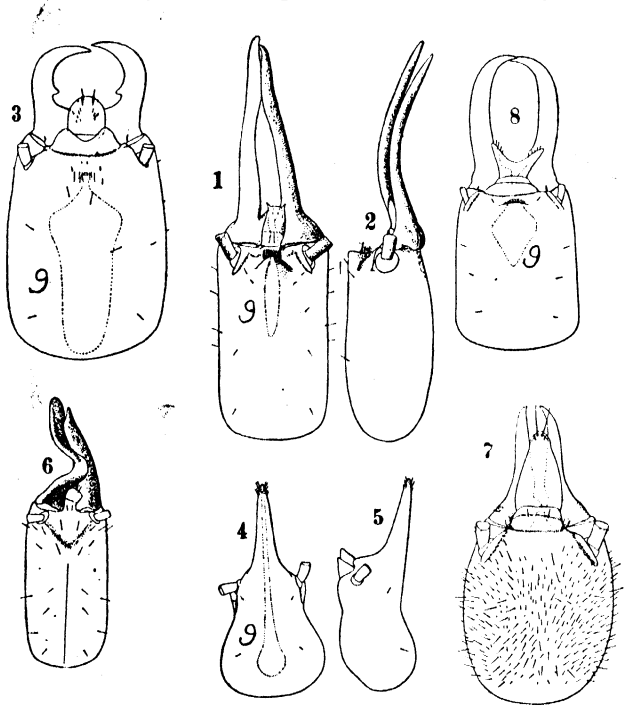


FIG. 291.—Heads of soldiers of African termites

1, 2, *Mirotermes*. 3, *Hamitermes*. 4, 5, *Eutermes*. 6, *Pericapritermes*. 7, *Microtermes*. 8, *Cubitermes*; *g*, frontal gland. *After* various figures by Silvestri, *Boll. Lab. Zool. Portici*, 9.

In the *cervix* there are two pairs of large and conspicuous lateral cervical sclerites, those of a pair being placed at right angles to one another: vestigial dorsal and ventral sclerites are also sometimes present.

In the *thorax* the terga are well developed: the pronotum is the most distinct, its many variations in form affording generic characters. It may be flattened and shield-like, heart-shaped, laterally lobed or very often saddle-shaped. The *meso-* and *metanotum* are of very nearly equal size and much less variable or pronounced in character. On the ventral surface, the sterna are membranous with their boundaries often difficult to distinguish. The *prosternum* is greatly reduced and definite shields are often wanting; in *Archoter-*

mopsis it consists of two small triangular plates which are separated from one another in the median line. The *mesosternum* is the largest of the three sterna and is a variably shaped shield; articulating with it posteriorly is a small rod-like *mesosternellum*. The *metasternum* is very wide and partially hidden from view by the bases of the middle pair of legs: a *metasternellum* is likewise present. In each segment the sides of the sternum are separately sclerotized to form laterosternites which also articulate with the *episterna*. The latter elements in the prothorax are strongly sclerotized bands which pass upwards to articulate with the under surface of the pronotum on either side. In the meso- and metathorax the episterna are large, and in the macropterous form reach the bases of the wings. The three pairs of *legs* are very similar: at their bases the epimera are well developed and the *coxae* very large and broad. In the middle and hind pairs a *meron* is marked off from the rest of the coxa by means of a deep suture. The tibiae are long and slender: among the most primitive genera they are armed with both terminal and lateral spines, but in the majority lateral spines are wanting. The tarsi are typically 4-segmented: the only exception is *Mastotermes* which has 5 complete segments. In *Archotermopsis* and the related genera *Zootermopsis* and *Hodotermopsis*, the tarsi are imperfectly 5-segmented, the 2nd segment being reduced. In the winged imagines of *Mastotermes*, some Kalotermitidae and some Hodotermitidae, an *empodium* is present between the claws of the feet; in other families this structure is wanting.

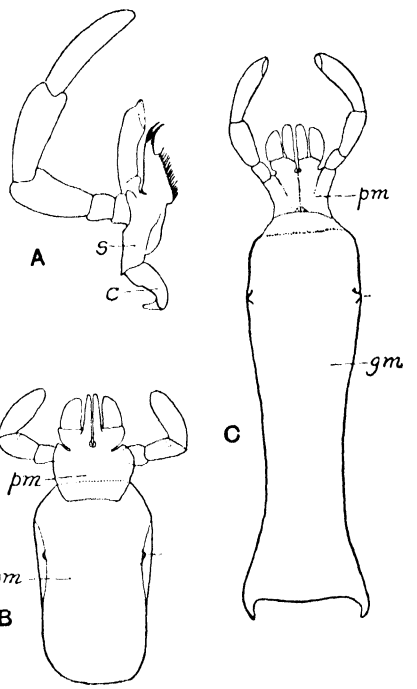


FIG. 292.—*Archotermopsis*

A, maxilla of soldier. B, labium of macropterous form. C, labium of soldier; *c*, cardo; *gm*, postmentum; *pm*, prementum; *s*, stipes.

The *wings* (Figs. 293, 294) of termites are characterized by the essential similarity in size, form and venation of the two pairs of those organs. The veins of the anterior portion of each wing are strongly sclerotized, while those distributed over the remaining area are much less pronounced and exhibit indications of degeneration. This feature has probably resulted from the slight use to which the wings are subjected, more durable organs being unnecessary. There is a striking absence of regular cross-veins, and the wing-membrane is stiffened in many cases by the presence of an irregular slightly sclerotized network between the veins. The veins distributed over the intermediate region of the wing are reduced to faint lines while, on the other hand, there is a large posterior group of accessory veins borne by the cubitus. The venation (Tillyard, 1931; Fuller, 1919) is primitive in a few genera (*Mastotermes*, *Archotermopsis*, *Zootermopsis*), but in the remainder of the order specialization by reduction is evident, affecting more particularly the radial and median veins. In the fore wing of *Mastotermes* there is no true costal vein: Sc is 2-branched, and R_{1-5} are recognizable as separate branches. Both M and

Cu are well developed, Cu_2 forms a curved *vena dividens* and there are no distinct anal veins. In the hind wing Sc is unbranched and M arises from the stem of R_{4+5}. Three anal veins are present and support a well-developed anal lobe (Fig. 314). The presence of the latter feature recalls the Blattid hind wing (Tillyard, 1937) and is a primitive character found in no other termites. *Archotermopsis* and *Zootermopsis* exhibit the first stage in reduction, R_{2+3} being undivided in the fore wing, and the anal lobe in the hind wing being vestigial. In the higher Isoptera, the costal margin is greatly thickened through the fusion of certain of the anterior veins, R is represented by a single stem, possibly R_{4+5}. M usually retains one or more branches and the remainder of the wing is occupied by the accessory branches of Cu. One of the most striking features of the termite wing is the presence of the *basal* or *humeral suture* which is a line of weakness along which the fracture and shedding of the wings takes place. *Mastotermes* is exceptional in that the hind wing has no fracture-line and is torn off irregularly. The stump of the wing, or that portion which lies between the humeral suture and the thorax, persists throughout life and is commonly termed the *scale*. This property of casting the wings is not entirely confined to the Isoptera. In the Blattid *Panesthia* the wings are torn off in a somewhat irregular manner in a certain proportion of individuals; in the Zoraptera (p. 396) they are likewise shed but the fracture is more regular although no basal suture is developed.

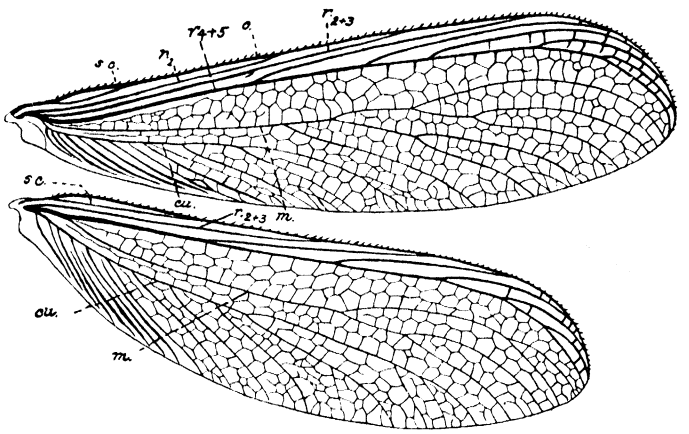


FIG. 293.—Fore and hind wings of *Archotermopsis*

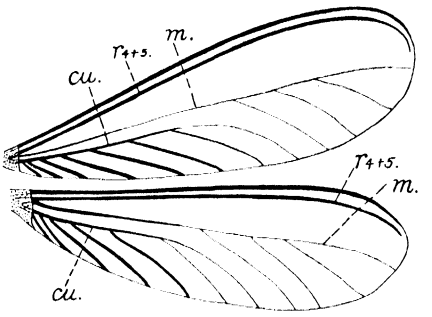


FIG. 294.—Fore and hind wings of *Eutermes* sp.

The *abdomen* has 10 visible terga, the 11th tergum probably being fused with the 10th, while the 11th sternum is represented by a pair of paraprocts. The 1st sternum is atrophied and the sternal plates differ markedly in the two sexes of the reproductive forms. In the males of many termites all the sterna are entire: in certain of the higher forms, however, the 9th sternum is divided. In the females the 7th sternum is greatly enlarged forming the subgenital plate which overlies the succeeding sterna. The terminal segment of the abdomen carries a pair of short *cerci* which are present in all castes. In *Archotermopsis* they are composed of 6–8 segments, in *Mastotermes* and *Zootermopsis*

of 5 segments, *Hodotermopsis* 3–6 segments, while in the family Termitidae they are, for the most part, reduced to the condition of 1- or 2-segmented tubercles. On the hind border of the 9th sternum a pair of small, unjointed *styles* is frequently present. They occur in both sexes of the soldiers and workers and in the nymphs of all castes: in the reproductive forms, with rare exceptions, they are present in the males only. External sexual differentiation is clearly evident in the soldiers and workers of *Mastotermes*, *Archotermopsis*, and a few other primitive forms. In the two first mentioned genera there is a similar differentiation of the terminal ventral plates as in the sexes of the reproductive forms. A reduced ovipositor of the Blattid type is present in *Mastotermes* and is still further reduced in the other families (Browman, 1935). The male has a membranous median copulatory organ.

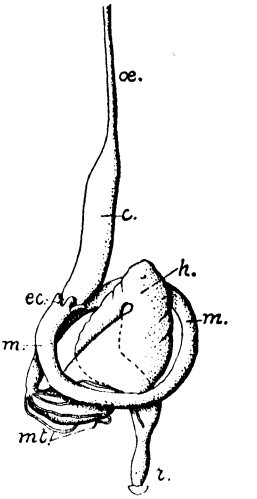


FIG. 295.—*Archotermopsis*, alimentary canal of soldier

oe, oesophagus; *c*, crop; *ec*, enteric caeca; *m*, mid intestine; *mt*, Malpighian tubes; *h*, hind intestine; *r*, rectum.

Internal Anatomy.—The *digestive canal* (Figs. 295, 296) is a coiled tube of moderate length and exhibits comparatively few important variations in structure (Sutherland, 1934). The mouth leads into an elongate *oesophagus* of narrow calibre which expands distally to form the *crop*. The latter organ is seldom capacious and frequently is only slightly emphasized. It is followed by the *gizzard*, provided with an armature of cuticular denticles: this organ is simple and ring-like in certain of the more primitive forms, becoming more pronounced among other termites. Beyond the gizzard the fore intestine protrudes into the cavity of the mid gut forming a large *oesophageal valve*. The mid gut is tubular, of uniform calibre throughout and often completely encircles the hind intestine. At the junction of the mid gut with the latter region are the *Malpighian tubes*; these are variable in number, eight being usually present in the Kalotermitidae and from two to four among the Termitidae. In some Hodotermitidae four or five *enteric caeca* arise as outgrowths from the anterior end of the mid gut; in *Capritermes* Holmgren (1909) mentions a pair of large berry-like glands arising near the origin of the Malpighian tubes. At its commencement, the *hind intestine* is a short narrow tube (or ileum), often separated by means of a valve from the *colon*. The latter region is usually an extensive chamber (the so-called rectal pouch) which, in the wood-feeding termites, is frequently distended owing to the presence of large numbers of Protozoa. The *rectum* is a narrow tube of very variable length and terminates in an ovoid or spherical chamber opening to the exterior by means of the anus. A peritrophic membrane is present (Platania, 1938).

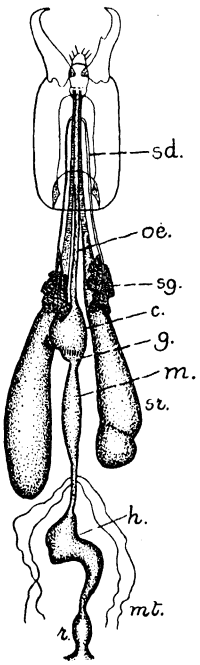


FIG. 296. — *Odontotermes ceylonicus*, alimentary canal of soldier

g, gizzard; *sd*, salivary duct with gland *sg* and reservoir *sr*. Other lettering as in Fig. 295. *After* Bugnion, *Rev. Suisse Zool.*, 1911.

Salivary glands are well developed and racemose in character; each gland

is provided with a salivary reservoir. The ducts, both from the glands and their reservoirs, eventually unite to form a common salivary canal opening at the base of the hypopharynx. Bugnion (1911) states that in the soldiers of *Odontotermes ceylonicus* the salivary glands are very large and secrete a viscous milky fluid probably defensive in function.

The *circulatory system* has been very little investigated; the *heart* consists as a rule of 8–10 chambers and is prolonged anteriorly as the *aorta* which communicates with the cephalic blood space just behind the brain.

The *fat-body* is more extensively developed in the reproductive forms than in the soldiers or workers. Feytaud (1912) states that in the kings and queens this tissue undergoes a complete change several years after swarming. Migratory cells (adipocytes) enter it in large numbers and undergo division, gradually building up a new fat-body at the expense of the old. In the course of its development the new tissue often assumes a regular columnar form which is lost when it becomes actively functional.

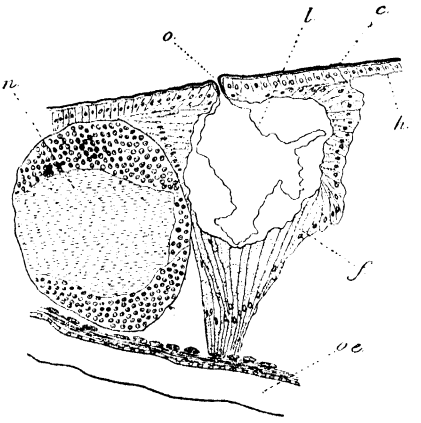


FIG. 297.—*Reticulitermes lucifugus*, section of frontal gland of macropterous form

c, cuticle of head; *f*, frontal gland; *h*, hypodermis; *l*, cuticular lining of gland; *n*, brain; *o*, frontal pore; *oe*, oesophagus. *After* Feytaud.

The *nervous system* presents no notable variations, excepting differences in the degree of development of the brain and eyes in the reproductive and sterile castes. In the ventral nerve-cord there are three thoracic and six abdominal ganglia. The sympathetic system is well developed and closely resembles that of the Orthoptera.

The *frontal gland* (Fig. 297) is a very characteristic termite organ and is formed by a differentiation of a group of hypodermal cells in the median line of the frons. It may be present in all castes but usually attains its greatest development in the soldiers (Holmgren, 1909; Feytaud, 1912; Thompson, 1916, 1917). In its completely developed condition it is a sac-like gland which communicates with the exterior by means of the *frontal pore*. The latter opens in a shallow depression of the surface of the head where the cuticle is pale-coloured and known as the *fontanelle*. The gland is, furthermore, connected with the brain by a median *fontanelle nerve*. In *Reticulitermes* the gland is well exhibited in an average degree of development. According to Feytaud in the macropterous caste of *R. lucifugus* it is a spherical sac, which opens to the exterior, and is lined by a cuticular membrane; beneath the latter is a layer of elongate epithelial cells. In the soldiers its configuration is very similar, but the gland is somewhat larger, while in the workers it is rudimentary, being merely represented by a group of hypodermal cells and devoid of a frontal pore. Thompson has made a more detailed study of the organ in *R. flavipes* and states that in this species it is largest in the macropterous caste. It is present in the newly hatched nymphs, although barely recognizable, and undergoes differentiation as development proceeds. The gland attains its greatest development in the soldiers of *Prorhinotermes* and *Coptotermes*; in these genera it is in the form of an extensive sac, reaching backwards to the extremity of the abdomen (Fig. 306), and discharges a milky latex-like secretion through an enlarged frontal pore. In the soldiers of *Termes* the gland

opens at the apex of a prominent *frontal tubercle*, and in the nasute soldiers of *Nasutitermes* the tubercle is prolonged into an elongate rostrum, through which the duct of the gland passes.

The nature and function of the secretion of the frontal gland is problematical: in some cases it appears to have defensive significance while in others the gland is so little developed as to appear to be non-functional. Thompson suggests that the frontal gland arose phylogenetically from the original median ocellus which is now wanting in termites. This view is based upon the position and the structural resemblances of the frontal gland and lateral ocelli, upon the presence of the fontanelle nerve in the same frontal section at which the lateral ocellar nerves enter the brain, and upon the resemblance of the cells of the gland in developing nymphs to visual cells. Facts enumerated by Holmgren bearing upon the morphology of the frontal gland and the phylogeny of termites, are also regarded by Thompson as lending support to this view.

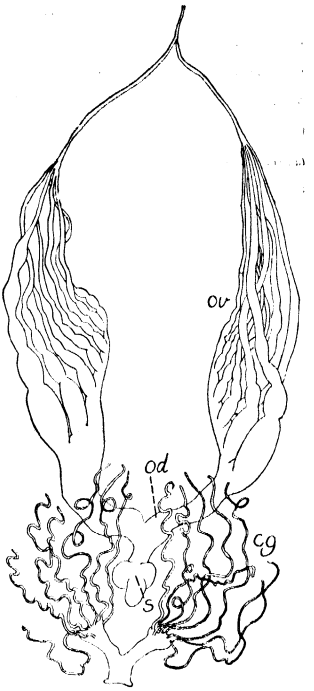


FIG. 298.—*Archotermopsis*, reproductive organs of winged female

ov, ovary; *od*, oviduct; *cg*, colleterial gland; *s*, spermatheca.

The *sexual organs* attain their complete functional development in the reproductive castes. In the soldiers and workers they are almost always aborted to a greater or less degree. Exceptions are met with, however, in *Archotermopsis* whose soldiers have fully developed sexual organs, which may be capable of functional activity, and Heath records members of this caste in *Zootermopsis* producing fertile eggs. Almost every grade in degeneration of the sexual organs can be traced among the soldiers of various genera, until the culminating point is reached in *Hospitalitermes monoceros* where, according to Bugnion (1909), no traces of these organs are to be found (Weyer, 1935; Stella, 1938, 1939). In the reproductive castes (Fig. 300), the *testes* are simple

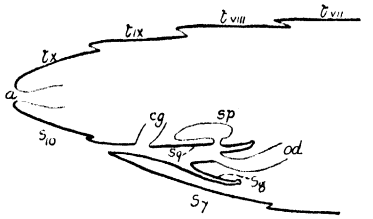


FIG. 299.—*Archotermopsis*, diagrammatic section of the apex of the abdomen of a female soldier

tvii–tx, terga; s_7–s_{10}, sterna; *a*, anus; *cg*, opening of colleterial glands; *sp*, spermatheca; *od*, oviduct.

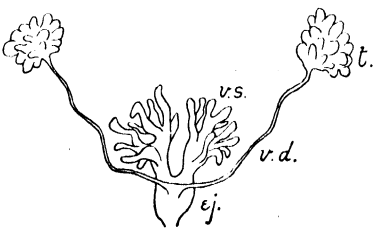


FIG. 300.—*Archotermopsis*, reproductive organs of winged male

t, testis; *vs*, vesicula seminalis; *vd*, vas deferens; *ej*, ejaculatory duct.

and consist of a variable number of short digitate lobes (usually about 8–10) situated in or near the 8th abdominal segment. The *vasa deferentia* are a pair of short tubes which converge and unite to form a muscular *ejaculatory duct*. At the point of union there is a pair of *vesiculae seminales*, each consisting of a

small group of tubules. Typically, the spermatozoa of termites are aberrant in being non-motile and lacking the usual tail. In *Archotermopsis*, however, they do not offer any exceptional features and the latter appendage is present. In the female (Fig. 298), each *ovary* consists of an extremely variable number of panoistic *ovarioles* (30–45 in *Archotermopsis*) which open separately into the oviduct. The two oviducts communicate by means of a common aperture with the genital pouch whose floor is formed by the enlarged 7th sternum (Fig. 299). The dorsal wall of the pouch receives the apertures of the *spermatheca* and the common duct of the colleterial glands. The latter organs consist of a large number of elongate and much convoluted tubules, whose function has not been ascertained.

The Castes of Termites

It has been mentioned previously that termites are polymorphic and live together in large communities. The individuals are divisible into reproductive and sterile forms, each of which comprises a number of *castes*—i.e. morphologically and functionally distinct terminal forms incapable of further transformation.

The **Reproductive Castes** consist of—(1) PRIMARY REPRODUCTIVES (Fig. 289). The members of this caste are the winged imagines of most authors and the 'adults of the first form' of Thompson (1917). They are to be regarded as the ancestral caste among termites from which the other forms, both fertile and sterile, have been derived. The two pairs of large membranous wings, nearly equal in size, afford the character upon which the name Isoptera is based. The body in these individuals is well sclerotized and often darkly coloured, compound eyes are fully developed, and there are frequently paired ocelli. The caste is adapted for a brief aerial life and its members are concerned with the foundation of new colonies. The brain is large, the frontal gland when present is relatively well developed, and the sexual organs attain a greater size than in any other caste.

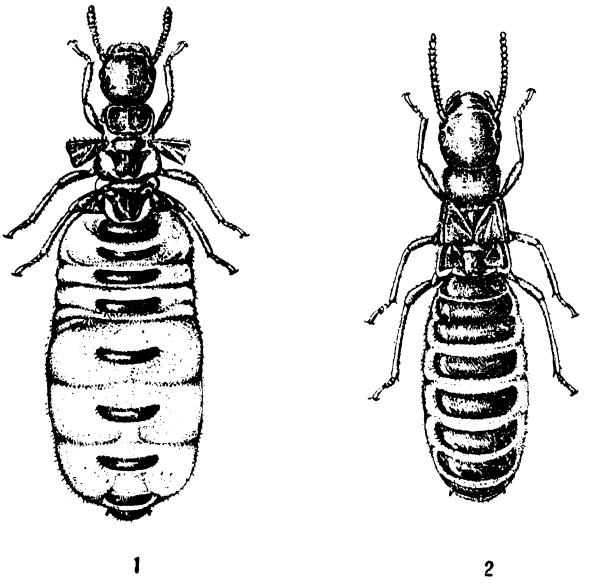


FIG. 301.—*Reticulitermes flavipes*. Deälated queen (1) and king (2) of macropterous form
After Banks & Snyder, *U.S. Nat. Mus. Bull.* 108.

(2) SUPPLEMENTARY REPRODUCTIVES (Fig. 302). The members of this caste have no aerial life, the body is usually much less sclerotized and pigmented than in the primary reproductives, being commonly straw-coloured or greyish-white and the compound eyes are generally reduced. Growth of the wings

is inhibited to a varying extent and they usually resemble wing-pads, though with some indications of venation. The brain, frontal gland and sexual organs are also somewhat reduced in size. Thompson (1917; 1919) considered that two types of supplementary reproductives could be distinguished: brachypterous ('adults of the second form') and apterous ('adults of the third form'), the latter having no wings and showing more complete reduction of the pigmentation and eyes. Weyer (1930), however, has found in *Microcerotermes* that a series of transitional forms occurs, varying from apterous specimens morphologically very similar to workers up to those which resemble primary reproductives in pigmentation, sclerotization and eye-development, but with shorter wings (which, of course, are not shed). Further studies of the variation among supplementary reproductives is desirable. The so-called 'pseudo-imagines' of *Kalotermes flavicollis* and *Reticulitermes lucifugus* (Grassé, 1949) which occasionally appear in colonies recently deprived of their queen, resemble primary reproductives but are not pigmented and, after tearing off their wings irregularly with the mandibles, become sexually functional without leaving the colony. They are probably to be regarded as extreme examples of supplementary reproductives.

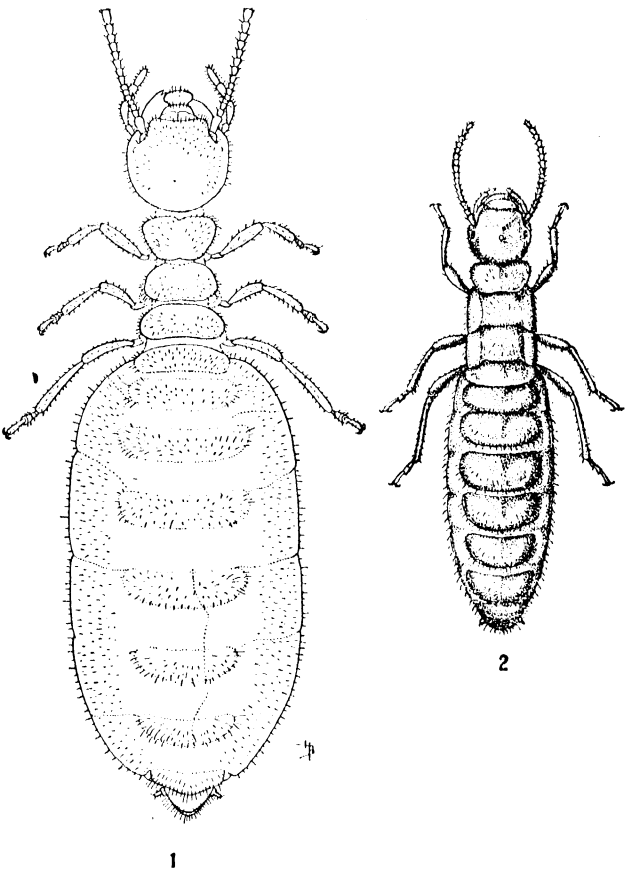


FIG. 302.—1, *Reticulitermes flavipes*, apterous supplementary queen. 2, *R. virginicus*, brachypterous supplementary queen

After Banks & Snyder, *loc. cit.*

Supplementary reproductives are not normally found in colonies headed by the original primary reproductives. They appear after a lapse of several weeks should one or both of these die and replace them so that the colony can continue to develop. There do not seem to be any general rules governing the number and sex of supplementary reproductives which develop after loss of the primary forms. When one of the primaries dies, supplementaries of that sex alone or of both sexes may develop and though many supplementaries frequently appear (e.g. 4–100 in the colonies of *Microcerotermes* studied by

Weyer, 1930), Grassé & Noirot (1946) report that in artificial colonies of *Kalotermes flavicollis* one pair of supplementaries sometimes attains dominance, the others disappearing (possibly through cannibalism). Further details of the role of supplementary reproductives and their differentiation from nymphal stages will be found below.

The reproductive castes exhibit a remarkable postmetamorphic growth which is initiated as a response to the stimulus exercised by the developing sexual organs after coitus has been effected. The fertilized females, or queens, of the more primitive genera betray this postmetamorphic growth only to a very slight degree: on the other hand, among the Termitidae they attain relatively enormous dimensions (Fig. 309). These gigantic queen termites often attain a length of 5 to 9 cm. or more: they have attracted the wonder of generations of naturalists, and the appetite of the savage who has prized them as a food delicacy. Although queens may be developed from both reproductive castes, they attain the largest dimensions when derived from the primary forms. Such queens are easily recognizable on account of the persistent bases of the cast-off wings (Fig. 301). The increase in size only directly affects the abdomen, the head and thorax remaining unchanged in appearance, forming a mere appendix to the greatly distended hind-body. The vast size of the latter is mainly due to the increased development of the ovaries and fat-body. The postmetamorphic growth does not affect the size of the external sclerites but, on the other hand, the intersegmental membranes develop to such a degree that they constitute almost the whole abdominal covering, leaving the original tergal and sternal plates as small sclerotized islands.

The changes undergone during postmetamorphic growth have been studied by Feytaud (1912) and Bugnion & Popoff (1912): the chief features of the process may be summarized as follows. The wing-muscles, which occupy the greater part of the thoracic cavity, degenerate and are broken down, partly by phagocytic action. The original fat-body, as mentioned earlier in the present chapter, undergoes complete transformation, being replaced by a new tissue. Certain changes supervene in the digestive system in conformity with an alteration in diet. The queen no longer partakes of ligneous or other hard matter but is nourished upon saliva or, in the fungus-growing species, upon fungal hyphae in combination with that secretion. The jaw-muscles in consequence become reduced in size and power: the stomach undergoes correlated changes, both structural and functional, the Malpighian tubes increase in length, while the hind intestine suffers marked curtailment and the intestinal Protozoa are lost. The volume of the blood-tissue is greatly increased, while the nervous system and dorsal vessel undergo elongation in conformity with the general extension of the abdomen. There is also hypertrophy of the corpora allata with histological signs of increased secretory activity (Pflugfelder, 1938). The most striking changes are exhibited in the reproductive system which monopolizes, as it were, the greater part of the abdomen and converts the queen into one vast, inert, egg-laying mechanism. The changes involved are those of size and, in its general morphology, the reproductive system of the queen does not differ from that of the same individual when in the winged stage though a postmetamorphic increase in the number of ovarioles may occur: in *Odontotermes redemanni* Bugnion mentions that one ovary alone consisted of the enormous number of 2,420 ovarioles.

Sterile Castes.—The two most important sterile forms are the workers and soldiers, which are apterous individuals in which the sexual organs are arrested in their development or atrophy, and are consequently non-func-

tional. Certain other forms, which do not warrant consideration as distinct castes, may also conveniently be described here.

(1) WORKERS. True workers are absent among the Kalotermitidae, many Hodotermitidae and probably also *Mastotermes*, their place being taken by nymphal stages or by pseudergates (see below). Where they occur, workers are numerically the most important members of the community. They are usually pale coloured with the integument but little sclerotized, and they bear a closer resemblance to the nymphs than to the adult members of other castes. External sexual characters are hardly perceptible. The head of the worker is directed downwards, it is relatively wider than in the reproductive castes, but never attains the dimensions found among the soldiers. Compound eyes are usually absent, but in certain species they are present in a vestigial condition; tolerably well developed faceted eyes occur in the workers of *Hodotermes*, which are active above ground during daylight. The mandibles resemble those of the reproductive castes but they are more powerful and adapted for gnawing wood and other vegetable tissue. In the configuration of the thorax the workers resemble the soldiers rather than the imagines. On the whole, distinctive characters are but little emphasized among the workers of the various species and, for this reason, it is usually a matter of great difficulty, or an impossibility, to determine their specific identity unless members of other castes are taken with them at the same time.

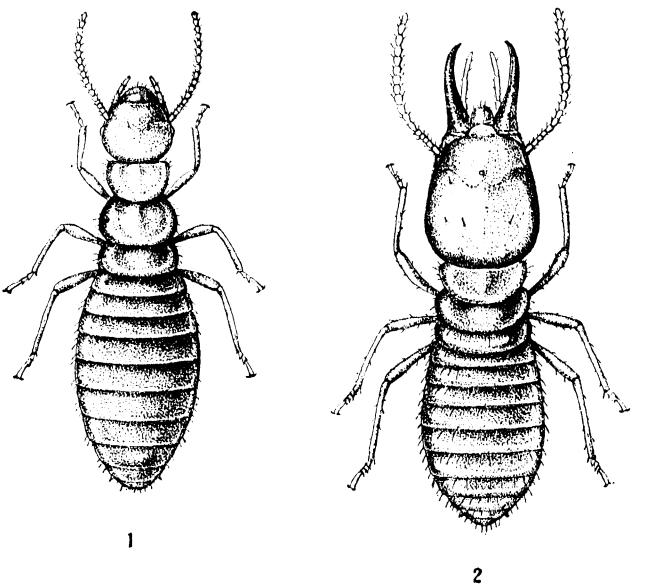


Fig. 303.—*Prorhinotermes simplex*. 1, worker, 2 soldier
After Banks & Snyder, *U.S. nat. Mus. Bull.* 108.

Not infrequently the workers are dimorphic, being divisible into major and minor forms. In such cases the head and mandibles, and often the body, of the major workers are distinctly larger than those of the minor individuals. In some species, however, it is impossible sharply to separate the workers into these two classes owing to the occurrence of numerous intermediate forms. Dimorphism among workers occurs, for example, in *Macrotermes estherae*, *Odontotermes obesus*, *O. redemanni*, *O. horni* and in many species of the genus *Trinervitermes*.

Although taking no part in reproduction, and seldom any part in the defence of the community to which they belong, practically all other duties devolve upon the members of this caste. They exhibit marked care for the eggs and young and, in times of danger, may remove them to situations which afford greater safety. They also feed and tend the queens, forage for food,

often at a distance from the nest and, in the fungus-growing species, attend to the cultivation of these lowly forms of vegetation which they plant in special chambers. In the case of lignicolous species, the workers excavate the galleries and tunnels which serve for the nest; in the mound-building forms they construct the termitarium, and repair any injuries sustained by the latter. Owing to their gnawing propensities the workers have earned for termites their unenviable reputation as destroyers of crops, woodwork and other materials serving the convenience of man.

(2) The SOLDIERS are structurally the most specialized members of the termite community but their occurrence in all families of termites and certain features of intercastes (see below) suggest that they are to be regarded as the primitive sterile caste. They appear to be wanting only in the genera *Anoplotermes* and *Speculitermes*. They may be readily recognized by the great size and strong sclerotization of the head. The mandibles also attain much larger dimensions than in other castes, and frequently assume striking or almost grotesque forms (Fig. 291). Two well-defined types of soldiers can be distinguished—(*a*) the mandibulate type with large and powerful jaws but no frontal rostrum; (*b*) the nasute type (Fig. 304) in which there is a median frontal rostrum but the jaws are small or vestigial. Soldiers conforming to either of these types may frequently be separated into major and minor forms as in the workers, and often in the same species. In other instances trimorphism obtains, large, intermediate, and small soldiers occurring within the limits of a single species. In certain other cases, however, the soldiers are extremely variable and, although separable into large and small forms, the two extremes are connected by numerous individuals of intermediate sizes.

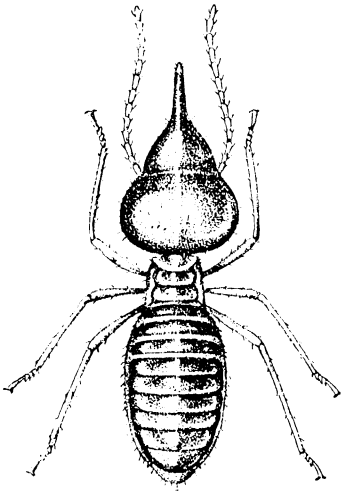


FIG. 304.—*Nasutitermes corniger*, nasute soldier

After Banks & Snyder, *loc. cit.*

As in the workers, the soldiers consist of both males and females but, except in those of *Mastotermes*, *Archotermopsis* and certain species of *Kalotermes*, external secondary sexual characters are slight, and the sex of the individual can be best ascertained from an examination of the gonads. Tolerably well developed faceted eyes occur in the soldiers of *Hodotermes*, and vestigial eyes are found in those of *Archotermopsis*, *Kalotermes* and other genera, but more often than not visual organs are totally wanting: a pair of reduced ocelli may also be present. The antennae usually consist of one or several segments less than in the reproductive castes.

Although numerous modifications are exhibited in the form of the head and mandibles among soldiers of various species, comparatively few of these differences can be interpreted as being special adaptations to particular functions. The soldiers are mainly concerned with the defence of the colony which they protect by seizing or repelling any intruders. Means of defence are afforded, in many cases, by the great size and power of the mandibles: in others it resides in the capacity of the individual for ejecting a repellent fluid. When disturbed the mandibulate soldiers may often be observed to assume threatening attitudes with the jaws outstretched, and they will usually seize

any object presented to them. Ants are among the bitterest enemies of termites, and the soldiers of the more courageous termites not infrequently seize them, and eject them when attempting to enter the nest. The highly specialized soldiers of some species are apparently of little service to the community. Those of *Capritermes*, for example, with their curiously twisted mandibles, are ill adapted for performing any utilitarian function. Any defensive role which such termites may possess would appear to be solely expressed in their general aggressive appearance and power of assuming threatening attitudes. In several species with exceptionally large heads the soldiers are stated to block up gaps in the walls of the nests, while the workers are undertaking repairs.

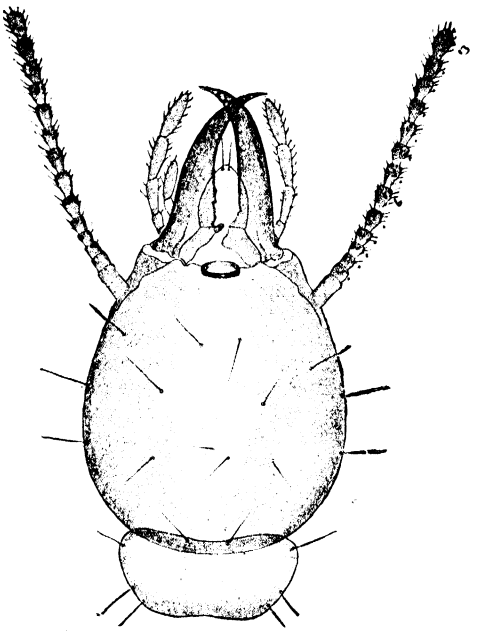


FIG. 305.—*Coptotermes ceylonicus*, head of soldier showing frontal pore
After Bugnion.

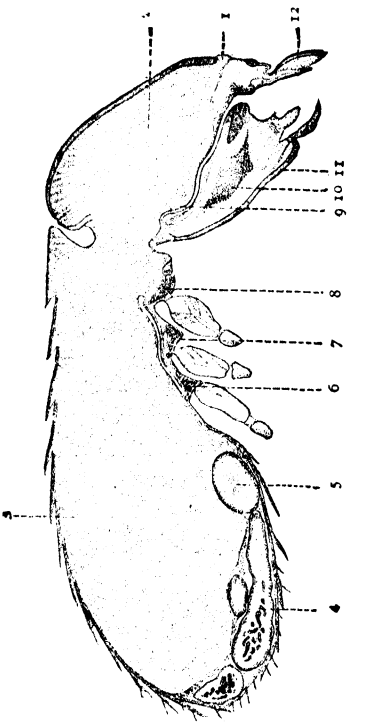


FIG. 306.—*Coptotermes ceylonicus*, median longitudinal section of soldier
1, frontal pore; 2, 3, frontal gland; 4, hind intestine; 5, mid intestine; 6, 7, 8, thoracic ganglia; 9, oesophagus; 10, suboesophageal ganglion; 11, mentum; 12, labrum. *After* Bugnion.

In the second method of defence, referred to above, a viscid secretion is emitted through the frontal pore, situated in the anterior region of the head (Fig. 305). The possessors of this type of defensive capacity have as a rule small or vestigial mandibles, or the latter are ill-adapted for their usual function. In *Coptotermes*, a profuse white secretion is produced by an extensive gland occupying the greater part of the thoracic and abdominal cavities (Fig. 306). According to Holmgren a similar capacious gland is present in *Rhinotermes nasutus*. In the nasute soldiers of *Nasutitermes* (Fig. 304) and other genera, the repellent secretion is the product of a retort-shaped glandular sac, situated in the head. A clear thick liquid is ejected through its duct which traverses the rostrum and opens at the apex of the latter. The soldiers of *Nasutitermes*, notwithstanding their small size, are usually not lacking in courage. When the nest is injured in any way, they issue through the broken

parts in large numbers, and stand on guard while the workers are busily engaged in executing repairs. Globules of secretion may often be seen at the apex of the rostrum of the soldiers and this protective fluid appears to have a very salutary effect upon any enemies. Haviland observed that the soldiers may be seen to eject a small quantity of the fluid on the antennae of their foes: ants, he remarks, are rendered *hors de combat* by this means. In *N. triodiae* Hill mentions that the secretion is ejected as a fine jet which has the appearance of a silken thread waving from the tip of the rostrum.

(3) PSEUDERGATES. Grassé & Noirot (1947) have designated as pseudergates the large, blind, apterous forms in *Kalotermes flavicollis* which carry out the functions exercised by workers in the higher termites. They consider that in a normal stable colony the pseudergates do not moult again, but under experimental conditions they have moulted into supplementary reproductives so that they can hardly be regarded as a true caste. Grassé considers that pseudergates occur in *Zootermopsis* and *Archotermopsis* and that the so-called workers of *Mastotermes* are probably also of this form.

(4) ACHRESTOGONIMES. The alate imagines produced in a colony normally all leave when swarming occurs but sometimes a small number remains; these lose their wings and their gonads atrophy. They remain xylophagous, retain their protozoal fauna and though they play no part in the maintenance of the colony are tolerated by its other members. Grassé & Bonneville (1935) refer to such forms as achrestogonimes and have found them in several species.

(5) INTERCASTES. Rather rarely, individuals are found which are morphologically intermediate between castes. Soldiers with wing-pads and forms intermediate between workers and soldiers are known, but worker-sexual intercastes have never been reported (Adamson, 1940). Though infection with parasites is apparently sometimes the cause of intercaste formation, other cases are readily intelligible in the light of what is known of the postembryonic differentiation of castes under the influence of environmental factors.

Postembryonic Development and Caste Differentiation

The study of the postembryonic development of termites is unusually difficult. Direct observation of the numbers of instars and of the course of caste differentiation is impossible in natural colonies and the plasticity shown in the development of the castes from nymphs of different stages renders it difficult to be certain how far some of the developmental processes revealed in artificial colonies are a regular feature of natural development. It is therefore not surprising that reasonably complete accounts of the process have been given for only a few species. Grassé (1949) has given a useful interpretative summary of available information and the diversity of modes of development there presented may serve as a warning against incautious generalization.

The eggs are normally deposited singly but *Mastotermes* lays clusters of 16–24 eggs cemented together with a gelatinous secretion and recalling a simple type of ootheca (Hill, 1925). The incubation period is rather long (periods of 24 to 90 days have been recorded for various species, while some eggs may overwinter in cooler regions) and the eggs are often tended by workers or nymphs. Postembryonic development is slow, e.g. Pickens (1932) records that workers of *Reticulitermes hesperus* in the U.S.A. take about 32 months to attain full development while Harvey (in Kofoid *et al.*, 1934) found that reproductives of *Kalotermes minor* took from 6 to 14 months to develop at 21° C. and 83 per cent. relative humidity. Such figures have little general significance, however, since the duration of development and the number of nymphal instars varies not only with the species, caste and the usual environmental factors, but also with the age, size and caste-composition of the colony. From four to ten nymphal stages have been recorded, the younger colonies

producing terminal forms (soldiers, workers or supplementary reproductives) after a smaller number of moults. There are commonly seven nymphal instars among the members of established colonies of the more primitive families while the primary reproductives seem almost invariably to have at least this number of developmental stages. Ecdysis is accompanied by cessation of feeding, loss of most or all of the intestinal contents, shedding of the mid gut epithelium and its renewal from regenerative cells (Weyer, 1935) and by a quiescent period which may last for several days (Snyder, 1913). This quiescent period is most pronounced in the moult giving rise to soldiers and primary reproductives and in the Macrotermitinae (Termitidae) where the insect lies on its side with the head flexed upon the ventral aspect of the thorax, while the limbs and other parts remain immobile (Fig. 307). Such a state presents some analogies with the pupal instar of endopterygote insects, but there is no reason to regard the resemblance as having a phylogenetic significance.

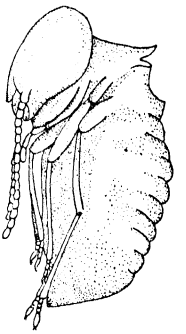


FIG. 307.—Quiescent nymphal phase of a termite (*Rhinotermes*)
After Holmgren, *Zool. Jb., Syst.*, 23.

Caste differences appear during the course of post-embryonic development. Thus, typically, the primary reproductives and the brachypterous supplementary reproductives are preceded by instars possessing wing-pads, the soldiers develop from apterous nymphs which have larger heads than those destined to become workers, while in species with polymorphic workers and soldiers, the major and minor forms may be distinguished among the

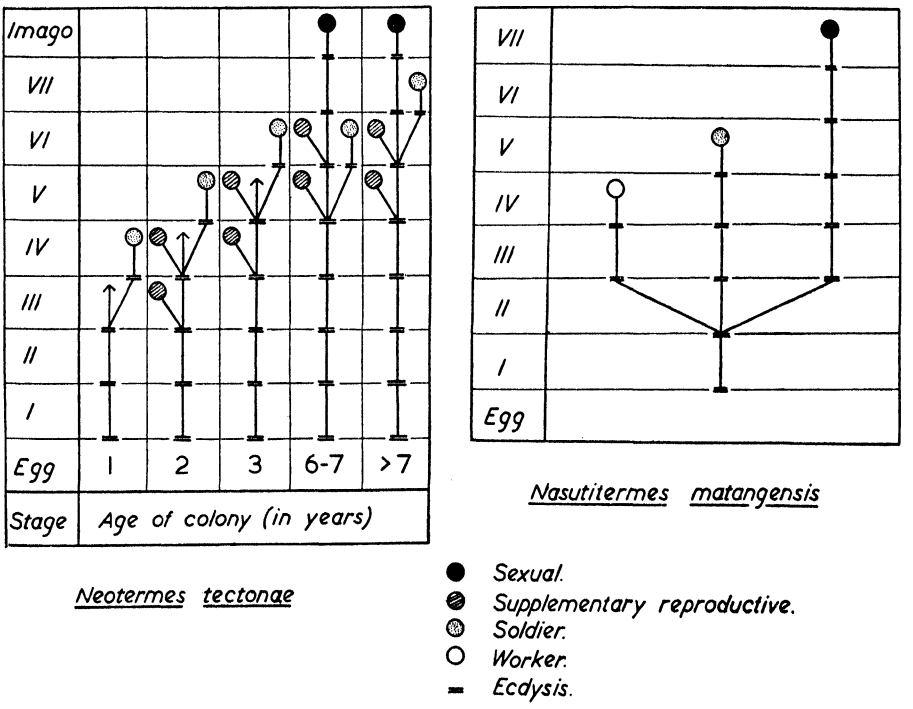


FIG. 308.—Diagrammatic representation of caste-differentiation in two species of Isoptera (based on figures in section Isoptères of *Traité de Zoologie*, Vol. 9 (1949), under direction of P. P. Grassé, Masson & Cie, Éditeurs)

preceding nymphal stages. Cases are known, however, where regressive moults occur, e.g. Grassé & Noirot (1947) found that pseudergates could develop in *Kalotermes flavicollis* either from apterous fourth-instar nymphs or from sixth- or seventh-instar nymphs by loss of the wing-pads; Miller (1942) working with *Prorhinotermes* and Grassé & Noirot (1946a) with *Kalotermes* have found that soldiers can develop in the same way from nymphs with wing-pads. The instar at which caste differences become apparent varies again with species, caste and colony age. Thus, in *Kalotermes* the first three instars show no differences in young colonies, while in older colonies caste distinctions appear only in sixth or later instars. On the other hand, in *Macrotermes gilvus* Bathellier (1927) finds that the second-instar nymphs are already differentiated into large and small apterous nymphs (destined to produce major and minor sterile castes respectively) and nymphs with wing-pads which give rise to primary reproductives. The variety of conditions occurring in postembryonic development are best represented diagrammatically as in the two examples given in Fig. 308. It is hardly surprising with the large number of developmental courses open to undifferentiated or partially differentiated nymphs that intercastes should occasionally arise.

Origin of Polymorphism

Several theories have been proposed to explain the mechanism of caste differentiation although interest has centred mainly on the distinction between reproductive and sterile castes rather than on attempts to account for the polymorphism among the latter. The problems involved are as yet far from being satisfactorily solved (Light, 1942–43).

Many early workers considered that the castes were genetically determined—a view for which support was claimed on the grounds of alleged caste differences between newly hatched nymphs—and schemes were proposed to account for them as segregates from heterozygous parents (e.g. Thompson, 1922). More critical examination of newly hatched nymphs, however, has shown that they do not display caste differences (Heath, 1927; Heath & Wilbur, 1927; Hare, 1934; Miller, 1942; Grassé & Noirot, 1946). Furthermore it has been demonstrated by several workers that nymphs which would normally have developed into sterile forms can give rise to supplementary reproductives in experimental colonies lacking these forms. Thus, Light & Illg (1945), working with *Zootermopsis* and Grassé & Noirot (1946) with *Kalotermes flavicollis* showed that all nymphs of the fourth or later instars can differentiate into supplementary reproductives in artificial colonies from which the reproductives are removed as they appear. Experimental production of soldiers under similar conditions has not given such clear results though Miller (1942) found that slightly fewer soldiers were produced in *Prorhinotermes* colonies containing an excess (more than 20 per cent.) of this caste. For these reasons it is held by almost all modern authorities that the newly hatched nymph is potentially capable of giving rise to any of the castes, the particular line along which it develops depending on environmental influences within the colony. Exactly what these environmental factors are and how they operate, however, is very uncertain and it will suffice to outline three theories.

1. ECTOHORMONAL CONTROL. Pickens (1932) first suggested that the sexual forms secreted some substance (an 'ectohormone') which was absorbed, possibly by feeding stomodaeally, proctodaeally or on the products of exudatory glands, by the developing nymphs and inhibited their development into further sexuals. Similarly it was suggested that soldiers produced a substance inhibiting the differentiation of further soldiers. Light (1944), Keene & Light (1944) and Light & Weesner (1951) have reported extensive experiments on the effects of feeding extracts of supplementary reproductives to nymphal colonies of *Zootermopsis* and although the results were far from decisive, they concluded that the balance of evidence favoured the view that extracts of female supplementaries tended to inhibit the development of further supplementary reproductives. There is no proof of inhibition by male supplementary reproductives or by soldiers. Further experimental work on ectohormonal inhibition is greatly to be desired.

2. ALIMENTARY CONTROL. Grassi & Sandias (1897) were the first to suggest that differential feeding of young nymphs induced caste differences, it being held that some nymphs received large quantities of saliva and developed into sexual forms while those nymphs which remained predominantly xylophagous gave rise to soldiers or workers. Variants of this theory have retained some popularity (e.g. Becker, 1948) but there is no direct evidence for it and certain indirect considerations argue against its likelihood. Thus, Grassé (1949) points out that young sexuals of some termites are known to depend largely on wood while a male and female nymph of *Kalotermes* reared together apart from the colony become supplementary reproductives without receiving a salivary addition to their diet of wood. Since so little is known of the role of nutrition in affecting fecundity in insects it would be premature to dismiss the possibility of a nutritional factor being involved in caste differentiation.

3. Grassé (1949) has suggested that tactile or olfactory stimuli operating within the colony may play some part in controlling caste differentiation. This view appears to rest solely on doubtful analogies with some social Hymenoptera and the phase differentiation of locusts.

The Termite Community and its Biology

In order to describe the biology of the termite community it is convenient to begin with an account of the founding and development of colonies and then to discuss some aspects of the organization and maintenance of established colonies. Much of the extensive literature on this subject has been summarized by Hegh (1922), Handlirsch (1930), Emerson (1939), Goetsch (1940) and Grassé (1949). Other important papers dealing with the biology of special groups include those of Emerson (1925), Bathellier (1927), Kemner (1934), Kofoid *et al.* (1934) and Grassé (1937, 1944–45).

Colony-founding.—The typical method of founding new colonies is by the emission of swarms of primary reproductives (Fuller, 1915; Grassé, 1942; Light & Weesner, 1948; etc.). Individuals of this caste appear in established colonies, usually at certain seasons, and accumulate in the colony for a short period before departing on their colonizing flight. During this period the gonads are not fully mature, especially in the female, the alates exhibit no sexual behaviour and in the primitive families they remain xylophagous. Prior to the flight the workers make exit holes where necessary in the walls of the termitarium and numerous members of this caste, along with soldiers, congregate around and often just outside these apertures while swarming is in progress. Males and females leave the nest in about equal numbers and may emerge in a continuous stream or a series of smaller batches. Swarming may be diurnal or nocturnal according to the species, those which swarm at night being frequently attracted to light. Swarming is often a seasonal occurrence of limited duration or may occur at times over a rather long period—e.g. *Reticulitermes lucifugus* swarms in S. France between May and August; many tropical species do so after the first rains of the rainy season. Many nests in the same area may produce swarms simultaneously but it is thought that most individuals eventually mate with another from their own nest. After leaving the nest the alates fly weakly for a short distance; *Kalotermes minor* is said to be able to fly about half a mile but in many species only a few yards are covered unless a light wind assists their flight. Attacks by birds, lizards and small mammals cause a high mortality among swarming alates but the survivors, on completing their flight, cast their wings and on encountering a deälate of the opposite sex show some epigamic behaviour before walking in tandem fashion (the male following the female) to seek a site where, in wood or the ground, they excavate a small nuptial chamber in which copulation takes place. The whole series of acts beginning with the emission of the swarm

and ending with the establishment of the royal pair in the nuptial chamber are closely linked together—e.g. alates captured before the end of the swarming flight fail to shed their wings and pair—but no detailed experimental analysis of the series has been made. External factors such as temperature and humidity probably exert some effect in deciding the time of swarming but conditions within the society are doubtless also of great importance.

Other methods of colony-founding have been described but are probably not very common. In *Reticulitermes*, which constructs a very diffuse nest, supplementary reproductives may develop among groups of nymphs remote, though apparently not completely isolated, from the parent couple and so give rise to secondary colonies (Pickens, 1932). It is said that in Italy *Reticulitermes lucifugus* forms new colonies only in this way, the alate forms never reproducing after swarming (Jucci, 1924). Grassé & Noirot (1951) have described the formation of new colonies of *Anoplotermes* and *Trinervitermes* through a large fraction of a colony, including all castes with even the primary founders, leaving the nest and breaking up into smaller groups which, if they lack the royal pair, develop supplementary reproductives. Finally, in *Microcerotermes amboinensis* and *Subulitermes undecimus*, Weyer (1930) has found that two or more pairs of primary reproductives may collaborate in starting a colony and Pickens (1932) says that the first offspring of several primary reproductives may be collected under one of the pairs in *Reticulitermes hesperus*.

Growth of the Colony.—Quantitative data on the growth and size of termite populations are given by Bodenheimer (1937). Egg-production by the primary queen is low at first—15–50 eggs may be laid in the first season, of which some are eaten by the parents. Later, the fecundity increases and mature queens of the Termitidae lay several thousand eggs per day (at least over short periods) though far fewer are produced by queens of the primitive families, e.g. *Kalotermes flavicollis* females reach their full egg-laying capacity after 3–4 years and then produce 4–6 eggs per day. The size attained by a mature colony is much smaller in the primitive genera, though *Mastotermes* sometimes forms exceptionally large societies. In *Kalotermes flavicollis* there are 15–20 members after one year and a maximum of 600–1,000 individuals is reached after several years. On the other hand, colonies of the Termitidae may contain over a million individuals, all derived from a single royal pair. The individuals produced in the early stages of a colony are always of the sterile castes; alate reproductives develop later, e.g. after about four years in *Zootermopsis* (Heath, 1927) when the colony comprises about 450 individuals. During the growth of the colony in higher termites the king and queen remain in the royal cell—usually deep in the termitarium—where the queen undergoes the postmetamorphic growth described above and is attended by numerous workers who feed her and the king and devour the secretions produced by the exudate glands which she develops and those issuing from the gonopore and anus. The king lives as long as the queen and copulation takes place frequently. Colonies containing two pairs of primary reproductives or 2–3 queens with one king have been described, but are exceptional. In *Nasutitermes amboinensis* Weyer (1930a) found colonies containing primary queens of different ages but this species appears to be unusual in the readiness with which colonies adopt foreign queens and Weyer was able to produce colonies with several queens artificially.

Members of the sterile castes probably live for 2–4 years. The longevity of the reproductive forms is not known accurately; it may be 15–50 years in the higher forms but is shorter in primitive families. The long life of the indi-

viduals in a colony is obviously an important factor in permitting the close relationship between successive generations which is the basis of insect social organization. Since the death of the primary queen is normally followed by the development of one or many supplementary reproductives, colonies would seem to be potentially immortal, and colonies of some Termitidae have certainly been estimated to be 40–100 years old. However, Kalshoven (1930) considered that large colonies of *Neotermes tectonae* died out at the age of 15–16 years, having attained a maximum population of nearly 3,000 individuals eight years previously, while smaller colonies died after 6–7 years. Newly developed supplementary queens lay more eggs than young primaries but never achieve the fecundity of mature primaries, though the development of many supplementaries to replace a lost primary may compensate for this.

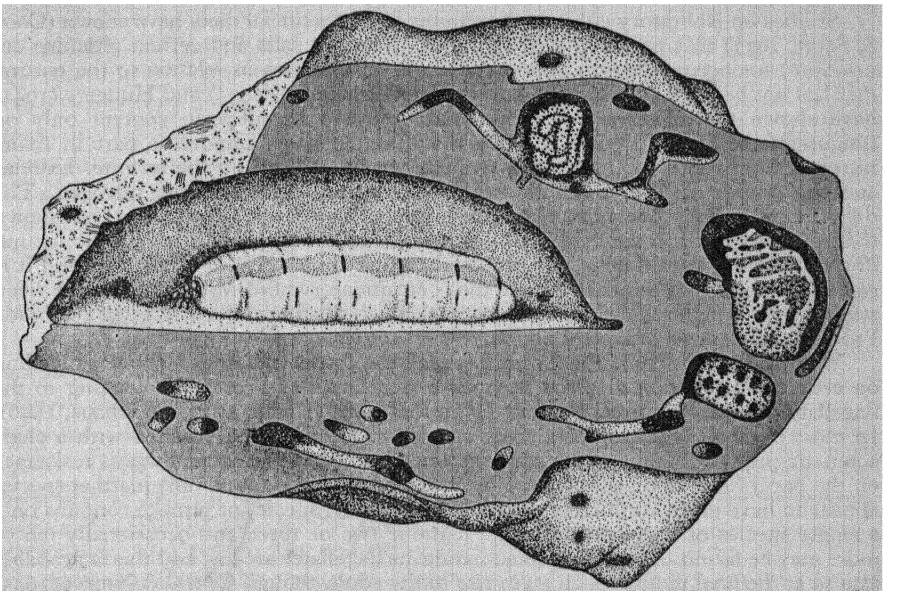


FIG. 309.—Section of royal cell with queen of *Odontotermes transvaalensis*, × ½. On the right chambers with fungus gardens

After Sjostedt.

There are several records (e.g. in Hill, 1942) of primary and supplementary reproductives being found together in the same colony.

Few quantitative data are available on the proportions of the different castes present in a colony. On general grounds and from the very limited experimental work on artificial colonies (e.g. Miller, 1942; Grassé & Noirot, 1947) one would expect considerable powers of social regulation leading to approximately constant proportions of the various castes in well-established colonies. Emerson (1939) states that the proportion of soldiers varies from 3 to 16 per cent. of the sterile castes.

Feeding Habits and Nutrition.—The food requirements and feeding habits of termites display numerous interesting features but the fact that the different castes and developmental stages may have widely different alimentary regimes makes the subject rather complex (Cleveland, 1925; Grassé & Noirot, 1945). Two main types of feeding habit may be distinguished: (*a*) feeding on sound or decaying wood or other plant materials such as humus, grass, fungi, etc. This is practised by the workers of all families which

possess them, the young reproductive forms of the Kalotermitidae and the older nymphal stages of most termites. (*b*) feeding on a diet prepared by other members of the colony. This includes (i) stomodaeal feeding, in which a mixture of varying proportions of salivary secretions and regurgitated intestinal contents is received from another insect and (ii) proctodaeal feeding, in which a drop of the contents of the rectal pouch is obtained from the anus of another insect in response to tactile stimulation by the soliciting termite. While the forms feeding primarily on wood etc. may also consume these prepared foods, the latter are the sole diet of soldiers, all young nymphal stages, the entire brood of the subfamily Macrotermitinae (Termitidae), the older sexual forms of the primitive families and the reproductives of all ages in the Termitidae, the food being passed on to them by workers or old nymphs.

Studies on laboratory cultures of termites fed on artificial diets have shown (Cook & Scott, 1933) that proteins, carbohydrates, inorganic salts and certain vitamins are necessary for normal growth. The precise role of vitamins in relation to the natural diet has not been studied but the observations of Hendee (1935) and Hungate (1941) have shown that *Zootermopsis* grows and increases its nitrogen content only on fungus-infected wood and it is likely that fungi play an important part in fixing nitrogen from soil sources in a form which can be utilized by the termite. Exuviae and the bodies of dead termites are also eaten and provide some nitrogen. The digestion of carbohydrates has received considerable attention. Cook (1943) has shown that many mono- and disaccharide sugars are readily assimilated, but in the natural diet of wood or plant tissues, the principal carbohydrate utilized is cellulose and it is probable that in all families except the Termitidae (whose nutrition has not been studied) this is made available to the insect through the metabolic activity of symbiotic Protozoa resident in the rectal pouch.

With the exception of the Termitidae, all the forms mentioned above as feeding on cellulose-containing material harbour a rich fauna of Protozoa belonging to the flagellate groups Polymastigina and Hypermastigina (Kirby, 1937; Steinhaus, 1946). In most cases all members of a given species of termite are associated with a characteristic protozoal fauna, although experiments to decide whether there is resistance on the part of the insect to infection by Protozoa normally found only in other species appear to have given conflicting results. Usually each species of termite contains only a single species of flagellate but some harbour two or three and occasionally ten or more may be found. At each nymphal moult the flagellates are lost and this is probably also so at the final moult which gives rise to the adult, though Grassé & Noirot (1945) claim that in *Reticulitermes* and possibly some others the flagellates are retained in the rectal pouch though its other contents are lost. After the moult the fauna is rapidly re-acquired, probably through proctodaeal feeding (Andrew, 1930).

It was shown by Cleveland (1924; 1925a) that the Protozoa could be removed artificially from the termites by a period of starvation, exposure to temperatures of about 36° C. or, best of all, by exposure to a pressure of 3–4 atmospheres of oxygen. Experimentally defaunated termites lose weight and eventually die if they are prevented from acquiring a new fauna. The absence of a cellulase from the digestive enzymes of the insect coupled with the facts that the protozoa can be seen to ingest wood particles and are capable of digesting cellulose *in vitro* indicate that they are essential because of their ability to supply the insects with the end-products of cellulose decomposition. Earlier workers considered that the main product of cellulose digestion by the Protozoa was glucose but the later researches of Hungate (1939; 1943) showed that *in vitro* degradation of cellulose by the Protozoa of *Zootermopsis* led to the appearance of carbon dioxide, hydrogen and simple organic acids (mainly acetic acid) and he considers that it is probably the acetic acid which is absorbed and metabolized by the termite. It should, however, be pointed out that preliminary experiments by Cook (1943) showed that the sodium salts of lactic and acetic acids killed the Protozoa in termites to which they were fed.

While the experimental evidence quoted above has convinced most workers of the symbiotic role of the flagellates in cellulose digestion, Pierantoni (1936) and Baldacci & Verona (1940) maintain that the breakdown of cellulose is actually accomplished by the bacteria which are known to occur within the bodies of the Protozoa. The evidence for this does not, however, seem compelling. Again, the earlier claims that

cellulose digestion is accomplished, at least to an appreciable extent, by bacteria living freely in the lumen of the gut has been rendered unlikely through the more critical work of Dickman (1931) and Hungate (1936). The physiology of carbohydrate utilization in the Termitidae—which lack the flagellates—is not understood but it may be noted that their food usually includes a high proportion of partially decomposed organic matter such as humus or includes fungi so that cellulose may not be such an important constituent of their diet.

The habit of foraging outside the nest is found in various species of Termitidae and in *Hodotermes*. The workers and soldiers of species of this genus possess well-developed compound eyes, and exhibit the unusual habit of foraging above ground during daylight. Sorties are made from the nest for the purpose of collecting grass, pine needles, etc., which are cut into short lengths, and carried to the mouth of the burrow. Here the material is either taken directly within, or allowed to accumulate to form a mound whose contents are subsequently removed into the nest. Among certain Termitidae the foraging habits of *Odontotermes latericus* and *Trinervitermes trinervius* in S. Africa are described by Fuller (1915). In the former species there are special cells or granaries within the nest, and lengths of green grass, together with large quantities of seeds are collected. *Nasutitermes triodiae*, in Australia, stores dried grass in chambers which are situated in the walls of the termitarium from the ground to the summit. Bugnion (1914) describes the habits of the 'black termite' (*Hospitalitermes monoceros*) of Ceylon. Long dense files of workers of this species set out about sunset, with the soldiers aligned up on guard on either side of the procession. The object of these expeditions is to gather fragments of lichens which serve to nourish the young. Having found a suitable tree, they remain the whole night gathering provender, and return the following morning. Bugnion calculated, by means of photographs, that there are, on an average, 1,000 termites to each metre of the moving column and, if the army marched out for five hours, moving at the rate of a metre per minute, about 300,000 termites would be involved in the procession.

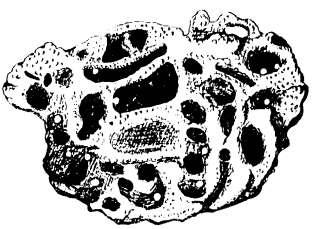


FIG. 310.—Fungus bed of *Odontotermes*, India: the small white fungal spheres are seen growing on the substratum. × 2

The habitations of the Macrotermitinae (Termitidae) contain what are commonly termed 'fungus gardens' (Grassé, 1944–45). These beds are composed of a spongy dark reddish-brown coral-like 'comb' which is constructed by workers from small balls of comminuted vegetable matter aggregated into masses varying in size from about 2 to 20 cm. across and providing a substrate on which fungal hyphae grow (Fig. 310). The chambers containing the fungus gardens are scattered throughout the nest, sometimes more or less concentrated near the royal cell. Two genera of fungi occur in these gardens—the Ascomycete *Xylaria* which, though not confined to termitaria, constantly occurs there but does not produce fructifications in inhabited nests, and a Basidiomycete, *Termitomyces*, which is exclusively termitophile and produces on the surface of the bed small white spheres composed of bundles of hyphae ending in swollen cells (Heim, 1940; 1942). These spheres form part of the food of workers and are mixed with the stomodaeal food fed to nymphs. It seems likely that they serve as a source of vitamins and organic nitrogen.

Termitophiles.—In addition to the normal occupants of a termite

habitation, there is also a very extensive termitophilous fauna consisting of various insects, and other arthropods, which are represented in almost every community by one or more species. The relations between these guests and their hosts are, so far as is known, very similar to those described later on between myrmecophilous species and ants. The termitophilous forms similarly include true guests or symphiles, indifferently tolerated guests or synoeketes, and synechthrans which are scavengers or predators. The largest number of termitophilous insects belong to the Coleoptera. The Carabidae are principally represented by the larvae of *Orthogonius*: the Staphylinidae include such genera as *Corotoca*, *Spirachtha*, *Termitobia*, *Termitomimus*, *Doryloxenus*, etc., while the Pselaphidae, Scarabaeidae, Tenebrionidae and other families have sundry representatives. Among the Diptera are certain remarkable Phoridae including *Termitoxenia*, *Termitomyia* and *Ptochomyia*: included in this same order are the equally remarkable Psychodid *Termitomastus*, and several genera of larval Anthomyidae. The Thysanura include a large number of termitophilous forms, there are also a few Collembola of similar habits, several larval Tineids and, among the Hemiptera, the anomalous genus *Termitaphis*. In addition to insects the list includes Acarina, Diplopoda and Chilopoda. The literature on termitophilous arthropods is extensive and is principally comprised in numerous papers by Wasmann (1894 onwards; 1934) and Silvestri (1903; 1905; 1914–20). Termite mounds also afford shelter to lizards, snakes and scorpions, while certain birds are even known to nest in them.

It is noteworthy that more than one species of termite may inhabit the same habitation and that a kind of social symbiosis exists in consequence. Thus *Anoplotermes*, which has no soldiers, is often associated with species of other genera. In S. America five species of termites, belonging to as many different genera, are recorded by Holmgren as sharing a habitation of *Syntermes dirus*, while no less than eight different species are mentioned by Escherich as living amicably with *S. chaquimayensis*. Certain members of the genus *Nasutitermes* particularly exhibit this habit of guest species. It should be noted, however, that termite colonies are generally hostile to individuals of the same or different species, that very few cases are known of termites found only in association with other species and that where two or more species occur together they may occupy gallery systems which are distinct. Termites and ants have often been recorded as inhabiting the same log, or other object, where they may occupy contiguous galleries or even intermingle. Under ordinary circumstances the relations between the two kinds of insects are friendly, unless the nest be disturbed, when the ants soon attack and carry off the termites.

The Habitations of Termites

A general account of termite nests has been given by Emerson (1938). The simplest kind of habitation is found in the wood-feeding species, which usually lack the worker caste, and include the most primitive members of the order. *Archotermopsis* and *Zootermopsis*, for example, live in moist decaying trunks and logs of conifers. The abodes of such termites consist of nothing more than a series of galleries, excavated in the wood, without any external manifestation of their presence (Fig. 311). Other genera such as *Mastotermes*, *Kalotermes*, *Neotermes* and *Cryptotermes* include species which bore into dry wood, often selecting posts and other structures, or furniture in buildings, as the seat of their habitations. *Neotermes militaris* and *N. greeni* are destructive

to tea in Ceylon where they burrow in the stems of the bushes. *Rhinotermes*, *Reticulitermes* and *Coptotermes* live in the ground and infest wood indirectly through the soil. They are exceedingly injurious to any woodwork of buildings in contact with the ground. They also frequently issue above ground in order to obtain access to woodwork in their vicinity. With this object in view they construct covered passage-ways of earth, or faecal matter, which enable them to work concealed from the light and from sundry enemies and, at the same time, surrounded by the requisite humidity. They are able, by means of these tubular communications, to pass from their underground chambers and reach the upper storeys of buildings or ascend lofty trees.

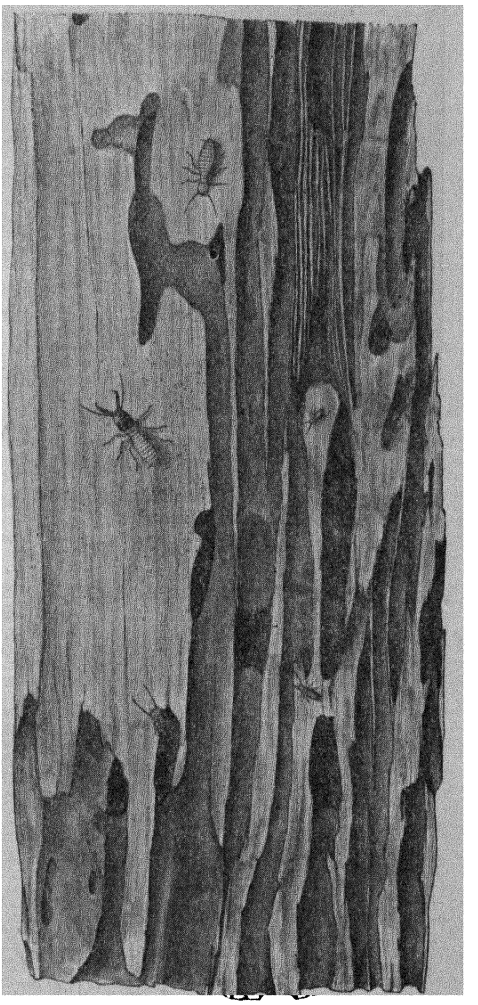


FIG. 311.—Portion of log of *Cedrus deodara* showing galleries of *Archoptermopsis*. × ½

In other cases very extensive structures known as termitaria (Fig. 312) are constructed, particularly by the African and Australian species of the Termitidae. These termite mounds are built of earth excavated in making subterranean chambers and were perhaps originally only a convenient method of disposing of this material. The outer walls and passages, and the royal cells of these habitations, are composed of earth particles cemented together to form a hard brick-like substance. The agglutinating fluid appears to consist either of saliva, or of the latter together with proctodaeal matter. The inner galleries, where the brood is contained, are of a softer consistency, and are composed of woody or other comminuted material which has passed through the alimentary canal. Some of the most remarkable of all termitaria are the lofty steeple-like structures constructed by *Nasutitermes triodiae* in Northern Australia. They are stated to exceed in size those of any known termite, and one recorded by Hill measured 20 feet high with a basal diameter of 12 feet. The greater bulk of the earth and sand used in their formation is collected on the surface, and not mined from below. The interior of such a termitarium presents a maze of irregular chambers and passages, and its walls are so resistant that it is difficult to make any impression upon them even with a sharp pick. The 'compass' or 'meridional' termite (*Omitermes meridionalis*) is widely distributed in Australia. The habitations of this species may attain a height of 8 to 12 feet, and are flattened from side to side in such a manner that the broad

sides face east and west, and the narrow ends north and south. It has been suggested that the reason for their being built according to this plan is in order to secure the maximum of desiccation, and to allow for the repairs, which are made during the wet season, being dried and hardened as speedily as possible.

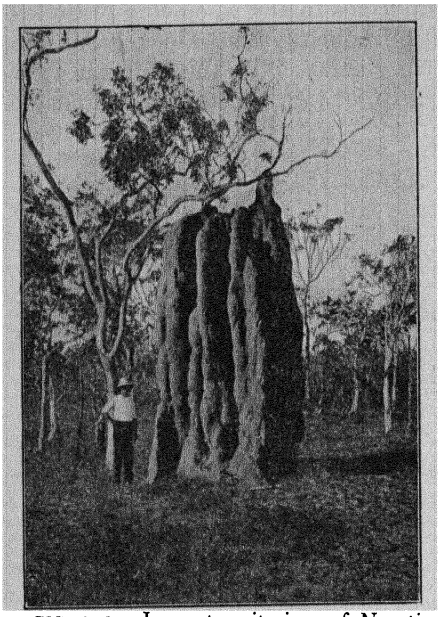


FIG. 312.—Large termitarium of *Nasutitermes triodiae*, Australia

After Hill, *Proc. Linn. Soc. N.S.W.*, 1915.

Other species of termites live in the ground, without constructing termitaria above the surface, or only forming small mound-like structures (Fig. 313). Many termites which exhibit this habit are exceedingly injurious to the roots of grass, field crops, and other vegetation. Although the type of habitation may be very constant for a particular genus or species, in other cases considerable variation obtains. *Odontotermes*, for example, includes both mound builders and subterranean forms, and the two habits may be exhibited in the same species as in the common Indian termite *O. obesus*. Certain species of *Nasutitermes* construct gigantic termitaria of the type already referred to, while others form arboreal habitations often more or less spherical in form.

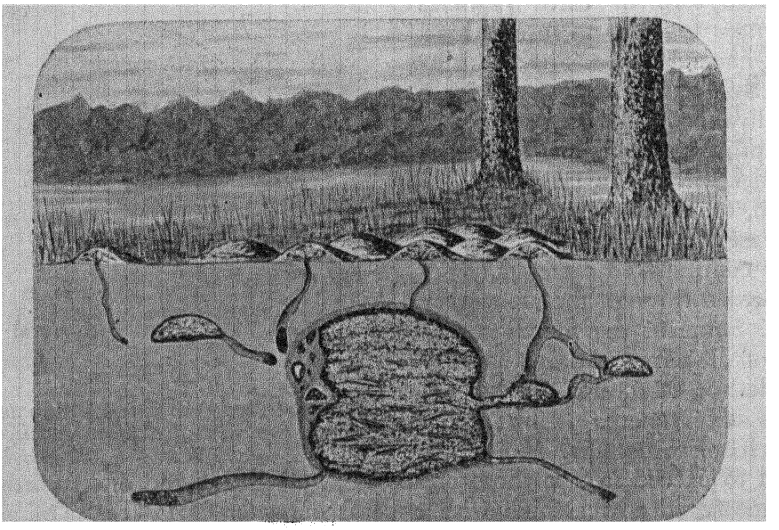


FIG. 313.—Vertical section of a nest of *Odontotermes badius* (S. Africa) and perspective, showing trees crusted by termites with clay: small surface mounds and descending shafts: great cavity and supplementary cavities filled with fungus garden; queen-cell attached to wall of cavity (left side) and radiating galleries. × $\frac{1}{36}$

After Fuller, *Ann. Natal Mus.*, 3.

The material used in constructing the latter appears to be comminuted wood, and the nest is composed of an outer envelope enclosing a comb-like mass of

internal chambers. Such habitations bear a superficial resemblance to the carton nests of arboreal Vespidae. In many cases they are connected by means of covered passage-ways with subterranean abodes.

The role of subterranean termites has been compared by Drummond (*Tropical Africa*) with that of earthworms. By means of their underground activities they keep the soil in constant circulation, rendering it permeable to air and moisture. Also the faecal matter of these insects serves to enrich the soil very much after the manner of the 'casts' of earthworms. In many parts of the tropics there is scarcely a cubic yard of soil that is free from the burrows of these insects, and their activities may exert an appreciable influence on the vegetation of the areas concerned.

Classification

The foundations of the modern classification of termites were laid by Desneux (1904), Silvestri (1909) and particularly Holmgren (1909–13). Later workers have created more families and genera and the classification given below is that recognized by such authorities as Sjöstedt (1926) and Snyder (1949), the latter having catalogued the fossil and recent species. Among the more important recent taxonomic works are those of Banks & Snyder (1920), Emerson (1925; 1942), Sjöstedt (1926), Bathellier (1927), Kemner (1934), Grassé (1937), Hill (1942) and Ahmad (1950).

A. Tarsi 5-segmented; hind wings with well developed anal lobe.

FAM. 1. MASTOTERMITIDAE.—Includes the single recent species *Mastotermes darwiniensis* from N. Australia (Fig. 314) and a few fossil genera.

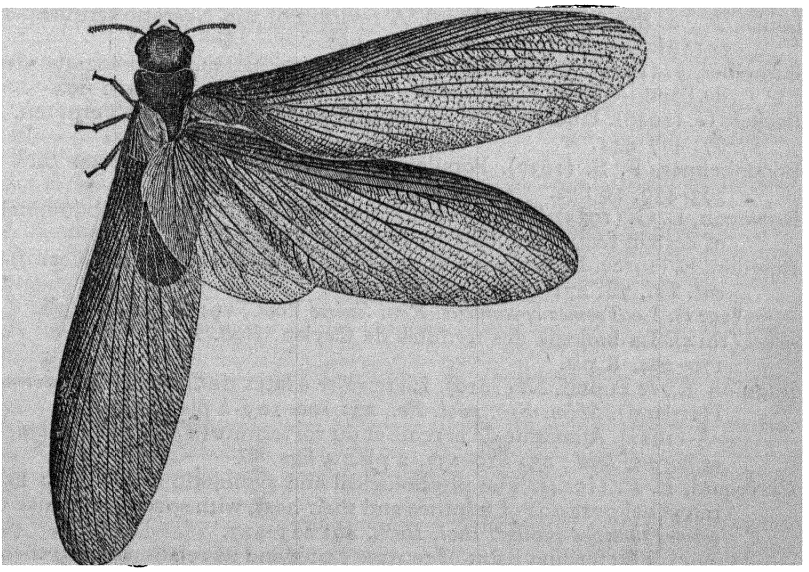


FIG. 314.—*Mastotermes darwiniensis* male, right wings extended
After Froggatt.

B. Tarsi 4-segmented or rarely imperfectly 5-segmented (some Hodotermitidae); hind wings without anal lobe.

FAM. 2. KALOTERMITIDAE.—*Fontanelle absent; ocelli usually present; pronotum flat, usually broader than head; anterior wing-scales long. No workers; wood-dwelling.* Representative genera: *Kalotermes, Neotermes, Glyptotermes.*

FAM. 3. HODOTERMITIDAE.—*Fontanelle and ocelli absent; pronotum saddle-shaped, narrower than head; anterior wing-scales short. Workers present in some genera; wood-inhabiting and subterranean species.* Representative genera: *Archotermopsis, Zootermopsis, Hodotermopsis, Hodotermes.*

FAM. 4. RHINOTERMITIDAE.—*Fontanelle present; pronotum of workers and soldiers flat, without anterior lobe; wings often reticulate, without hairs; anterior wing-scales usually long. Workers present; almost all subterranean.* Representative genera: *Psammotermes, Reticulitermes, Coptotermes, Termitogeton, Rhinotermes.*

FAM. 5. TERMITIDAE.—*Fontanelle present; pronotum of workers and soldiers narrow, with raised median anterior lobe; wings only slightly reticulate if at all, wing-membrane and margin more or less hairy; anterior wing-scales short. Workers present; all ground-dwelling with wide range of food habits and colony-structure.* Includes about two-thirds of recent Isoptera. Representative genera: *Serritermes, Anoplotermes, Termes, Capritermes, Macrotermes, Odontotermes, Microtermes, Nasutitermes, Trinervitermes.*

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Order 15. ZORAPTERA

Winged or apterous insects with 9-segmented moniliform antennae. Y-shaped epicranial suture present. Normal maxillae, 3-segmented labial palps. Wings, when present, capable of being shed by means of basal fractures; venation specialized by reduction. Prothorax well developed. Tarsi 2-segmented. Cerci very short, 1-segmented. Ovipositor absent; male genitalia specialized, sometimes asymmetrical. Metamorphosis slight.

The first Zoraptera were described by Silvestri in 1913, among insects obtained from W. Africa, Ceylon and Java. Gurney (1938) recognizes 16 species from all zoogeographical regions except the Palaearctic. The known species belong to the genus *Zorotypus* which constitutes the family Zorotypidae: they are minute insects, less than 3 mm. long, and the alate forms have a wing-expanse of about 7 mm. They occur under bark, in decaying wood, humus, etc., and are sometimes found near the galleries of termites. Though the alate forms of some species have not yet been described, two distinct types can be recognized in most species of the Zoraptera. The commoner form is apterous, only slightly pigmented and without compound eyes or ocelli while the rarer alates are darker, with eyes and ocelli and differ in details of thoracic structure (Delamare-Debouteville, 1948). The causes of this dimorphism are not known, but it is not a caste-difference since each form is made up of sexually functional males and females.

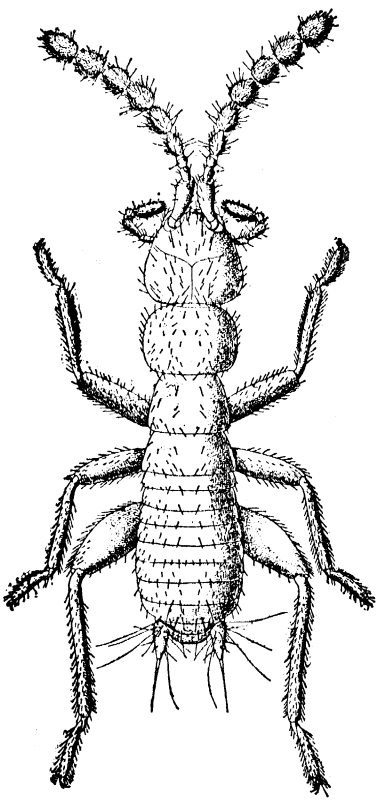


FIG. 315.—*Zorotypus guineensis*, Africa
After Silvestri. *Boll. Lab. Zool. Portici*, 1913.

The mouthparts of the Zoraptera are of a generalized type (Fig. 317). The mandibles are more or less quadrangular and adapted for mastication: the maxillae do not call for special mention and their palpi are 5-segmented: the labium is characterized by the completely divided prementum, and 3-segmented palpi. The wings are capable of being shed as in termites, but the fractures are not very definitely located though they are situated near the bases of the

veins. The wing-stumps persist in deälated individuals as in termites. The venation (Fig. 316) is greatly specialized by reduction and according to Crampton (1922) it approaches that of some Psocoptera, probably through parallel evolution. The abdomen is 11-segmented and genitalia are wanting in the female: in the male, genitalia are present but their homologies are not known (Snodgrass, 1937). There are ten pairs of spiracles, two being thoracic and the remainder abdominal in position. The internal structure has been only partially investigated (Silvestri, 1913; Gurney, 1938). The digestive system is characterized by the large crop which extends backwards to about the 5th abdominal segment; the mid gut is an ovoid obliquely disposed sac, and the hind intestine is convoluted. There are six Malpighian tubes and six

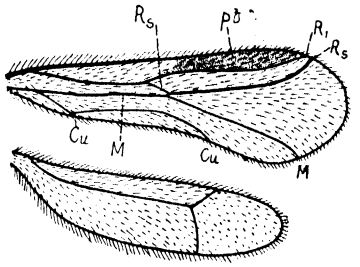


FIG. 316.—*Zorotypus snyderi*, right wings

pt, pterostigma.

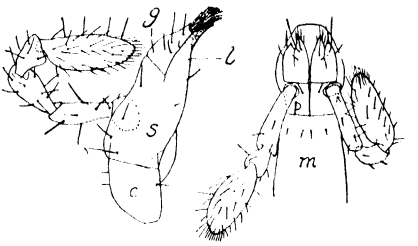


FIG. 317.—*Zorotypus guineensis*, maxilla and labium

c, cardo; *s*, stipes; *g*, galea; *l*, lacinia; *p*, prementum; *m*, postmentum. *After* Silvestri, 1913.

rectal papillae. The nervous system is highly specialized, there being three thoracic and only two abdominal ganglia, the first of the latter being located in the thorax. The testes are ovoid paired bodies communicating by slender vasa deferentia with a large seminal vesicle. From this runs a long ejaculatory duct at the base of which is a pair of accessory glands. The female reproductive system consists of 4–6 panoistic ovarioles on each side and a spermatheca connected with the region of the genital chamber by a long slender duct.

The eggs are simple ovoidal structures and eclosion is assisted by an egg-burster on the head of the embryonic cuticle which is cast off as the young nymph emerges. The number of nymphal instars is unknown but two types of nymphs, corresponding to the adult forms, occur. Though the Zoraptera are gregarious there is no evidence of any form of social organization. Fungal spores and the remains of mites have been found in the alimentary canal.

The affinities of the Zoraptera are uncertain. The concentrated nervous system and few Malpighian tubules are suggestive of the Psocoptera but the presence of cerci and the structure of the head-capsule, mouthparts and thorax indicate an Orthopteroid ancestry perhaps near to the point at which the Psocoptera also originated.

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Order 16. **PSOCOPTERA** (**Copeognatha**: Booklice or Psocids and their allies)

Insects with long filiform antennae of 12–50 *segments.* Y*-shaped epicranial suture present; post-clypeus enlarged. Maxilla with a rod-like lacinia which is partially sunk into head-capsule; labial palps much reduced,* 1- *or* 2*-segmented. Prothorax generally small. Tarsi* 2- *or* 3*-segmented. Cerci absent.*

The Psocoptera are small or minute insects with rather soft, stout bodies and, in many cases, with delicate membranous wings. Individuals or generations of the winged species sometimes occur with the alary organs rudimentary; in other cases the micropterous condition appears to be an attribute of the female, and there are further species in which the possession of rudimentary wings is a constant feature in both sexes. Among the Liposcelidae most of the species never possess any traces of wings. Several of the latter insects are familiar to the non-entomological observer and are common among accumulations of books and papers, in uninhabited and other apartments, being known as booklice or dustlice. They feed upon the paste of book-bindings, also on fragments of animal and decaying vegetable matter (Broadhead, 1950). Flour, meal and other cereal products are also frequently resorted to while, at times, collections of insects, and other dried natural history specimens, suffer from depredations by Psocids. These insects sometimes occur in houses in such numbers as to constitute a pest, and are usually introduced in the stuffing of mattresses, etc. They are also often abundant among straw and chaff in barns. The majority of Psocids, including the alate species, occur out of doors and are to be met with on tree-trunks, under bark, on weathered palings and walls, in birds' nests, etc., and often in situations where there are growths of lichen or algae: others are found among vegetation. They live on fragments of animal or vegetable matter, particularly on fungi, unicellular algae and lichens: some species pass their whole lives among fungi of various kinds. Although sometimes stated to eat paper, certain species feed upon moulds growing thereon and in this way reveal the injury done to the paper. Most Psocids carry foreign matter entangled among their body-hairs and in this way disseminate fungus-spores. Many Psocids live gregariously and clusters of individuals, of various ages, are sometimes met with on bark, each colony being covered by a canopy of fine silken threads. The winged forms are curiously reluctant to take to flight. At times, however, they fly in considerable numbers and drift through the air after the manner of winged aphids. They have occasionally been recorded as occurring in buildings in large swarms, the commonest species concerned being *Lachesilla pedicularia.*

External Anatomy.—The head (Fig. 318) is large and very mobile, with the epicranial sutures more or less distinct. The compound eyes are markedly convex and protrude from the surface of the head: in apterous Liposcelidae they are vestigial and reduced to two small groups of ommatidia. Three ocelli

are present in the winged species but these organs are wanting in the apterous forms. The *labrum* is well developed and attached to the *ante-clypeus*: the *post-clypeus* (prefrons of some authors) is a conspicuous sclerite often presenting an inflated appearance. The *antennae* are long and filiform: they are frequently 13-segmented, but the number of segments is variable and may be as high as fifty. The mouthparts (Fig. 319) have been investigated by many authors, especially Badonnel (1934), Weber (1936) and Cope (1940). The *mandibles* are relatively large and strong, each with a broad striated molar area and a denticulate cutting edge. The *maxillae* are considerably modified. The cardo and stipes are apparently not always clearly separated, but the 4-segmented maxillary palp is well developed. The galea is a large, fleshy lobe, medial to which is a strongly sclerotized rod (the 'pick'), the basal half of which is sunk into the head. The innervation of the small internal cavity of the pick by a branch of the maxillary nerve and the attachment to it of retractor muscles comparable with the cranial flexors of the lacinia in other insects suffice to identify it as a highly modified lacinia. The pick is said to be used for scraping food from the substrate but Pearman (1936) was unable to confirm this, the mandibles alone being used in the feeding Psocids which he studied. In the *labium*, the mentum is oblong, the prementum is divided and the ligula carries a pair of membranous paraglossae. The inner lobes or glossae are represented by a pair of minute structures forming the external conduit of the labial glands. The labial palpi are reduced to the condition of single or, rarely, 2-segmented lobes. The *hypopharynx* is well developed and its complex structure has received diverse explanations. The free extremity of the lingua bears a pair of small delicate lobes, the *superlinguae*, while its ventral surface is thickened locally to form a pair of oval *lingual sclerites*. The latter are connected by a sclerotized filament to the conspicuous *sitophore sclerite* (sometimes misleadingly called the oesophageal sclerite) which, following Badonnel (1934) and Snodgrass (1944), is to be regarded as the basal part of the cibarial surface of the hypopharynx. Directly opposite the sitophore sclerite, the dorsal wall of the

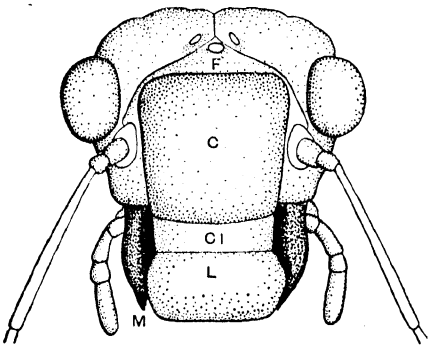


FIG. 318.—Frontal view of the head of a psocid

F, frons. *C*, post-clypeus. *C1*, ante-clypeus. *L*, labrum. *M*, mandible.

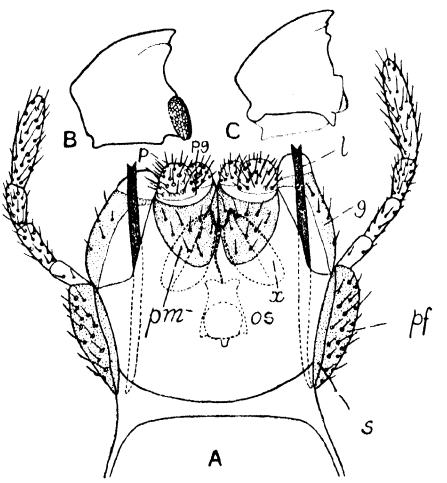


FIG. 319.—A, ventral view of the head of a Psocid. B, right mandible (ventral). C, left mandible (dorsal)

g, galea; *l*, lacinia; *os*, sitophore sclerite; *p*, labial palp; *pf*, palpifer; *pg*, paraglossa; *pm*, prementum; *s*, stipes; *x*, lingual sclerite.

cibarium bears a sclerotized knob-like process which Weber (1936) suggests can be moved against the sitophore sclerite so that the two act like a mortar and pestle and help to break up food particles. The sitophore sclerite, lingual sclerites and sclerotized filament correspond to similar structures in the Mallophaga.

The *thorax* of the winged forms is characterized by the reduction of the prothorax, which is largely concealed between the head and mesothorax. The meso- and metathorax are very similar, the nota being subdivided clearly into scutum and scutellum, followed in each case by a phragma-bearing postnotum. The pleura consist of the typical elements. The sterna are reduced to narrow strips lying between the legs, each being subdivided into a sternum and sternellum and provided with well-developed furcal arms. In apterous forms the prothorax is larger and in some (Liposcelidae) the tergites and sternites of the meso- and metathorax are united into a continuous shield. The *wings* (Fig. 320) are membranous with prominent although reduced venation: the anterior pair is considerably the larger and the wings, when not in use, are steeply inclined in a roof-like manner over the body, with the hind margins uppermost. In flight the fore and hind wings are coupled. In some species the wings are conspicuously marbled and these organs together with the body and appendages may bear scales of varied form not unlike those of Lepidoptera. The venation is discussed in detail by Enderlein (1903) and Tillyard (1926): a pterostigma is present on the fore wing, and there is a reduction in the branches of the principal veins: Sc is unbranched, R and M are each normally 3-branched and there is a fusion of the main stems of M and Cu. M may also be associated with the basal part of R_s. Cu_1 usually branches distally into Cu_{1a} and Cu_{1b}, the cell enclosed by the fork (the so-called *areola postica*) being either free, connected with M by a cross-vein or fused with it as in Fig. 320. In the hind wing reduction is carried still further, M being represented as a rule by a single branch. In *Psocus*, and other genera, the wings are effectively braced on account of the somewhat tortuous courses of the veins, and there is a striking absence of cross-veins. The latter exist, however, in certain members of the order.

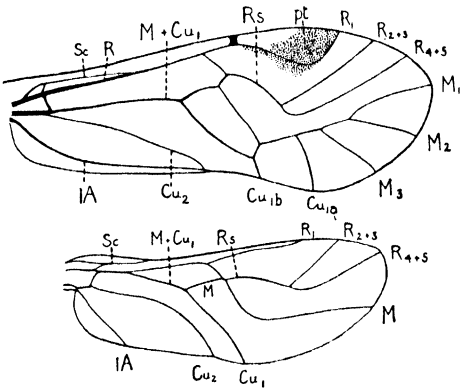


FIG. 320.—Right wings of *Amphigerontia bifasciata*
pt, pterostigma.

The legs show no special adaptive modifications. In many species there occurs on the inner face of each posterior coxa a structure known as Pearman's organ. This is believed to be stridulatory and consists typically of a sculptured prominence near which lies an area of thin cuticle—the mirror or tympan (Pearman, 1928). According to Cope (1940) the Psocoptera share with the Mallophaga, and with them alone, the peculiarity of a ventral articulation between the anterior coxae and the prosternum, the middle and hind coxae having only the normal pleural articulation. The pretarsus bears two claws, beneath which occur pulvilli of varied form, but there is no empodium.

The morphology of the abdomen, and particularly of its terminal segments and the genital appendages, is by no means clear. Nine segments are generally recognized, together with a dorsal terminal epiproct and a pair of paraprocts flanking the anus. It is, however, uncertain whether these latter structures are homologous with the similarly named sclerites of other insects. The small ovipositor is partly concealed by the enlarged sternum of the 8th abdominal segment and consists, when fully developed, of three pairs of valves of which the anterior pair arises from the 8th sternum and two pairs from the 9th sternum. Atrophy of all the valves may occur. The male genitalia, which are concealed by the enlarged 9th sternum, consist of a pair of parameres between which lies the aedeagus. The homologies of the genitalia are not established but the terminalia provide valuable taxonomic characters.

There are two pairs of thoracic spiracles and seven or eight abdominal pairs.

Internal Anatomy.—The principal recent works on the internal anatomy of the order are those of Badonnel (1934), Weber (1936) and Finlayson (1949) who also review earlier work.

In the *digestive system* the oesophagus is elongate and extends into the abdomen, the mid gut is sharply curved and U-shaped and leads into a very short unconvoluted hind intestine bearing six rectal papillae: the Malpighian tubes are four in number. There are two pairs of labial glands which extend into the abdomen and whose ducts open at the base of the labium. One pair, normally dorsal in position, is composed of cells with an acidophil cytoplasm and, in all but a few species, secretes silk, while the other pair, made up of basophil cells, is salivary and is usually ventral to the silk glands (Weber, 1938). The spinning glands provide silken threads which form the webs often associated with colonies of these insects. The *nervous system* is highly concentrated: in addition to the brain and suboesophageal ganglion there are only three other ganglionic centres. The first of these belongs to the prothorax, the meso- and metathoracic ganglia are fused into a common centre, and the single abdominal ganglion has shifted forwards so as to lie partly in the thorax. The connectives are extremely short but are double throughout their course. A pair of large abdominal nerves extend to the posterior extremity of the body. The *female reproductive organs* are of an extremely simple type: each ovary consists of from three to five polytrophic ovarioles, the oviducts are very short and a small globular spermatheca opens into the dorsal aspect of the vagina. A peculiar type of accessory gland was described by Nitsche in *Clothilla* many years ago: it contains from one to four small sacs each opening by a narrow canal into a common duct. The *male reproductive system* consists of a pair of testes—which may be simple pyriform organs or three-lobed—leading by short, narrow vasa deferentia into the large seminal vesicles. The latter are somewhat complex structures in some species, consisting of two chambers and responsible for secreting material used in the formation of the spermatophore, a detailed account of which is given by Finlayson for *Lepinotus*. The seminal vesicles open into a short ejaculatory duct.

Development.—Females—except in viviparous forms—lay 20–100 eggs which are ellipsoidal or bluntly rounded at one end. They may be scattered singly or laid in groups and are sometimes covered by an incrustation of bark, algae, etc., or by a silken web (Fig. 321). Eclosion is assisted by an egg-burster on the head of the embryonic cuticle, which is shed before emergence is complete. There are usually six subsequent nymphal instars differing from the

adult in possessing a smaller number of antennal segments, fewer ommatidia, two tarsal segments and the gradually developing wing-pads and genitalia (Weber, 1931; Söfner, 1941; Broadhead, 1947; Finlayson, 1949). Facultative parthenogenesis is not infrequent and males of some species are unknown. The Psocoptera occurring in N.W. Europe usually have one or two generations per year but some species of *Caecilius* have several generations while the domestic species breed continuously. Overwintering usually occurs in the egg.

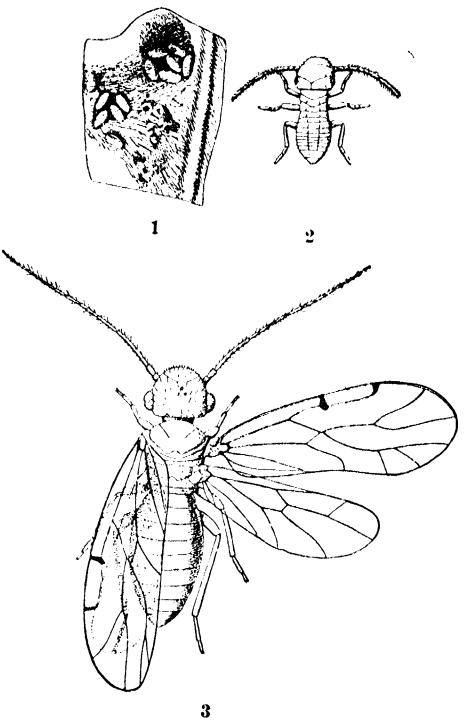


FIG. 321.—*Peripsocus phaeopterus*. 1, portion of leaf with eggs beneath silken threads; 2, young nymph; 3, imago
After Silvestri.

Classification. — The group was first given ordinal status by Enderlein (1903) but this author's classification, based primarily on tarsal segmentation, is not now accepted. Tillyard (1926) and Karny (1930) have emphasized the importance of venational characters and Roesler (1944) has proposed the classification indicated in the following key based on his work. This classification incorporates many features of Tillyard's scheme together with those of an outline sketch by Pearman (1936). Roesler estimates that about 1,000 species have been described, of which 80 per cent. belong to the suborder Eupsocida and about 70 species are British. Most of the species occurring in N.W. Europe can be identified with the aid of works by Enderlein (1927) and Badonnel (1943) while Roesler (*op. cit.*) has a key to the genera of the world.

Key to adult Psocoptera (Roesler, 1944)

1. Antennae with more than 20 segments, never secondarily annulated; tarsi 3-segmented; labial palps 2-segmented (**Trogiomorpha**) 2

–. Antennae usually with 13 segments, sometimes 15–17, in which case some are annulated; tarsi 2- or 3-segmented; labial palps 1- or 2-segmented . . 4

2. Head short and transverse; inner side of 2nd segment of maxillary palp with peg-like sense-organ; if macropterous Cu_2 and 1A end separately at edge of fore wing 3
–. Head long and vertical; maxillary palp without sense-organ; Cu_2 and 1A of fore wing converge to a point (nodulus) . . . . PSYLLIPSOCIDAE

3. Claws not toothed, body and wings never scaled . . . . TROGIIDAE
–. Claws with preapical tooth; body and wings usually scaled . LEPIDOPSOCIDAE

4. Antennae with 12–17 segments, some or all of the flagellar segments annulated; labial palps 2-segmented; tarsi 3-segmented (**Troctomorpha**) . . 5

–. Antennae almost always 13-segmented; labial palps 1-segmented; tarsi 2- or 3-segmented, if latter then flagellar segments not annulated (**Eupsocida**) . 8

5. Antennae usually 15-, sometimes 17-segmented; wings usually greatly reduced or absent; body and wings never scaled; meso- and metanota often fused . 6
–. Antennae with 12–13 segments; wings seldom reduced, never absent; body and wings usually scaled; meso- and metanota separate 7

6. Body normally convex, short; hind femora not broadened PACHYTROCTIDAE
–. Body strongly flattened, longer; hind femora flat and broad LIPOSCELIDAE

7. Fore femora with saw-like row of longitudinal teeth; body and wings usually scaled; areola postica free . . . . . AMPHIENTOMIDAE
–. Fore femora simple; without scales; areola postica united with media. . PLAUMANIIDAE

8. Labial palps short and appressed, somewhat semicircular; apical third of lacinia equally broad or broadened towards apex, usually markedly toothed . 9
–. Labial palps broadly triangular, laterally diverging; lacinia pointed apically, usually without marked teeth 16

9. Labrum on inner side with 2 strongly sclerotized ridges, often fused at fore margin and showing through outer surface; outer margin of mandible bluntly angled 10
–. Labrum on inner side with only a small sclerotized tubercle on each side; outer margin of mandible smoothly curved 13

10. Fore wing with no trace of cross-vein joining R_1 and R_s behind stigma; females sometimes apterous 11
–. Fore wing with an incomplete cross-vein between R_1 and R_s or a fusion between them; never apterous 12

11. Tarsi 3-segmented; two anal veins in fore wing . . . PTILONEURIDAE
–. Tarsi 2-segmented; one anal vein in fore wing . . . EPIPSOCIDAE

12. Tarsi 2-segmented; hind wing with forked media . . CALLISTOPTERIDAE
—. Tarsi 3-segmented; hind wing with simple media . . . PSILOPSOCIDAE

13. Fore wing with aerola postica united with media; if females occasionally brachypterous, then with glandular hairs on head 14
—. Areola postica free or absent; often brachypterous or apterous but head never with glandular hairs 15

14. Tarsi 3-segmented . . . . . MYOPSOCIDAE
—. Tarsi 2-segmented . . . . . PSOCIDAE

15. Tarsi 3-segmented . . . . . MESOPSOCIDAE
—. Tarsi 2-segmented . . . . . PSEUDOCAECILIIDAE

16. Venation reticulate in outer half of fore wing; Cu_{1b} little shorter than Cu_{1a}; 1A almost as long as Cu_2 . . . . . NEUROSEMIDAE
—. Venation not reticulate; Cu_{1b} extremely short; 1A about half as long as Cu_2. POLYPSOCIDAE

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Order 17. **MALLOPHAGA** (Biting Lice or Bird Lice)

Apterous insects living as ectoparasites mainly of birds, less frequently of mammals. Eyes reduced. No ocelli. Antennae 3- to 5-*segmented. Mouthparts of a modified biting type: maxillary palpi* 4-*segmented or wanting: ligula undivided or* 2-*lobed, labial palpi rudimentary. Prothorax evident, free: meso- and metathorax often imperfectly separated: tarsi* 1- *or* 2-*segmented, terminated by single or paired claws. Thoracic spiracles ventral. Cerci absent. Metamorphosis wanting.*

The Mallophaga are very small or small (0·5 to 6 mm. long), flat-bodied, active insects entirely adapted for an ectoparasitic life. The majority of the species infest birds and a smaller number occur on mammals. Most Mallophaga feed on fragments of feathers, hair and other epidermal products, but Ewing (1924) says that *Gyropus ovalis* and *Gliricola porcelli* obtain sebum and possibly serum by probing into the hair-follicles of their hosts while Crutchfield & Hixson (1943) find that *Menacanthus* spp. feed habitually on blood in addition to feathers. Other species do not neglect the opportunity of imbibing blood from wounds, as, for instance, when a bird is shot. Hosts seem able to withstand the usual degree of infestation without obvious ill-effects but with exceptionally heavy infestations there may be some loss of plumage and deterioration in condition due to irritation. Dust-baths and 'anting' in birds may possibly be attempts to rid themselves of these parasites. Mallophaga tend frequently to be restricted to special areas of the host's body. For example, on the pigeon, *Columbicola columbae* is found mainly on the remiges of the wing while *Goniocotes bidentatus* occurs on the small feathers of the neck (Beier, 1936). In populations of *Bovicola bovis* on cattle, Craufurd-Benson (1941) found that there was some segregation into breeding clusters and nymphal colonies though this was complicated by seasonal changes in the distribution of infestation over the host's body. After the death of the host, Mallophaga are capable of survival for only a short period (a few hours to

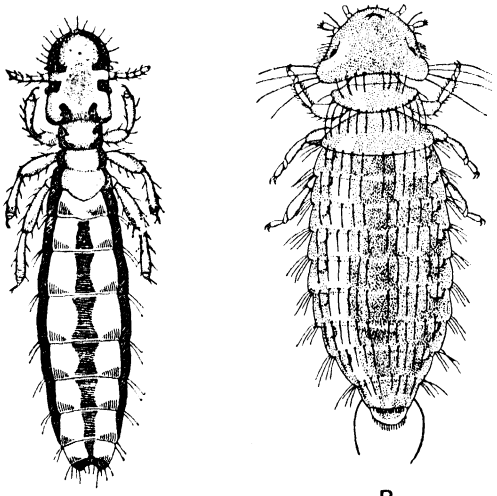


FIG. 322.—Mallophaga of domestic fowl
A, *Lipeurus caponis* L. *After* Denny. B, *Menopon pallidum* Nitz. *After* Bishopp & Wood, *U.S. Farmer's Bull.*, 801.

three days). Migration from one host to another probably occurs mainly through bodily contact of the hosts though recorded instances of Mallophaga clinging to Culicid and Hippoboscid flies suggests that phoresy may play some part in their spread. There appears to be a definite relation between the evolution of the lice and that of their hosts so that groups of closely related host species tend to be infested by similar Mallophaga (Hopkins, 1942; 1949). Several authors have suggested that this type of host-association may aid in elucidating the phylogeny of the hosts. Thus, the flamingoes (Phoenicopteridae) have four Mallophagan genera in common with the ducks (Anatidae) but only one with the storks (Ciconiidae), thus indicating a closer relationship with the former. Many Mallophaga show an interesting symbiotic association with bacteria which, in nymphs and males, occur in specialized mycetocytes distributed among the fat-body. In adult females the bacteria accumulate in the ovarial ampullae, whence they pass into the eggs before they are laid and are so transmitted to the progeny (Ries, 1931). Lice from which the symbionts have been eliminated soon die. The symbionts tend to occur in those species which normally or occasionally imbibe blood and it has been suggested that one factor helping to determine the host-specificity of biting lice is the inability of the symbionts to flourish in a louse feeding on the blood of an abnormal host species.

The most notorious member of the order is the Common Chicken-Louse *Menopon pallidum*. Ducks are infested by several species, among which a common form is *Philopterus dentatus*. Pigeons are almost always infested by an elongate and very slender louse, *Columbicola columbae*. The species living on domestic mammals belong to a few Trichodectid genera: thus the dog is often infested by *Trichodectes canis* and cats by *Felicola subrostratus*. Horses and donkeys harbour several species while *Bovicola bovis* troubles cattle all over the world. The host-relations of the Trichodectidae are discussed by Hopkins (1949).

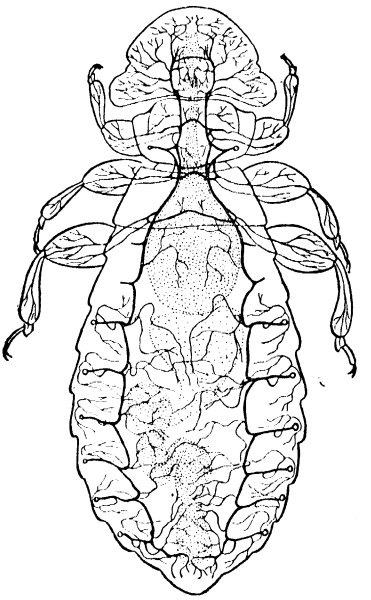


FIG. 323.—Tracheal system of *Myrsidea cucularis*
After Harrison, *Parasitology*, 8.

External Anatomy. — The body is usually very much flattened dorsoventrally with the integument well sclerotized. Over the abdomen the tergal, pleural, and sternal regions are separated by very distinct areas of membrane. The *head-capsule* is large and horizontal and many of its sutures have been obliterated though the labrum is distinct and a clypeofrontal suture may be retained; the tentorium is often reduced (Symmons, 1952).

The *antennae* differ very markedly in the two suborders: in the Amblycera they are generally capitate, and concealed in deep fossae, while among the Ischnocera they are filiform, exserted and may be modified as clasping organs in the male. The *mouthparts* (Snodgrass, 1944; Qadri, 1936) are of the biting type with large dentate *mandibles*, which differ in their insertion in the two suborders (Fig. 324). Among the Amblycera they lie parallel with the ventral surface of the head, so that each condyle is ventral and the ginglymus dorsal.

In the Ischnocera each mandible is inserted more or less at right angles with the head, the condyle being posterior and the ginglymus anterior. The *maxillae* are single-lobed and lack differentiation into the usual sclerites: they are, furthermore, attached to the lateral margins of the labium and, for this reason, their palpi were formerly regarded as belonging to that region. In certain genera a pair of minute forked rods have been described, but are very fragile and easily overlooked. They are evidently homologous with the similar, but more prominent, laciniae of the Psocoptera. The maxillary palpi are 4-segmented in the Amblycera and wanting in the Ischnocera. The *labium* is composed of a submentum, mentum and prementum; the palpi are reduced to small lobes, and the ligula is either entire or represented by a pair of fleshy processes, probably homologous with paraglossae. The mouthparts of *Haematomyzus* are highly modified. The head is produced into a long rostrum at the end of which are a pair of mandibles with laterally developed biting edges which work outwards. Small structures which may be vestigial maxillae and labium are also present in biting lice and a long tubular food meatus traverses the rostrum to open posteriorly into a cibarial sucking pump. The Mallophagan *hypopharynx* shows some variations in structure (Cummings, 1913; Qadri, 1936), but basically it bears a very strong resemblance to that of the Psocoptera (q.v.). Posteriorly there is a strongly developed sitophore sclerite (the 'oesophageal sclerite' of some authors) from which arises a trachea-like sclerotized filament which runs forwards and divides into two, the branches uniting on each side with well-developed oval lingual sclerites. The latter have been referred to as lingual glands but there is no evidence that they are associated with secretory cells. The sitophore and lingual sclerites are absent in a few cases. In *Trochilocoetes*, Clay (1949) has found that the hypopharynx is produced into three stylet-like structures which appear to be adapted for piercing.

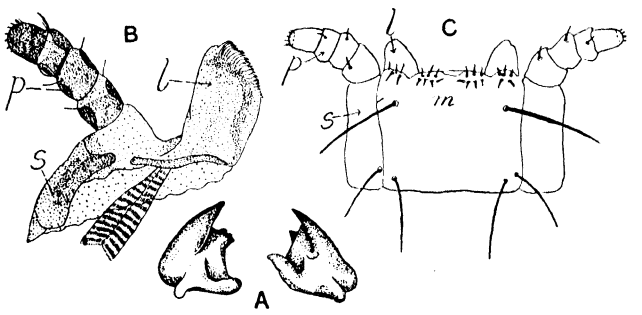


FIG. 324.—Mouthparts of Mallophaga. A, mandibles. B, maxilla (*Laemobothrion*). C, labium and maxillae (*Ancistrona*)

l, galea; *m*, mentum; *p*, maxillary palp; *s*, stipes. Adapted from Snodgrass, 1899, 1905.

In the *thorax*, the prothorax is well developed and almost invariably free. Cope (1940; 1941)—who has given a detailed, though in places unorthodox, account of the thoracic morphology of two species—has suggested that the presence of a ventral articulation between prosternum and fore coxae is a character peculiar to the Psocoptera and Mallophaga, but not all lice possess it. The meso- and metasterna are fused together but the nota of the pterothorax may be separate (Amblycera) or united (Ischnocera). Postnotal sclerites are not differentiated. The thoracic segments are completely fused in *Haematomyzus*. The legs are rather similar throughout the order. The coxae are widely separated and the 1- or 2-segmented tarsi commonly bear a pair of claws, though in the Trichodectidae and Gyropidae, which infest mammals, the claws are single. There are no pulvilli, nor is an empodium developed.

The morphology of the abdomen and the genital appendages requires further investigation. The number of visible abdominal segments present in the adult varies from eight to ten. In *Lipeurus heterographus* the reduction to nine segments has been shown by Wilson (1936) to result from the fusion of the 1st and 2nd during embryonic development and of the 9th and 10th in postembryonic growth. The male genitalia are represented by a median eversible aedeagus, often of complex structure, but no other appendicular parts are present (Qadri, 1936). The ovipositor may be absent or represented by a pair of small appendages on the 8th segment.

Internal Anatomy.—A general description of the internal organs is given by Snodgrass (1899). The *alimentary canal* (Fig. 325, A) is either an almost straight tube, or slightly convoluted, but always comparatively short. It is characterized by the well-developed crop, the large mid intestine, and short simple hind intestine. A pair of large enteric caeca extend as outgrowths of the stomach on either side of the crop. There are four Malpighian tubes and a whorl of six prominent rectal papillae. Among the Amblycera, the crop is a simple expansion of the oesophagus: in the Ischnocera it is greatly developed, and is either connected with the gut by means of a narrow duct-like tube, as in *Trichodectes*, or assumes a more or less fusiform shape, and extends into the body-cavity to one side of the alimentary canal. In both the main suborders a pair of labial salivary glands, lying beneath the suboesophageal ganglion, opens by a median duct at the base of the labium. In the Ischnocera there is also a pair of thoracic salivary glands, each accompanied by a reservoir, which opens into the anterior part of the gut by an unpaired duct and also two supplementary glands with ducts opening separately into the front of the crop. In the Amblycera there is a pair of sausage-shaped or conical glands opening into the oesophagus in front of the crop and possibly corresponding to the supplementary glands of the Ischnocera. The *nervous system* is highly specialized: in *Eurymetopus taurus* the brain is laterally expanded in such a manner as to be U-shaped, the suboesophageal ganglion is exceptionally large, and is united with the thoracic chain by means of short thick connectives. The thoracic ganglia are three in number and connectives are wanting: there are no ganglia in the abdomen, the latter region being innervated from the metathoracic ganglion. The *tracheal system* (Harrison, 1915) is disposed in two main trunks, opening to the exterior by means of seven pairs of spiracles (Fig. 323): of the latter, the first pair is prothoracic, and the remainder are abdominal and situated typically on segments 3 to 8 or, more rarely, on

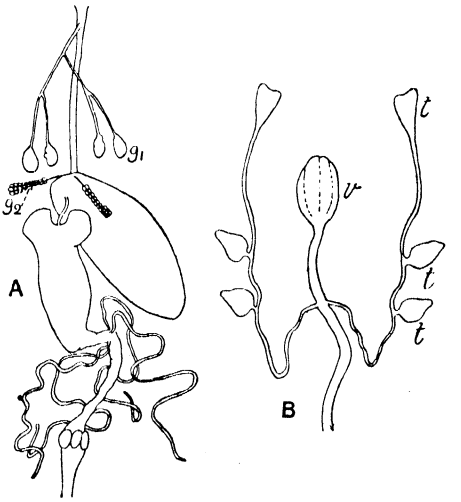


FIG. 325.—A, digestive system of *Eurymetopus taurus*

g_1, salivary glands; g_2, supplementary glands.

B, male reproductive organs of *Physostomum diffusum*

t, testis; *v*, vesicula seminalis. *After* Snodgrass, *Occas. Papers Calif. Acad. Sci.*, 1899.

segments 2 to 7. In *Trimenopon* and *Gliricola* there are five pairs of abdominal spiracles located on segments 3 to 7, while *Harrisoniella densa* is peculiar in possessing a pair of metathoracic spiracles. Details of spiracular structure are given by Webb (1946). The *heart* (Fulmek, 1906) is situated in the 7th and 8th or 8th segment of the abdomen. It is an extremely short chamber provided with two or three pairs of ostia, and is continued forwards as the aorta: the latter is swollen into a bulbus arteriosus at its junction with the heart. The *female reproductive organs* consist of a pair of ovaries, each organ being usually composed of five panoistic ovarioles: in the Amblycera there is a tendency to reduction, and the ovarioles may be restricted to three. The common oviduct leads into a vagina and the latter opens behind the 8th sternum. An unpaired accessory gland, which secretes the cement used for attaching the eggs, is usually present, together with a spermatheca which may assume various forms, often being two-lobed or divided into two in the Amblycera. At the base of the ovarioles in certain forms is developed an ampulla containing mycetocytes. With regard to the *male reproductive organs* (Fig. 325, B), the testes are composed of three (Amblycera) or two (Ischnocera) ovoid or pyriform follicles, which are quite separate from one another. Those of a side communicate with the corresponding vas deferens, and the two latter canals frequently discharge into the vesicula seminalis. This organ is compact and bilobed, often large, and is continuous distally with a tortuous ejaculatory duct.

Postembryonic Development.—The eggs, of which each female usually produces less than 100, are cemented to the feathers or hair of the host, usually in certain favoured areas. They are small, elongate-oval and provided at the anterior pole with a cap, near the margin of which occur several micropyles. Posteriorly there is the so-called egg-stigma, consisting of a group of canals which partly or completely traverse the chorion and which assists in the attachment of the egg. Eclosion (Weber, 1939) occurs through internal pressure breaking off the cap around a preformed line of weakness and the rupture of the extra-embryonic membranes by a group of sharp cephalic hatching spines on the embryonic cuticle. The latter is then ruptured before the thorax and its appendages have emerged from the egg and the newly hatched nymph leaves it behind in the egg-shell. There are three nymphal instars which differ from the adults in their smaller size, lighter pigmentation and different chaetotaxy. Little is known of the duration of development but Martin (1935), who bred *Columbicola columbae* on pigeon-feathers in an incubator at 37° C. found the egg stage to last four days and each of the nymphal stages about seven days.

Classification.—About 2,600 species of Mallophaga are known (about 260 British) and for their taxonomy reference should be made to Kellogg (1908) and numerous more recent papers by authors such as Bedford, Clay, Ewing, Kéler and Werneck. Hopkins & Clay (1952) give a list of the genera and species of the world and Séguy (1944) has monographed the species found in France. The classification adopted here recognizes three suborders. There is no general agreement on the number of families which may be distinguished, Kéler, for instance, according family status to groups which other authors treat as subfamilies.

Suborder 1. AMBLYCERA

Antennae capitate, 4-segmented, concealed. Mandibles horizontal. Maxillary palpi 4-segmented. Meso- and metathorax usually separate.

1. Infesting birds (e.g. *Menopon, Trinoton*) . . . . . MENOPONIDAE
–. Infesting mammals 2

2. Tarsi with one claw (*Gyropus*) . . . . . GYROPIDAE
–. Tarsi with two claws (*Boopia, Heterodoxus*) . . . . BOOPIIDAE

Suborder 2. ISCHNOCERA

Antennae filiform, 3- to 5-segmented. Mandibles vertical. Maxillary palpi absent. Meso- and metathorax usually fused.

1. Antennae 5-segmented; tarsi with paired claws; infesting birds (*Lipeurus*, Fig. 322, A; *Goniodes*) . . . . . PHILOPTERIDAE

–. Antennae 3-segmented; tarsi single-clawed; infesting mammals (*Trichodectes*). TRICHODECTIDAE

Suborder 3. RHYNCHOPHTHIRINA

Head prolonged anteriorly into a rostrum. Mandibles at apex of rostrum, working outwards. Labium and maxillae vestigial. Contains only one family, the Haematomyzidae, with a single species, *Haematomyzus elephantis*, found on *Elephas* and *Loxodonta* (Ferris, 1931; Weber, 1939).

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Order 18. **SIPHUNCULATA** (**Anoplura** of some writers: Sucking Lice)

Apterous insects living as ectoparasites of mammals. Eyes reduced or absent. Ocelli absent. Antennae 3- to 5-segmented. Mouthparts highly modified for piercing and sucking, retracted within the head when not in use. Thoracic segments fused: tarsi 1-segmented, claws single. Thoracic spiracles dorsal. Cerci absent. Metamorphosis wanting.

The insects included in this order are exclusively blood-sucking ectoparasites of mammals and about 225 species have been described. Of these, two species infest man and about a dozen occur on domestic animals: the remainder have been taken from a wide range of mammals including monkeys, rabbits, mice, seals, elephants, etc. There is no doubt that the greater number of species are, as yet, undescribed and only a beginning has so far been made in the study of these insects. As in the Mallophaga (q.v.) there is considerable host-specificity and closely related host species tend to be infested by similar Siphunculates, e.g. *Enderleinellus* is restricted to squirrels (Sciuridae) and *Pedicinus* to the Cynomorph monkeys. A comprehensive and critical review of Siphunculate host-relations is given by Hopkins (1949) while Webb (1949) has discussed phylogenetic aspects of the host-parasite association for the lice of Ferungulate mammals. Kellogg (1913) pointed out the close physiological relationships between certain of these parasites and the specific blood-characters of their hosts as determined by precipitin tests and it is possible that a lethal effect of abnormal host-blood on the essential symbiotic bacteria which occur in most Siphunculates is a factor helping to determine host-specificity.

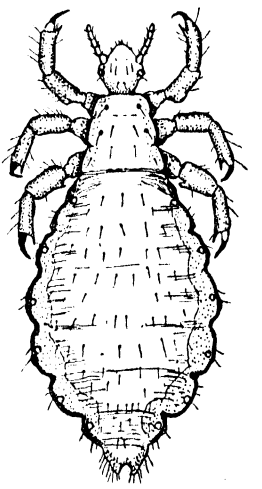


FIG. 326.—Body louse (*Pediculus humanus*), female, magnified

The best known species of Siphunculata is *Pediculus humanus*, the common louse of man (Fig. 326). It infests people living under unhygienic conditions and who, through neglect or force of circumstances, go for a number of days without any change of clothing. This insect exists in at least two races which have been regarded as separate species; they are *P. humanus capitis*, the head louse, and *P. humanus corporis* (*vestimenti*), the body louse. A detailed comparison of the two forms has been made by Busvine (1948) and earlier workers, whose results, however, do not coincide in all details. Morphologically, populations of the two forms differ significantly in total body size, head dimensions and antennal length, the body louse being larger with a

larger head and longer antennae though there is appreciable overlapping in the frequency distributions of the measurements. Biologically they differ in that body lice live between the clothes and skin of the infested person and are more resistant to starvation than the form *capitis* which is confined to the hair of the head. The two forms breed together readily under experimental conditions, the fertile hybrids being morphologically intermediate between the parents but in the F_2 and F_3 generations they become identical with the body strain. Earlier investigations suggested that the differences between the two forms were environmentally induced and that *capitis* reared on the body underwent a transformation to *corporis*. Busvine, however, found that head-lice reared on the body for 43 generations did not change systematically in biometric characters.

The extensive literature on the biology and control of *Pediculus humanus* has been summarized by Buxton (1947). The species is of considerable medical importance since in addition to the relatively unimportant effects of irritation and inflammatory reaction caused by its feeding, it transmits four more serious diseases. The most important of these is epidemic typhus, caused by the micro-organism *Rickettsia prowazeki* which is ingested by the louse when feeding on an infected person, multiplies in the gut and passes out in the faeces. Contact of the faeces (even after they have dried or when a louse is crushed) with a skin abrasion leads to infection, though it is likely that the disease is also acquired when dried, infective louse faeces are inhaled or come into contact with the conjunctiva. The disease is not transmitted by the feeding of infected lice. Another rickettsial disease transmitted by *Pediculus humanus* was the Trench Fever which appeared during the 1914–1918 War but afterwards died out completely. The mode of transmission probably resembled that of epidemic typhus. A third disease, murine typhus, related to the epidemic form, is normally flea-borne but there is evidence that it may sometimes become louse-borne. Finally, one form of relapsing fever (due to infection by *Spirochaeta recurrentis*) is carried by the body louse, transmission occurring when a louse infected by feeding is crushed and the spirochaetes in its haemolymph enter through abraded skin.

The only other Siphunculate infesting man is *Pthirus pubis*, the Crab Louse, which is restricted mainly to the hair of the pubic and peri-anal regions but is more rarely found on other hairy parts of the body. So far as is known it does not transmit any disease.

Among other genera of the order one of the most prevalent is *Haematopinus* which is mostly parasitic upon ungulates: *H. suis* (Fig. 329) is the well-known hog louse which occurs on domestic and wild pigs in many parts of the world (Florence, 1921): *H. tuberculatus* is found on the buffalo in E. Europe and the Orient, and *H. eurysternus* occurs on domestic cattle and may, at times, prove a pest. Species of *Polyplax* find most of their hosts among the Muridae, and *P. spinulosus* transmits *Trypanosoma lewisi* from rat to rat. *Echinophthirius*, and its allies, exclusively infest marine mammals (seals, sea-lions and walruses), and the anomalous genus *Enderleinellus* occurs only on Sciuridae.

External Anatomy.—The body of a louse is dorsoventrally flattened and only the abdomen is distinctly segmented. The head is more or less conical and pointed and, in *Linognathus*, it is much attentuated and relatively little broadened behind the antennae. Though some of the sutures of the typical insect head are visible in the nymphs they are mostly obliterated in adult lice. There is no tentorium. The antennae are short and 3- to 5-segmented: in

Pediculus and *Pthirus* they are 3-segmented in the first instar, but afterwards become 5-segmented, and in *Pedicinus* they are 3-segmented throughout life. The eyes are reduced and sometimes absent but are relatively well developed in *Pediculus* (Webb, 1948).

The mouthparts (Fig. 327) are difficult to investigate owing to their minute size and delicacy of structure. Numerous, somewhat discordant, accounts have been given and these are summarized by Stojanovich (1945), whose description of the structure and homologies of the mouthparts in four species forms the basis of the following account (see also Snodgrass, 1944). The labrum forms the dorsal wall of a small snout-like proboscis which is armed internally with small teeth and which is everted to grip the host during feeding. Both cibarium and pharynx are well provided with dilator muscles and together form a powerful sucking pump. Opening off the ventral side of

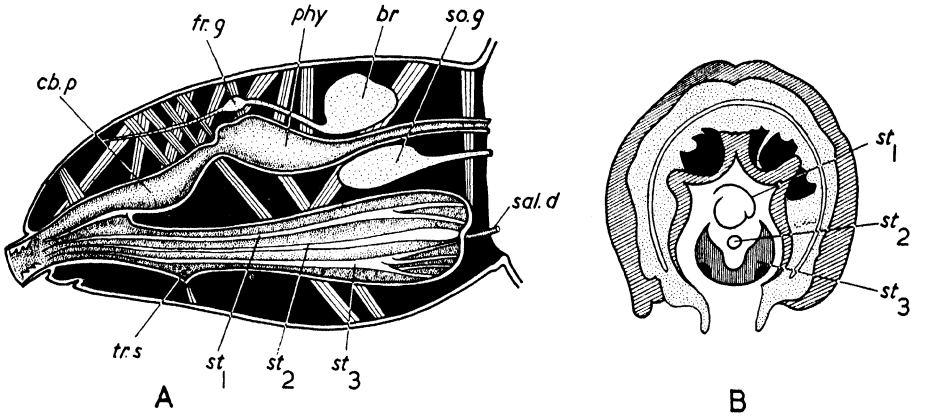


FIG. 327.—A. Longitudinal section through head of Siphunculate louse (*after* Snodgrass, 1944). B. Transverse section through head and trophic sac of *Pediculus* (*from* Snodgrass, 1944, *after* Vogel, 1921)

br, brain; *cb.p*, cibarial sucking pump; *fr.g*, frontal ganglion; *phy*, pharynx; *sal.d*, salivary duct; *so.g*, suboesophageal ganglion; *st* 1–3, stylets; *tr.s.*, tropic sac.

the cibarium is a well-developed pouch, the trophic sac, in which are accommodated three stylets, lying one above the other with the dorsal and ventral ones forked at their bases. These are the effective piercing organs. The dorsal stylet probably represents a highly modified hypopharynx, the middle stylet is regarded as a modification of the opening of the salivary duct and is pierced throughout its length by this duct while the ventral stylet is believed to be the greatly modified labium. Schölzel (1937), in his account of the embryological development of the mouthparts, showed that the mandibular rudiments disappear and it seems that a pair of small sclerotized structures situated latero-ventral to the trophic sac are derived from the maxillary rudiments. It should, however, be mentioned that Fernando (1933) gives a somewhat different account of the development of the mouthparts, asserting that the dorsal stylet is formed of the fused maxillae and Ferris (1951) reaches a similar interpretation by considering the musculature and innervation of this stylet. When the insect feeds its mode of action is probably as follows. The rostrum is everted and its denticles maintain a hold on the skin of the host. Special muscles come into play which draw the cibarium and pharynx forward, with the result that the cibarium and the opening of the trophic sac

come into contact with the skin. The contraction of protractor muscles associated with the stylets brings the latter into action and they perforate the skin: at the same time saliva enters the puncture. By the periodic contraction of the cibarial and pharyngeal dilators blood is then sucked up from the wound.

The *thorax* is relatively small and only imperfectly segmented. The legs are strongly developed in accordance with a mode of life which requires appendages adapted for maintaining a firm hold on the host. The tarsi are single-segmented, and each is terminated by a powerful claw which works against a tibial process.

The *abdomen* is 9-segmented: the terga and sterna are, as a rule, thinly sclerotized, while the pleura are strongly developed and deeply pigmented. A copulatory organ is well developed in the male, and in the female there is a pair of short gonopods which are used during oviposition for grasping the hair and directing the alignment of the eggs. Cerci are wanting in both sexes.

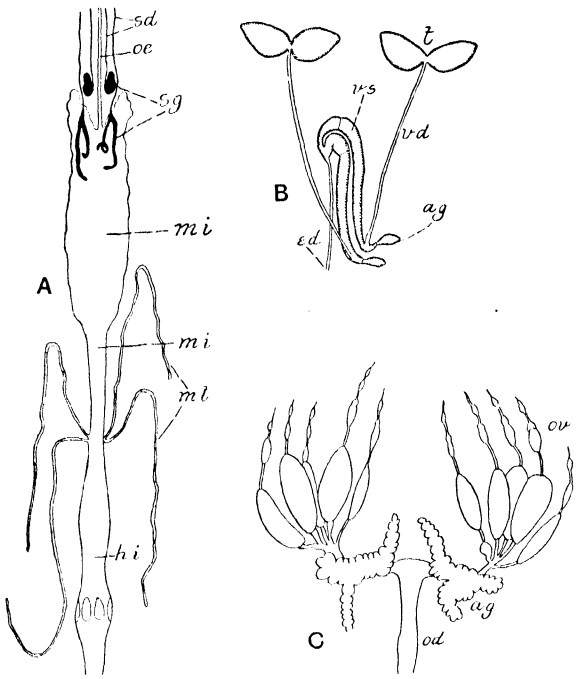


FIG. 328.—*Pediculus*. A, digestive system. B, male and C, female reproductive organs

ag, accessory gland; *ed*, ejaculatory duct; *hi*, hind intestine; *mi*, mid intestine; *od*, oviduct; *oe*, oesophagus; *ov*, ovary; *sg*, salivary glands and ducts *sd*; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis. Adapted from Patton and Cragg.

Internal Anatomy (Fig. 328).—Most of what is known concerning the internal anatomy is relative to *Pediculus* and *Haematopinus*. The anterior portion of the fore intestine has already been referred to, and the oesophagus passes directly to the stomach, both crop and gizzard being undeveloped. The stomach is a large chamber which narrows posteriorly, and occupies the greater portion of the abdominal cavity: in *Pediculus* a pair of large enteric caeca is present anteriorly. The hind intestine presents no convolutions and receives four Malpighian tubes, and the rectum is provided with a whorl of six sclerotized rectal papillae. There are two pairs of salivary glands which are situated in the thorax: one pair is elongate and tubular, the other being compact and reniform: their ducts apparently combine to form the salivary canal already mentioned in relation to the mouthparts. A pair of glands, known as Pawlowsky's glands, open into the stylet sac and their secretion possibly serves to lubricate the stylets. The *tracheal system* exhibits a general agreement with the simpler Mallophagan type (Harrison, 1915): there are usually seven pairs of spiracles, a mesothoracic pair being dorsal, and the abdominal spiracles opening on segments 3 to 8. The detailed structure of the

spiracles has been described by Webb (1946; 1949) who considers that they provide characters of considerable phylogenetic importance. The *female reproductive organs* consist of five polytrophic ovarioles to each ovary and there is also a pair of accessory glands but a spermatheca is not always present. The *male reproductive organs* are composed of a pair of compact bilobed testes and the slender vasa deferentia either open into a pair of tubular vesiculae seminales (*Pediculus*) or discharge separately from the latter into the ejaculatory duct (*Pthirus*). In *Pediculus* copulation takes place at frequent intervals and this fact is probably related to the absence of a receptaculum in the female and presence of well-developed vesiculae seminales in the male: according to Bacot one male may fertilize 10 to 18 females. The *nervous system* is highly concentrated, the thoracic and abdominal ganglia being fused into a common mass. The majority of Siphunculates possess symbiotic bacteria localized in mycetocytes which may occur separately in the gut-wall or grouped together in a special organ usually rather closely associated with the gut. In mature females the mycetocytes are found only in the ovarial ampullae, from which they pass into the eggs (Ries, 1931).

Postembryonic Development.—Though *Pediculus humanus* often lays its eggs scattered and unattached, the other Siphunculates cement them to the hairs of the host in a manner similar to the Mallophaga. There is an egg-stigma at the posterior end which assists attachment and at the anterior pole is an approximately oval lid pierced by micropylar canals (5–24 in *Pediculus*) and often a group of micropylar chambers ('air cells'). *P. humanus* lays about 300 eggs at the rate of 8–12 daily; *Haematopinus eurysternus* not more than 24 (Craufurd-Benson, 1941). Eclosion (Weber, 1939) is very similar to the same process in the Mallophaga (q.v.). There are three nymphal instars, each usually having a distinctive chaetotaxy. The rate at which development occurs has been investigated for only a few species, e.g. under normal conditions *Haematopinus eurystenus* has an incubation period of 12 days and its nymphal development takes a further 12 days while for *Pediculus humanus* the corresponding figures are 8 and 16–19 days. Sexual maturity is attained after 1–3 days of adult life.

Classification.—Ferris (1919–35; 1951) has monographed the species of the world but the supra-generic classification of the order has not yet been satisfactorily settled. Webb (1946, 1949) has devised a classification based primarily on spiracular structure but it seems desirable that other characters should also be taken into account and the key below is based on the work of Ferris (1951). It should be noted that the limits of the families recognized by this authority differ in important respects from those of earlier workers.

Twenty-four species occur on indigenous or domesticated British mammals, and in addition to Ferris's monographs the keys of Freund (1935), Jancke (1938) and Séguy (1944) may be used to identify the species of N.W. Europe.

Key to Families of Siphunculata

1. Body densely clothed with thick setae, sometimes modified into scales; abdomen never with sclerotized tergal, paratergal or sternal plates; confined to Carnivora Pinnipedia . . . . . ECHINOPHTHIRIIDAE
–. Body less densely clothed with thinner setae, arranged in rows and rarely modified into scales; never parasitic on Carnivora Pinnipedia 2

2. Abdominal paratergal plates absent; abdomen almost invariably membranous except for genital region 3
–. Abdominal paratergal plates present on at least one segment; abdominal tergal and sternal plates frequently present 4

3. Only 1 pair of abdominal spiracles present (on 8th abdominal segment); thoracic sternal plate divided into two . . . . . NEOLINOGNATHIDAE
–. 6 pairs of abdominal spiracles; thoracic sternal plate, if present, entire . LINOGNATHIDAE

4. Abdominal paratergal plates with an apical margin which projects freely from the body; abdominal tergal and sternal plates usually distinct HOPLOPLEURIDAE
–. Paratergal plates without freely projecting apical margin; tergal and sternal plates absent or indistinct 5

5. Abdominal cuticle unwrinkled, membranous except for genital region . . PEDICULIDAE
–. Abdominal cuticle finely wrinkled; indistinct tergal and sternal plates sometimes present . . . . . HAEMATOPINIDAE

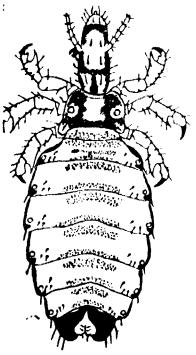


FIG. 329. — Female hog louse (*Haematopinus suis*)

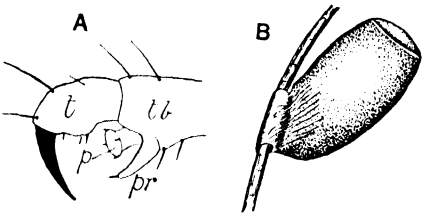


FIG. 330.—*Haematopinus suis*. A, extremity of leg. B, egg attached to a bristle
t, tarsus; *tb*, tibia; *pr*, process of tibia; *p*, tibial pad.

Literature on Siphunculata

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Order 19. **HEMIPTERA** (**Rhynchota:** Plant Bugs, etc.)

Two pairs of wings usually present; the anterior pair most often of harder consistency than the posterior pair, either uniformly so (Homoptera) or with the apical portion more membranous than the remainder (Heteroptera). Mouthparts piercing and suctorial, palpi atrophied; the labium in the form of a dorsally grooved sheath receiving two pairs of bristle-like stylets (modified mandibles and maxillae). Metamorphosis usually gradual, rarely complete.

The Hemiptera or Bugs are most easily recognized by the form of the mouthparts. They are, without exception, sucking insects, and this habit, along with the general structure of the mouthparts, is retained throughout life except in male Coccoidea where the mouthparts of the adult are atrophied. The wings present great variation in structure and for this reason no general definition is sufficiently comprehensive to include them all.

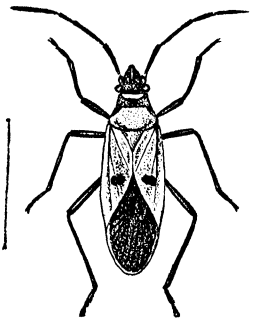


FIG. 331. — *Dysdercus cingulatus*

After Distant in *Fauna of British India.*

As Sharp observes, probably no other order of insects is so directly concerned with the welfare of man on account of the vast amount of direct, and indirect, injury its members entail to vegetation. Among the most destructive species are the Cotton Stainers (*Dysdercus*, Fig. 331), the Chinch-bug (*Blissus leucopterus*), Tea Blight (*Helopeltis*), Leaf-hoppers (Jassidae and related families), White Flies (Aleyrodidae), Plant Lice (Aphidoidea), and the Scale Insects and Mealy Bugs (Coccoidea). Certain Homoptera act as vectors transferring the viruses of such diseases as 'mosaic', 'leaf-roll', 'yellows', etc., from plant to plant by means of their piercing mouthparts. Aphides are the most important in this respect and *Myzus persicae* alone is known to be able to carry the viruses of over 50 separate plant diseases including mosaic and yellows of sugar-beet and leaf-roll of potato. Jassidae are also concerned with the transmission of aster yellows, 'curly-top' of sugar-beet and 'streak' of maize.

An all-important factor bearing upon the devastation entailed by Hemiptera is the extraordinary rapid rate of reproduction found in many members of the suborder Homoptera. The calculations of Réaumur and Huxley regarding the fecundity of parthenogenetic aphides are well known. Buckton, however, regards their conclusions as greatly underestimated, and showed that the progeny of a single aphid at the end of 300 days—if all the members survived—would be the 15th power of 210! With regard to leaf-hoppers Perkins, on the supposition that each hopper lays 50 eggs (and the sexes are about equal), calculates that if there are six generations in the year the undisturbed progeny of one female would amount, at the end of twelve months, to very little less than 500,000,000.

Among certain Heteroptera a propensity for animal food has been acquired, particularly in the predacious families Reduviidae, Nabididae and Anthocoridae and in most Cryptocerata. The Cimicidae, Polyctenidae, and the Reduviid genus *Triatoma* are active blood-suckers of mammals or birds, the habit being prevalent in both sexes.

Hemiptera afford many instances of resemblance to insects of their own and other orders. Certain of the ant-like forms are very remarkable; thus the Coreid *Dulichius inflatus* (brachypterous form) closely resembles and associates with the ant *Polyrachis spiniger*, and is furnished with pronotal and other spines, rather similar to those possessed by the ant. Another Coreid, *Alydus calcaratus*, is often found in England in company with *Formica rufa* and other ants, which its nymph closely resembles. Further cases of resemblance to insects pertaining to other orders are met with in the Reduviidae.

Aquatic Hemiptera afford excellent examples of the relation of structural modifications to differences of environment, particularly with regard to locomotion and respiration (vide Bueno, 1916, and Weber, 1930). In the surface dwellers (Gerroidea) the adaptations are less pronounced, the antennae free and unconcealed, and the legs not highly modified. These insects are clothed with velvety pile to prevent wetting, and respiratory devices are but little complicated. The Cryptocerata, on the other hand, have the antennae concealed, the long antennae of above-water forms obstructing the freedom of motion of submerged insects. The legs are highly adapted for purposes of swimming and respiratory modifications are complex.

External Anatomy

General accounts of the external anatomy of the order are given by Ekblom (1926–30), Weber (1930), Beier (1938), Pesson (1951) and Poisson (1951); see also Kramer (1950).

The **Head.**—The head (J. W. Evans, 1938; Spooner, 1938) is very variable both in form and in the inclination of its longitudinal axis, being porrect in most Heteroptera and usually deflexed in the Homoptera. In almost all cases the sclerites are compactly fused (Fig. 332), a distinct frons being visible only in some Psyllids and, less clearly, in Cicadids where, in both cases, it bears the median ocellus. The clypeus is subdivided, the post-clypeus being a large sclerite, frequently much swollen in the Auchenorrhynchan Homoptera but less conspicuous in the Heteroptera where it extends well back on the dorsal surface of the head and its posterior limits are not recognizable externally. A small ante-clypeus and labrum are also present, the latter often narrow and acuminate. At the sides of the head are two pairs of more or less distinct sclerites associated internally with the bases of the mouthparts: the mandibular plates (sometimes known in the Homoptera as the lora) are probably parts of a modified hypopharynx (q.v.) while the maxillary plates, which are often fused with the genae, arise—at least in part—from the embryonic maxillary rudiments. In all Heteroptera the maxillary plates meet and fuse ventrally to form the gula whereas this latter region remains small and membranous in the Homoptera. The tentorium is absent in Heteroptera and present, though sometimes reduced, in Homoptera. It may be mentioned that the frons and clypeus of many taxonomists are really the post- and anteclypeus respectively. Ocelli are usually present and frequently two in number (Heteroptera, and most Auchenorrhyncha); three are present in Cicadidae, and many Sternorrhyncha. They are wanting in Pyrrhocoridae, Cimicidae,

some Jassidae and most Cryptocerata, etc. In addition to compound eyes, ocular tubercles or supplementary eyes are present in close relation to the

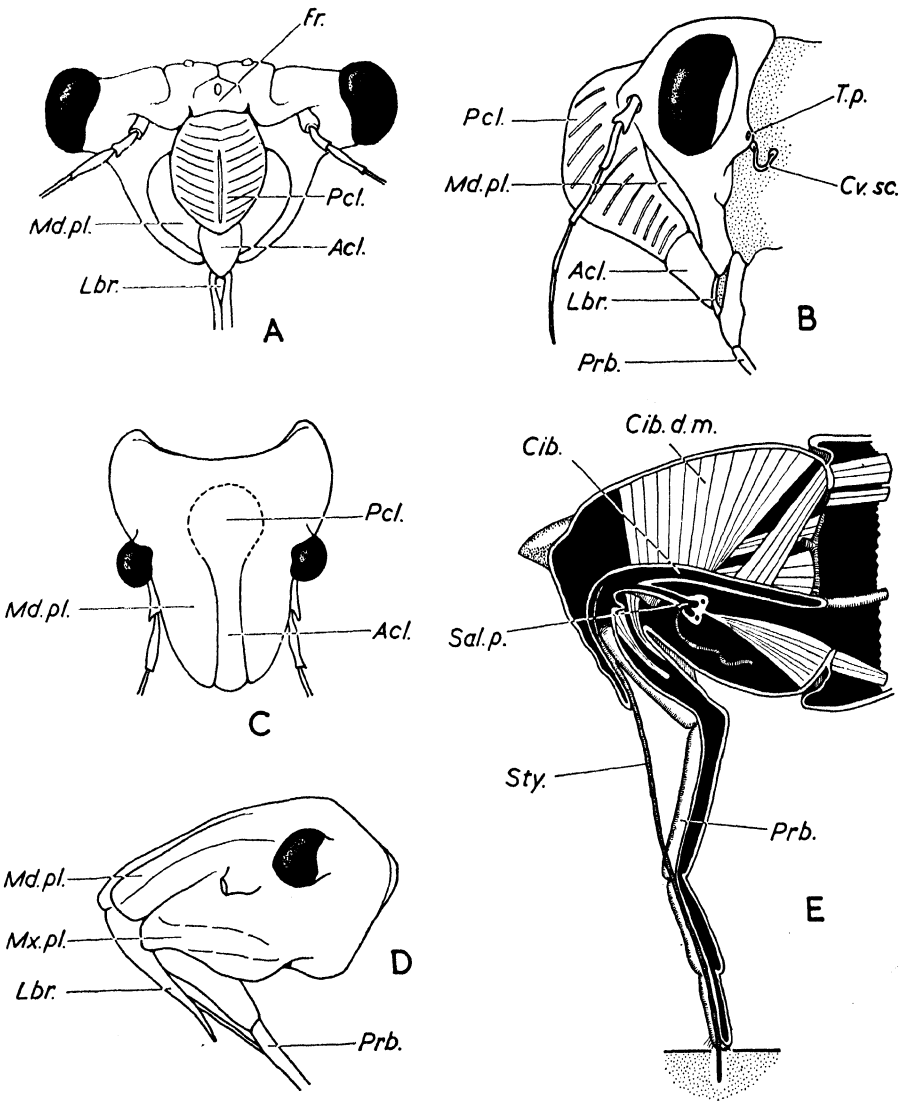


FIG. 332.—Head and mouthparts of Hemiptera. A, B. Frontal and lateral views of *Magicciada septendecim* (*after* Snodgrass, 1935). C, D. The same of a Pentatomid, *Euschistus variolarius* (*after* Snodgrass, 1935). E. Section of head of *Graphosoma italicum*, in feeding position (*after* Weber, 1930)

Acl, anteclypeus; *cib*, cibarium; *Cib.d.m*, cibarial dilator muscles; *Cv.sc*, cervical sclerite; *Fr*, frons; *Lbr.* sbrum; *Md.pl*, mandibular plate; *Mx.pl*, maxillary plate; *Pcl*, postclypeus; *Prb*, proboscis (labium); *Sal. p*, salivary pump; *Sty*, stylets.

former in *Livia* and many aphides. The antennae have few segments, frequently only four or five; their maximum number is attained in the Sternorrhyncha, where 10 segments are found in Psyllids and 25 in the males of a few Coccids.

The **Mouthparts** (Fig. 333).—These organs (Weber, 1928a; Pesson,

1944) are very alike in general structure in the different families, the similarity being correlated with the uniform nature of the feeding habits throughout the order. They are exclusively adapted for piercing and suction, the mandibles and maxillae being modified to form slender bristle-like stylets which rest in the grooved labium. The embryological studies of Newcomer (1948) and earlier workers have demonstrated that the mandibles and maxillae develop quite normally from the first two pairs of postoral embryonic appendages. They subsequently become sunk to some extent within the head, and enclosed at their bases in pockets whose lining is continuous with the general integument. Both pairs of stylets are hollow seta-like structures, capable of limited protrusion and retraction by means of muscular action. In many Homoptera and a few mycetophagous Heteroptera such as the Aradidae the stylets are extremely long and, in some cases, greatly exceed the total length of the insect. In these instances they are capable of being looped or coiled upon themselves, and withdrawn into a pocket connected with the channel of the labium. This pocket takes various forms but in Coccoidea (Fig. 358 A) is lined by thin membrane, is situated between the central nervous system and the ventral body-wall and is known as the crumena.

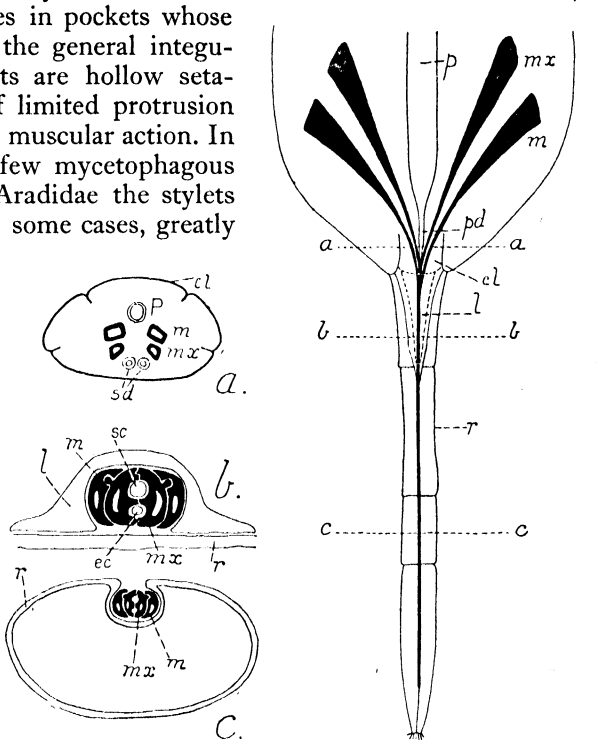


FIG. 333.—Diagram of the mouthparts and adjacent region of the head of an Hemipterous insect

On the left are transverse sections across the regions bearing corresponding lettering; the magnifications of these sections are not uniform. *cl*, clypeus; *ec*, ejection canal with salivary duct; *l*, labrum; *m*, mandible; *mx*, maxilla; *p*, pharynx; *pd*, cibarial pump; *r*, rostrum; *sd*, salivary ducts; *sc*, suction canal with pharyngeal duct.

The mandibular stylets form the anterior (outer) pair and, although usually free, may be closely interlocked with the maxillae as in *Lygus*: at their apices they are usually serrated. The posterior (inner) pair of stylets constitute part of the maxillae: the embryonic rudiments of the latter become bi-segmented at an early stage, and the basal segment thus formed gives rise to the maxillary plate, and the distal part to the maxillary stylet. Maxillary palps are absent. Each maxillary stylet tapers to a fine point and is grooved along its inner aspect: the groove is divided into two parallel channels by means of a longitudinal ridge which traverses the length of stylet. Seen in cross-section, the latter is shaped like a W, and the pair of stylets, by the approximation of their channels, form two extremely fine tubes. The dorsal one functions as the suction canal and communicates with the cibarial sucking pump: the ventral tube is the ejection canal and receives the saliva discharged through the salivary duct. Within the head the maxillary stylets diverge towards their bases, but externally they are closely interlocked, and appear as a

single structure, as in *Anasa* (Tower, 1914), and *Psylla* (Grove, 1919); or the interlocking arrangement is wanting and they are simply apposed to one another (*Eriosoma*). At the enlarged proximal ends of both pairs of stylets are ovoidal areas of tissue known as the *retort-shaped organs*, which are responsible for the secretion of the new stylet which is developed at each nymphal moult. In many Hemiptera the bases of the stylets are attached to the head-capsule by means of mandibular and maxillary levers (Ekblom, 1926–30). These latter are sclerotized rods which extend outwards in a transverse direction, and afford attachment to certain of the stylet muscles. The stylets themselves are enclosed in a sheath (rostrum) formed almost entirely by the labium which is dorsally grooved for their reception. At its base, however, the labial groove is wanting and in this region the sheath is roofed over by the labrum. If the latter be raised with the point of a needle the stylets can be discerned beneath. Distally, the lips of the labial groove are approximated or fused to form a tube and, as the lumen of the latter is very small, the stylets fit tightly therein. In the majority of Hemiptera the labium is either 4-segmented (Pentatomidae, Miridae, Lygaeidae, etc.) or, by reduction of the basal segment, apparently 3-segmented (most Reduviidae, Cicadidae, Psyllidae and Aleyrodidae); in Coccoidea and Corixidae it is always short and 1- or 2-segmented. Its apex is provided with sensory setae and it performs no part in perforating the tissues of the host-plant. Labial palpi are wanting, the so-called palps of Nepidae and Belostomatidae being small, secondary structures. The hypopharynx in Hemiptera is highly specialized. Part of it is visible as a small, well-sclerotized structure lying between the bases of the stylets where its median portion (sitophore) forms part of the floor of the cibarial sucking pump. Laterally, its walls are expanded and lamellate, becoming exposed externally as the mandibular plates. Such a condition is clearly seen in sections through the head of some Homoptera (Snodgrass, 1950), but in the Heteroptera the reduction of the lateral lamellae makes it less easy to see that the mandibular plates are actually part of the hypopharynx. Beneath the hypopharynx lies the salivarium which is modified into a powerful salivary pump, the walls of which are strongly sclerotized and into which runs the salivary duct.

The feeding mechanisms of Hemiptera have been studied by Weber (1928a), Pesson (1944) and others. While at rest the rostrum is concealed by being flexed beneath the body, with its apex directed backwards. When the insect is about to feed, the rostrum is extended from its position of repose and inclined downwards. In the great majority of Hemiptera the stylets are only slightly longer than the rostrum, and consequently some mechanism is necessary by means of which the latter becomes retracted to admit of the insertion of the stylets into the plant. In Aphididae, for example, this is brought about by the proximal portion of the rostrum being withdrawn or telescoped into the body (Davidson). In *Lygus*, and other Heteroptera, the stylets are able to penetrate the tissues owing, it is stated, to the bending or looping of the rostrum about its basal hinge (Awati, 1914). In Coccoidea and some Heteroptera the rostum is very short, and the stylets extremely long, and the mechanism by which the latter are inserted into the plant, and afterwards withdrawn and looped within the body, is as follows. Contraction of the protractor muscles of the stylets forces the latter into the plant for a short distance. They are then held, as in a clamp, by a specially modified muscular region of the labium while the contraction of the retractor muscles and relaxation of the protractors take up a little of the slack in the coiled or

looped stylets, thus preventing their withdrawal. The protractors then begin a repetition of the cycle so that by degrees the stylets are forced deeper and deeper into the plant. It seems probable that all four stylets are not protracted simultaneously but that the mandibles are first pushed in one after the other, followed by the maxillae. The path of the stylets in the plant has been traced in aphides and Jassids by several workers (e.g. Smith & Poos, 1931; Dykstra & Whittaker, 1938). Most of these insects feed upon the contents of phloem vessels and reach this tissue by a path which is mainly intercellular in aphides, but often passes through cortical cells in the leaf-hoppers. Once penetration has started, saliva is injected into the plant by the salivary pump and this reacts with the plant sap to form a tubular sheath, of uncertain function, around the stylets. It is also probable that enzymes in the saliva initiate extra-intestinal digestion, though only an amylase seems to have been detected so far (Davidson, 1923). The withdrawal of sap into the alimentary canal of the feeding insect is usually said to occur through the activity of the cibarial sucking pump which is provided with powerful dilator muscles arising on the post-clypeus. The physics of this process do not seem to have been investigated and it is possible that capillarity and the turgor pressure of the pierced plant cells may also play some role in the ascent of liquid through the feeding canal.

The **Thorax.**—The morphology of the hemipterous thorax has not been extensively investigated, but a comparison of a number of genera has been made by Taylor (1918) while Larsén (1945; 1945a) has studied many Heteroptera (see also Weber, 1928; 1929; 1935). Among Heteroptera the pronotum is tolerably uniform in its characters: it is always large, rarely marked off into separate sclerites, and forms the greater part of the thorax when viewed from above. The mesonotum frequently exhibits a five-fold division, thus presenting the maximum number of sclerites. Of these the most prominent is the scutellum, which is always well developed: in certain Pentatomoidea it extends posteriorly to the extent of entirely covering the wings, and imparts to the insect an apterous appearance. The metanotum is very variable: it may be well developed, as in *Anasa*, or reduced to a small region concealed beneath the mesoscutellum. It is never conspicuous, and is covered by the unexpanded wings. The sternites are, for the most part, fused with the respective pleura.

Among Homoptera there is more diversity of structure, though the Cicadidae may be regarded as fairly typical of the suborder. The pronotum is almost always small and frequently collar-like, except in Membracidae where it assumes incredibly bizarre and grotesque forms and extends backwards over the abdomen. The mesothorax is the largest and most typical region, exhibiting the primary divisions into prescutum, scutum, scutellum and postnotum. In almost all Fulgoridea it bears well-developed tegulae, which are vestigial or absent in these species with reduced wings. The metanotum is usually well developed, and in Jassidae it is nearly as long as the mesonotum.

The **Wings.**—Among Heteroptera there is a marked difference in the consistency of the two pairs of *wings*, as is implied by the name of that suborder. The fore wings are termed hemelytra (*hemi-elytra*) and their proximal area is well sclerotized, resembling an elytron, only the smaller distal portion remaining membranous. The hind wings are always membranous and, in repose, are folded beneath the hemelytra.

The hemelytra (Fig. 334) exhibit much diversity of structure and, for this reason, have been largely utilized for purposes of classification. The

hardened basal portion is composed of two regions separated by a concave vein, Cu_2—the *clavus* or narrower area next to the scutellum (when the wings are closed), and the *corium* or remaining broader portion. In the families Ceratocombidae and Anthocoridae a narrow strip of the corium, bordering on the costa, is demarcated from the remainder by R + M, and is known as the *embolium*. In the Miridae and Velocipedidae a triangular apical portion of the corium is separately differentiated to form the *cuneus*. Among Tingidae and some Gerroidea the differentiation into corneous and membranous regions is less distinct. In some cases the membranous area is much reduced or wholly absorbed, but in the Henicocephalidae the hemelytra are entirely membranous. The two pairs of wings exhibit evident departures from the primitive venational type (Tillyard, 1918; Hoke, 1926; China & Myers, 1929).

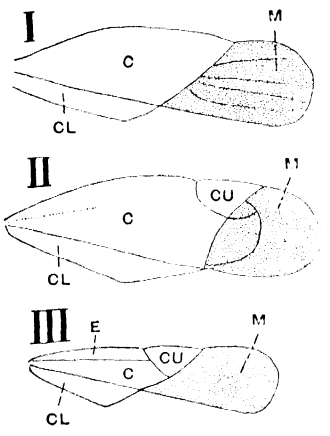


FIG. 334.—Diagrams of the hemelytra of—I, a Lygaeid; II, a Mirid; III, an Anthocorid

C, corium; *CL*, clavus; *CU*, cuneus; *E*, embolium; *M*, membrane.

Among Homoptera the fore wings are of uniform texture (Fig. 336) and are frequently of harder consistency than the hind pair. Apterous forms are the rule in female Coccoidea and Aphidoidea (sexuales), as well as occurring in some parthenogenetic forms of the latter group; both apterous and alate males are sometimes present in both Aphidoidea and Coccoidea. Although there is great diversity of venation which is dealt with under the different families, the occurrence of fossil forms (Tillyard, 1926) and the pre-existent tracheae in the nymph have made it possible to determine the homologies of the wing-veins (Tanaka, 1926).

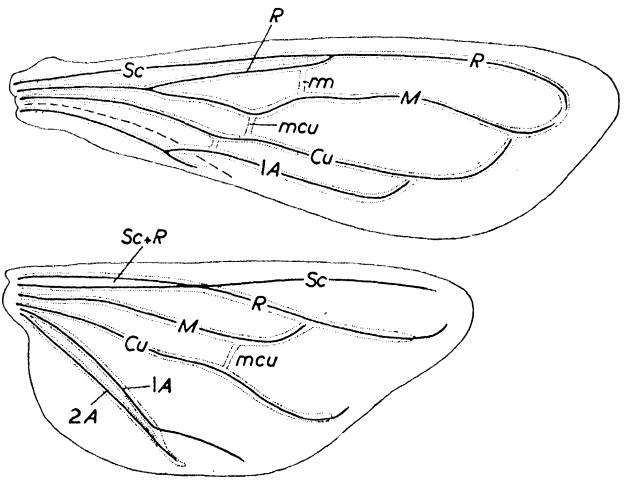


FIG. 335.—Venation (dotted lines) and tracheation (full lines) of wings of *Triatoma* (*after* Usinger)

The little-understood phenomenon of alary polymorphism is prevalent in different families. That is to say, in the same species there may be two or more forms of alary organs which, furthermore, may be correlated with sex or may not. There are two well-marked types of individuals—the apterous and macropterous, sometimes with intermediates or brachypterous forms. The phenomenon is evident, for example, in the Gerroidea (Larsén, 1931), Anthocoridae and Reduviidae among Heteroptera, and certain Fulgoroidea

(Delphacidae) and Jassidae among Homoptera. In *Perkinsiella* (Delphacidae) there is much specific variation in this respect: thus *P. saccharicida* has macropterous males and polymorphic females, while in *P. vitiensis* and *vastatrix* both sexes are dimorphic.

In certain African Reduviidae (*Edocla*) the males are winged and the females apterous and physogastric: in other species of the genus both sexes are alike and physogastric. In *Paredocla*, there are both winged and apterous males; the latter resemble the females, which are also apterous, and all forms are found together (Jeannel, 1919).

Many explanations have been advanced to account for alary polymorphism (Kirkaldy, 1906). It has been variously correlated with climate, season, mimicry, capability for leaping or rapid locomotion, and mode of life, whether arboreal or otherwise. Thus, in Africa, Jeannel states that most of the apterous and brachypterous genera of Reduviidae inhabit the hotter regions. In the European *Pyrrhocoris apterus* both pairs of wings may be either normally developed, or reduced to merely the sclerotized basal portions of the hemelytra, and the two forms vary very greatly both in local and seasonal occurrence. The phenomenon offers a wide field for research, particularly from the genetic point of view.

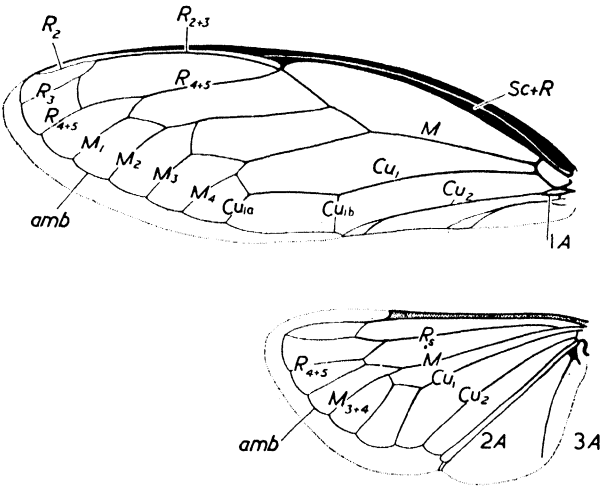


FIG. 336.—Wing-venation of *Cicada orni* (*after* Silvestri, 1934, with Tillyard's nomenclature)
amb, ambient vein.

The **Abdomen.**—In its least modified condition, as in many Auchenorrhynchan Homoptera, 11 segments are present though the first two may be modified in connexion with sound-producing organs (Cicadidae), the 8th and 9th undergo changes due to the development of external genitalia and the 10th and 11th are small annuli at the end of which the anus opens. Reduction of the number of well-defined segments is frequent. Thus, among the Homoptera, Crawford (1914) finds that the first three are suppressed or greatly reduced in Psyllidae while in Aphidoidea and female Coccoidea (Ferris, 1951)—where segmentation is often obscure—not more than 9 segments can be recognized. In the Heteroptera, the 10th and 11th segments are fused together and the first one or two may be reduced or absent. Cerci are never found in the Hemiptera.

The ovipositor is exhibited in a complete condition in many Auchenorrhynchan Homoptera (Snodgrass, 1933: Müller, 1942) where it consists primitively of a pair of valves, each articulating with a small basal sclerite, on the 8th sternum, another similar pair on the 9th sternum and a third pair, softer, sheath-like and more dorsal in position, also developed from the 9th sternum. Their homologies seem to be similar to those of the

corresponding valves of such Saltatorial Orthoptera as the Tettigoniidae (q.v.). Some Heteroptera, particularly those which insert their eggs into plant tissues, retain a similar, well-developed ovipositor, but other members of this sub-order have a smaller structure made up of only two pairs of valves, while some Sternorrhyncha (Aphidoidea and Coccoidea) have no ovipositor.

The morphology of the male external genitalia has been discussed by Singh-Pruthi (1925) but the homologies of some of the structures are undecided (Qadri, 1949; Marks, 1951). The most primitive condition occurs in the Auchenorrhyncha and the Heteroptera where the enlarged 9th sternum carries a pair of lateral claspers (probably the modified coxites and styles of this segment) while the membrane between the 9th and 10th sterna is invaginated to form a genital cavity in which are found a median penis and a pair of parameres. In the Sternorrhyncha the claspers alone (Psyllidae, Aleyrodidae) or both claspers and parameres (Aphidoidea, Coccoidea) are absent.

Sound-producing Organs are of frequent occurrence among Heteroptera and five important types will be mentioned (see also Leston, 1954).

(1) The PROSTERNAL FURROW of many Reduviidae and Phymatidae studied by Handlirsch (1900). This furrow is cross-striated and stridulation is produced by the rugose apex of the rostrum working thereon; it is well seen in *Reduvius personatus* and *Coranus subapterus*.

(2) The STRIGOSE VENTRAL AREAS of certain Pentatomidae (Scutellerinae). According to Handlirsch these are found on either side of the median line of the apparent 4th and 5th abdominal sterna. On the inner side of the hind tibiae are wart-like tubercles, each bearing a subapical tooth. When the insect bends the tibia against the femur, and again extends it, the spinous tubercles pass across the strigose areas, thus enabling the insect by rapidly repeating the movements to produce an audible sound.

(3) The PEDAL STRIDULATING ORGANS of Corixidae. The males of some Corixidae produce sounds when a spinose area on the inside of each front femur is drawn over the edge of the clypeus (Mitis, 1935). The pala is not a stridulatory organ, nor has it been shown conclusively that the peculiar strigil of these insects is concerned with sound production.

(4) COXAL STRIDULATORY ORGANS. In *Ranatra* Bueno (1905) describes two opposing rasps, one on each coxa near the base with longitudinal striations, the other on the inner surface of the cephalic margin of the lateral plate of the coxal cavity. The latter plate is exceptionally thin and probably functions as a resonating organ.

(5) The DORSAL STRIDULATORY ORGANS which are found in both sexes of *Tessaratoma papillosa* (Pentatomidae). The sound-producing organ consists of a striated surface or file situated one on either side of the dorsum of the abdomen close to the metathorax. On the under-surface of each wing, near the base, is a comb of strong teeth. The sclerite supporting the files is able to move backwards and forwards across the comb (Muir, 1907).

Among Homoptera, the sound-producing organs of the Cicadidae are complex structures peculiar to the family, and situated one on either side of the ventral aspect of the base of the abdomen (vide p. 117). The remaining Auchenorrhyncha are usually regarded as being silent, but Ossiannilsson (1949) has shown that several leaf-hoppers possess the power of very quiet stridulation, the organs concerned being homologues of those found in the Cicadidae.

Spiracles.—According to Schiödte 10 pairs of spiracles are normally present in Heteroptera, and this conclusion is confirmed by Handlirsch (1900a). They are present on the following segments: 1st pair, on the membrane between the pro- and mesothorax, and only to be observed with difficulty: 2nd pair, between the meso- and metathorax; 3rd pair, dorsal, lying between the metanotum and 1st abdominal tergum, hidden by the wings:

4th and following pairs, on the ventral (or, occasionally, dorsal) side of the pleural folds of the consecutive abdominal segments. This general rule is subject to modification particularly in aquatic families. Thus in *Nepa* there are 10 pairs of open spiracles in the nymph, but in the adult most of these are either closed or non-functional. Maulik (1916) regards the first three pairs as being functional although closed; the only other functional pair is at the base of the respiratory siphon. The 4th, 5th and 9th pairs have atrophied and the 6th, 7th and 8th are highly modified sieve-like structures which are regarded by Dogs, and also Baunacke (1912), as being modified into sensory organs. The spiracles of *Notonecta* have been investigated by Brocher (1909), who states that there are 9 pairs. The anatomy of the Heteropteran spiracle has been studied by Mammen (1912).

In the Auchenorrhyncha there are 10 pairs of spiracles as a general rule, but among the Sternorrhyncha there is a wide range of variation. In Aphididae there are usually 9 pairs, situated respectively on the pro- and metathorax and on the first 7 abdominal segments. Among Psyllidae Witlaczil (1885) finds 2 thoracic and 7 abdominal spiracles in the nymph of *Trioza*, while in the adult *Psylla mali* Awati (1915) states there are 2 thoracic and 3 abdominal pairs. In the Aleyrodidae the nymphs are closely applied to the leaf surface, and as the spiracles lie ventrally they are concealed. Air is conveyed thereto by means of special breathing folds of the integument. Two pairs of thoracic spiracles are present,—one pair between the anterior legs and the other pair between the posterior legs. Spiracles are also present behind the 2nd thoracic pair apparently on the 1st abdominal segment, and a 4th pair exists alongside the vasiform orifice. Vestigial spiracles are apparently found in some genera on other of the abdominal segments. In the adult the distribution of the spiracles is very much the same as in the nymph. The respiratory system of both Psyllidae and Aleyrodidae, however, requires detailed investigation.

In the nymphs and females of the Coccoidea there are commonly 2 pairs of spiracles on the ventral aspect of the thorax; abdominal spiracles are present, however, in certain groups (Ferris, 1918). The primitive number of 2 thoracic and 8 abdominal pairs is found in *Xylococcus* (Oguma, 1919); in *Orthezia* (List, 1886) and *Monophlebus* (Savage) there is one pair less on the abdomen. In *Icerya purchasi* the abdominal spiracles are reduced to 2 pairs, and in certain other species of that genus there are at least 3 pairs present (Ferris).

Internal Anatomy

The **Alimentary Canal.**—The entrance to the alimentary canal is the aperture of the cibarial sucking pump (Weber, 1928a; 1930; Snodgrass, 1935) which is situated at the base of the maxillary stylets. The walls of this tubular pump are strongly sclerotized and dilator muscles run from it to the post-clypeus. In the region of the epipharyngeal surface of the labrum there is, in most Hemiptera, a gustatory organ whose sensory cells communicate with the lumen of the cibarium through perforations in a sclerotized plate, which is a specialized development of the epipharyngeal membrane. The cibarial pump is followed by a small pharynx, the dilator muscles of which are attached to the frontal region of the head and the pharynx, in turn, communicates by a short oesophagus with the mid gut. The latter is modified considerably, but in different directions in the two suborders.

In Heteroptera the mid gut is frequently divisible into four sharply

differentiated tracts (Fig. 337): (1) An anterior sac-like chamber; (2) a tubular region; (3) an ovoid chamber smaller than the first; (4) a narrow tubular portion from which, in many families, numerous gastric caeca take their origin. In certain of the strictly predacious groups these divisions are less evident, and the tubular 4th region is absent in those families which lack the gastric caeca. The hind intestine is very contracted and consists of a small bladder-like chamber, which receives the Malpighian tubes, and a very large rectal chamber, often much more extensive than the 1st division of the mid gut and possessing one or two ampulla-like diverticula in the Cryptocerata. The remarkable

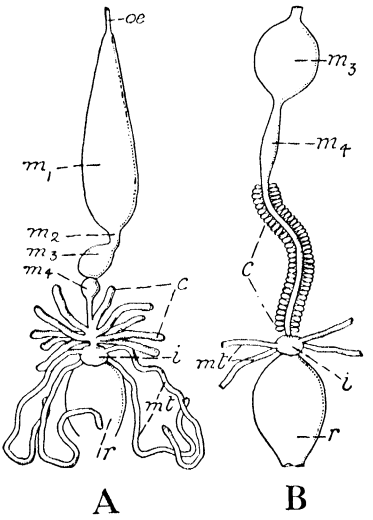


FIG. 337.—Digestive system of Lygaeidae. A, *Blissus leucopterus*. B, *Oedancala dorsalis* (posterior portion only)

c, gastric caeca; *i*, ileum; m_1–m_4, chambers of mid intestine; *mt*, Malpighian tubes; *oe*, oesophagus; *r*, rectum. *After* Glasgow (reduced).

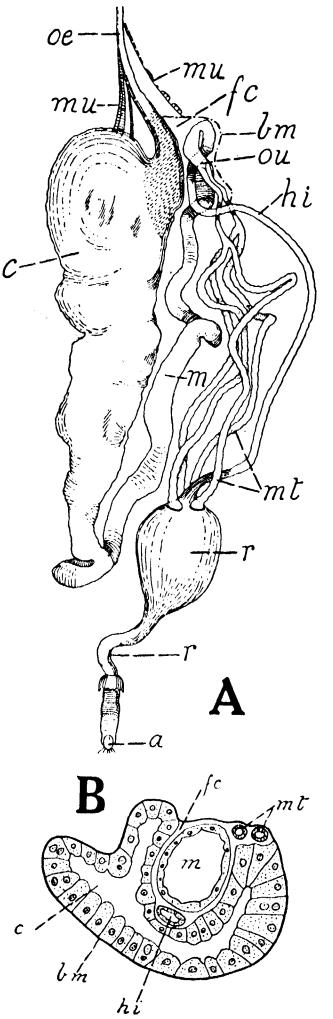


FIG. 338.—A, Digestive system of a Membracid (*Tricentrus albomaculatus*). B, Transverse section taken just below line *ou* in A

a, anus; *bm*, basement membrane; *c*, crop-like dilation of mid gut; *fc*, filter chamber; *hi*, hind intestine; *m*, mid intestine; *mt*, Malpighian tubes; *mu*, muscles; *oe*, oesophagus; *ou*, point of origin of Malpighian tubes; *r*, rectum. *After* Kershaw.

gastric caeca have been studied by Glasgow (1914), and they present many variations in form, number and arrangement. In *Blissus leucopterus* there are 10 finger-like caeca present, in *Anasa tristis* there are several hundreds in the form of closely compacted pockets, while in *Dysdercus* they are few in number (six in the male and none in the female). The caeca are invariably filled with bacteria and, furthermore, the association is hereditary, the organisms being present in the gut of the developing embryo. Their function is uncertain but may be that of inhibiting the growth of foreign bacteria, and so excluding the latter from the mid gut. A remarkable feature occurs in the alimentary canal of a few Heteroptera (e.g. the Lygaeid *Ischno-*

demus sabuleti and some Plataspididae): the mid gut is either closed anteriorly through the obliteration of its lumen and the reduction of its walls to a thin strand or it ends blindly and separate from the hind gut which receives the Malpighian tubules. In the males of *Coptosoma*, both interruptions of the gut are found (Schneider, 1940).

Among many Homoptera the oesophagus leads into a very capacious crop-like distension of the mid gut which occupies a large part of the abdominal cavity. The remainder of the mid gut is long and tubular and reflected on the first part in an ascending manner, with the result that its junction with the hind intestine comes to lie very far forwards alongside the oesophagus (Fig. 338). Owing to this disposition, the insertions of the Malpighian tubes are likewise anteriorly situated, and these organs, together with the mid gut and the hind intestine, form a complex coil of tubes lying in the thorax (Kershaw, 1914). In the Membracid *Tricentrus albomaculatus*, Kershaw (1913) states that the basement membrane, and the external muscles of the crop and of the base of the oesophagus, separate from the epithelial walls of those parts, and enclose the twisted knot formed by the above visceral complex. The result is that the latter comes to lie in a chamber bounded externally by the basement membrane. A similar arrangement of the viscera is found in Cercopidae (Licent, 1912) and in the Sternorrhyncha (Weber, 1930; 1935). The chamber or cavity thus formed is termed by Berlese the *filter chamber*. This authority suggests that, owing to the large surface presented by the mid gut, where it is applied to the wall of the oesophagus and crop, the excess of liquid in the food will pass directly by osmosis through the intervening walls to the mid gut, and thence through the wall of the latter into the hind intestine. In this manner liquid is quickly eliminated, while solid matter passes by the usual course through the whole digestive system. There is no filter chamber in the Coleorrhyncha, Fulgoroidea, Jassidae and some aphides.

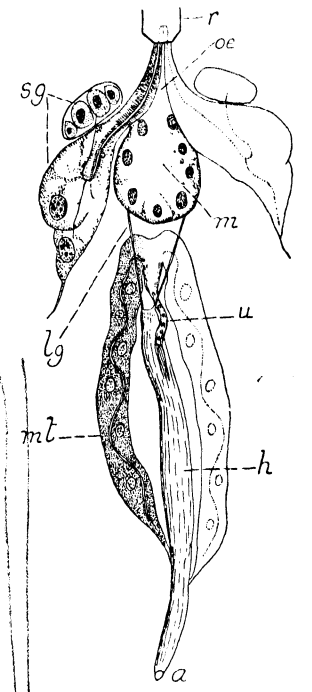


FIG. 339.—Digestive system of *Lepidosaphes fulva* × 80

lg, ligament; *oe*, oesophagus; *r*, rostrum; *sg*, salivary glands; *u*, ureter. Other lettering as in Fig. 338. *After* Berlese, *Riv. di Pat. Veg.*, 5.

In the Diaspididae the mid gut is a closed sac (Fig. 339), devoid of a functional connexion with the hind intestine, and the digestive juices render the food-contents capable of passing by osmosis into the main haemocoelic cavity. The waste substances therefrom are then taken up by the greatly enlarged Malpighian tubes (Berlese, 1893–96). (See also Pesson, 1942.)

The prevalent number of *Malpighian tubes* in Heteroptera is 4, but in *Lethocerus* there are 2 (Locy, 1884). Among Homoptera they are more variable; thus, in Membracidae there are 4 united proximally in pairs (Kershaw, 1913), and the same number is present in *Cicada*. Among Coccoidea there are generally 2 tubes of very large calibre and but little convoluted, but in *Icerya* there are 3 (Johnston, 1912) and in *Xylococcus* 4 (Oguma, 1919). Among Aphidoidea Malpighian tubes are absent.

Salivary Glands.—These organs exhibit a marked uniformity of structure

among Heteroptera, and have been very fully investigated by Baptist (1941) and earlier workers. The principal gland (Fig. 340) is ordinarily bi- or multilobed and situated in the thorax; the accessory gland is most often filiform. The main salivary duct arises at the point of junction of the lobes of the principal gland and, in the same region, it receives the long sinuous duct of the accessory gland of its side. The two main ducts of opposite sides converge to form a common canal opening into the *salivary pump*. In the zoophagous forms (*Harpactor*, *Reduvius personatus* and the Cryptocerata) the accessory gland is thin-walled and modified to form a reservoir. In some forms (*Naucoris*) the principal gland is very large and may extend into the abdomen.

In *Fulgora* there are three pairs of glands corresponding to the anterior and posterior lobes of the principal gland and the accessory gland of Heteroptera. In *Cicada* there are likewise three pairs of glands. Among aphides 2 pairs of simple sac-like glands are located in the prothorax in *Eriosoma* and *Lachnus*; in *Viteus vitifolii* and *Adelges lapponicus* 3 pairs have been described. Among Coccids the glands are bilobed in *Lepidosaphes* and *Xylococcus*; in *Icerya* each gland is reduced to 3 multinucleate spherical cells (Johnston, 1912).

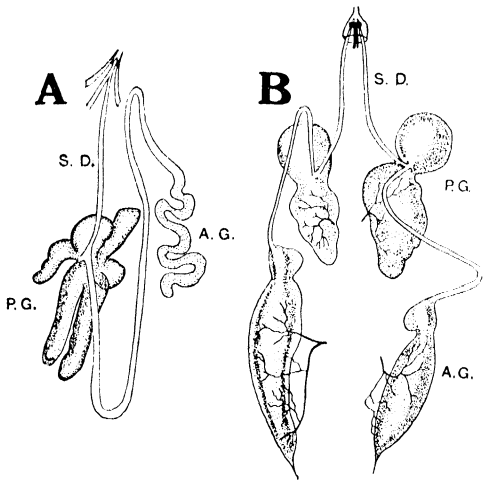


FIG. 340.—Salivary glands of A, *Lygaeus apuans*: B, *Notonecta maculata*

SD, salivary duct; *AG*, accessory gland; *PG*, principal gland. *After* Bugnion, 1908 (reduced).

The *salivary pump* or 'syringe' has been mentioned in connexion with the feeding mechanism.

Odoriferous Glands.—Odoriferous or repugnatorial glands are characteristic of a large number of Heteroptera, and open to the exterior by means of a pair of ventral pores or slits situated near the coxae of the hind legs. Each opening is surrounded by an evaporating surface, which retains the secretion while it volatilizes and prevents its more extended diffusion: the surface of this area is usually finely rugose or granulated (see p. 172).

In *Lethocerus* the glands form a pair of convoluted tubes and their odour is said to resemble that of ripe pears or bananas (Locy, 1884): very similar glands have been found by Bordas (1905) in *Gerris*. In the nymphs the metathoracic glands are wanting, their place being taken in some families by dorsal abdominal glands which assume the form of small integumentary invaginations (Gulde, 1902; see also p. 172).

Wax Glands.—These are prevalent in many Homoptera. They are usually unicellular (though multicellular wax glands are frequent in female Coccoidea) and may occur either singly or in groups (vide p. 169). They are well exhibited in the oriental *Phromnia marginella*, where they are situated beneath series of sclerotized plates on the dorsum of the abdomen: each plate is studded with pores which are the apertures of the wax glands. In various Aphidoidea (*Pemphigus*, *Adelges*, *Eriosoma*, *Lachnus*, etc.) the plates are segmentally

arranged in longitudinal series. The product of the glands is commonly in the form of a powdery secretion, or of dense flocculent threads.

The **Nervous System** (Brandt, 1879; Pflugfelder, 1937) exhibits a very uniform and complete degree of concentration. The abdominal ganglia are to a large extent fused up with the thoracic, though the connectives persist as the main single or paired abdominal nerve which gives off lateral segmental branches. Various degrees of concentration are recognizable in the ventral ganglia.

(1) Three ventral ganglia present (*Lygaeus*, *Capsus*, *Notonecta*, *Aphrophora*, etc.). The suboesophageal and 1st thoracic ganglia are separate, while the abdominal ganglia are fused with those of the 2nd and 3rd thoracic segments to form a common centre.

(2) Two ventral ganglia present (Aphididae). The first is the suboesophageal ganglion, while the thoracic and abdominal ganglia are merged into a common centre. In the Nepidae the prothoracic and suboesophageal ganglia are apparently fused since the nerves supplying the first pair of legs issue from the latter centre.

(3) A single ganglionic centre formed by the coalescence of all the ventral ganglia (*Hydrometra* and Coccoidea).

The **Dorsal Vessel** has been very little investigated: a 5-chambered heart is present in *Lethocerus* (Locy), and other Heteroptera have 4 or 5 chambers and 3 or 4 pairs of ostioles. A well-developed heart is found in the Auchenorrhyncha and Psyllidae and may extend over 6 or 7 segments. In other Sternorrhyncha it is usually smaller and posterior in position and is apparently absent in some aphides (*Phylloxera*, *Eriosoma*), and some Coccoidea (Diaspididae).

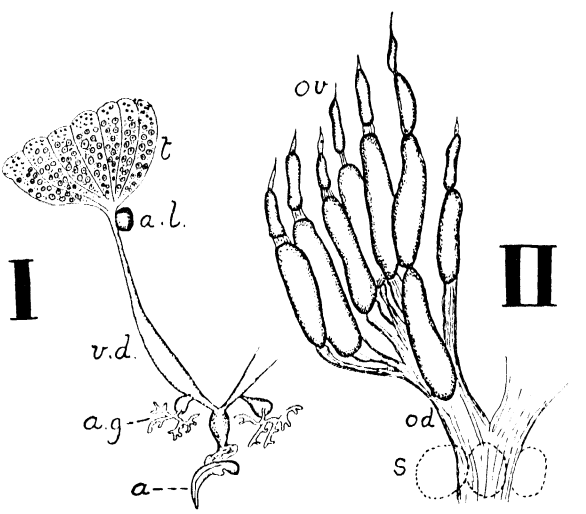


FIG. 341.—Reproductive organs (right side only) of *Cimex rotundatus*. I, male; II, female

a, aedeagus; *a.g*, accessory gland; *a.l*, accessory lobe of testis; *od*, oviduct; *ov*, ovary; *s*, spermathecae; *t*, testis; *vd*, vas deferens. Adapted from Patton & Cragg.

Pulsatile Organs occur in various aquatic Heteroptera and some terrestrial ones. They are present in each pair of legs and, owing to the opacity of the integument, are best observed in the nymphs. Brocher (1909a) has studied these organs among Cryptocerata: they are present at the base of the 1st tarsal segment of the anterior legs, and at the base of tibia in the other pairs. In *Ranatra* each organ consists of a pulsatile membrane lying longitudinally in the cavity of the limb; it serves to ensure the circulation of the blood in the extremities. Pulsatile organs are also present in the tibiae of *Philaenus* (Gahan) and in aphides (Richardson).

Reproductive System (Figs. 341, 342).—Each ovary has a variable number of ovarioles which are composed of a small number of follicles (usually 1 to 4). In structure the ovarioles are commonly of the acrotrophic type, but their histology has not been extensively studied in this order: in

certain Heteroptera protoplasmic cords connect the nutritive cells with the developing oocytes. In this suborder the ovarioles are few in number, generally 7 but sometimes 4 or 5 (Woodward, 1950). Holmgren (1899) figures the reproductive system of certain Auchenorrhyncha and the ovarioles varied in the examples studied from 3 in *Eupteryx* to 9 in *Philaenus*. Among Sternorrhyncha there are 8 or 9 very short ovarioles in *Psylla mali* (Awati, 1915), but in *P. alni* there are 40–50 (Witlaczil, 1885). In Coccoidea they are numerous, each consisting of a single follicle arising from a wide oviduct; in *Icerya* (Johnston, 1912), the oviducts are united anteriorly, forming a broad loop. In Aphidoidea the number of ovarioles varies in individuals of the same species, and different phases of the life-cycle. Thus, in *Viteus vitifolii*, in the apterous parthenogenetic forms they vary from one or two to thirty according to conditions (Foa, 1912), each containing two follicles; in the alate females there are usually two, and in the sexuales of this species and also *Eriosoma lanigerum* (Baker, 1915) there is a single unpaired unilocular ovariole. Spermathecae are very generally present among Hemiptera: in *Triatoma* they are small and paired, but there is usually a single dorsal or ventral organ, often of complex structure. Accessory glands, two or three in number and either tubular or globose, are of general occurrence, but are wanting in the Diaspididae (Berlese, 1893–96).

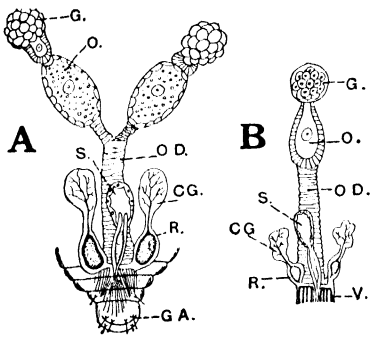


FIG. 342.—Female reproductive organs of *Viteus vitifolii*

A, of winged agamic form: B, of sexual form. *CG*, colleterial gland and reservoir *R*; *G*, germarium; *GA*, genital aperture; *O*, ovum; *OD*, common oviduct; *S*, spermatheca; *V*, vagina. *After* Balbiani.

In *Cimex* there is a small rounded body, known as the organ of Berlese, which is situated in the ventral region of the abdomen (vide Abraham, 1934). It is unpaired and lies on the right side, its external opening being in close association with a small longitudinal incision on the posterior edge of the 4th sternum. The organ functions as a copulatory pouch which receives the spermatozoa discharged during coition. After the latter process is accomplished the spermatozoa pass in large masses through the haemocoele into the spermathecae. The latter organs are stated to be unconnected with the common oviduct and it appears that the spermatozoa migrate from the spermathecae through the walls of the paired oviduct in order to reach the eggs. It is probable that the excess spermatozoa are utilized by the female as nutriment during oviposition—a process which is termed by Berlese 'hypergamesis' and which involves the absorption of the surplus spermatozoa by specialized mesodermal cells of the female. This unusual method of fecundation appears to occur in other Cimicids, though the position of Berlese's organ varies (Jordan, 1922). More recently Carayon (1952) has found an organ of Berlese in *Xylocoris* (Anthocoridae) while in *Lyctocoris* and the Nabidids *Prostemma* and *Alloeorhynchus* the spermatozoa pass from the vagina into the haemocoele before entering the oviducts for fertilization (Carayon, 1950). Spermatozoa have also been found in the haemocoele of the Polyctenid *Hesperoctenes* (Hagan, 1931).

The male organs are very variable. In the Heteroptera each of the paired testes usually comprises 7 follicles, but deviations from this number are not uncommon (Woodward, 1950), *Ranatra fusca*, for instance, having 6 follicles enclosed in a scrotum. The vasa deferentia are usually swollen at some point to form seminal vesicles and most Heteroptera possess 1 or more pairs of variously shaped accessory glands. Each testis in the Homoptera may consist of only a single follicle (Coccoidea) but more usually of a small number (e.g. 4 or 5 in Psyllidae) which may be free or united in a common sheath.

Accessory glands are present and in Psyllidae and Aleyrodidae part of the ductus ejaculatorius is modified to form a sperm pump.

The **Mycetome.**—Most Homoptera (some Typhlocybine Jassids are a notable exception) harbour allegedly symbiotic bacteria or yeasts which are most frequently confined to specialized cells, the mycetocytes. These cells may occur scattered in the gut-wall or fat-body (e.g. some Coccoidea) but more often are grouped into definite organs known as mycetomes. The latter vary greatly in size and position according to the insect and are sometimes very conspicuous structures. The physiological relations between insect and micro-organism have not been adequately studied but in many cases it is known that symbionts in female insects migrate into the maturing egg and are thus transmitted to the offspring. Apart from the intra-cellular symbionts of the alimentary canal, mycetomes harbouring comparable micro-organisms are reported for some Heteroptera. There is a large literature on these topics: see especially Uichanco (1924), Buchner (1953), Walczuch (1932), Profft (1937), Müller (1940; 1949) and Rau (1943).

Metamorphoses

The eggs of Heteroptera (Fig. 343) exhibit great diversity of form, chorionic structure, and colouring (vide Heidemann, 1911; Poisson, 1933; Michalk, 1935). The various types are peculiarly constant for different families and, when further studied, will evidently afford characters of classificatory value. Many are adorned with delicate sculpturing and spines or filiform appendages. In several families (Pentatomidae, Coreidae, Reduviidae, Phymatidae, Cimicidae, etc.) there is a conspicuous operculum (Fig. 364), often of complex structure, which is usually liberated at the time of hatching. At the upper pole of the egg, notably among Pentatomidae, Tingidae, and Reduviidae, there is a circlet of peculiarly shaped chorionic processes disposed around the rim of the operculum. These were originally termed by Leuckart 'seminal cups' from the belief that they afforded a means by which the spermatozoa entered the egg: by certain more recent observers they are regarded as also forming a mechanism to ensure the access of air to the interior of the egg (see Wigglesworth & Beament, 1950). A T-shaped denticle, or egg-burster, is present in the newly hatched nymphs of Pentatomidae and Coreidae; it is cast during the first moult, before the insect completely issues from the egg, and is usually found adhering to the empty chorion.

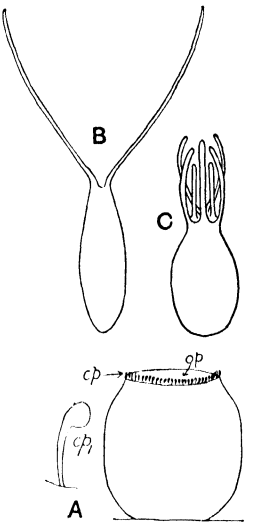


FIG. 343.—Eggs of Heteroptera

A, a Pentatomid, *Euschistus* (*after* Heidemann). B, *Ranatra* and C, *Nepa* (*after* Schouteden). *op*, operculum; *cp*, chorionic processes; cp_1, one of the latter more enlarged.

Among the Homoptera the eggs, as a general rule, are ovoid and of much simpler structure: in the Aleyrodidae and *Psylla*, however, they are often provided with a filamentous prolongation at one pole (p. 188): an egg-burster is present in aphides. Viviparity occurs in the Polyctenidae (Hagan, 1931) and among parthenogenetic forms in the Aphidoidea, while all stages from oviparity through ovoviviparity to viviparity occur in the Coccoidea.

Postembryonic development in Hemiptera is gradual, but colour changes are often very marked. The most sharply pronounced modifications are concentrated in the last ecdysis from the final nymph to the imago. The external morphological changes during development involve the segments of the antennae and tarsi, the latter frequently not attaining their full number

until the adult instar. The shape of the head and thoracic segments, more particularly the pronotum, undergo marked changes in different instars. Wing-rudiments are small or scarcely distinguishable in the 3rd instar but are evident in the 4th. Among Heteroptera the usual number of instars (including the adult) is 6; *Dindymus sanguineus*, however, is exceptional in passing through 9 instars (Muir and Kershaw).

In Homoptera the number of instars is subject to great variation; in *Psylla* and *Empoasca* there are 6, in aphides 5 except in the apterous Phylloxeridae, where there are 4, and the latter number is recorded in Aleyrodidae. The highest observed number is 7 (in *Magicicada septendecim*) and the lowest in Coccoidea where, as a rule, there are 3 instars in the females, and 4 in the males. In the males of Coccoidea the last instar but one is the so-called pupa, and the same obtains in both sexes of Aleyrodidae.

Classification

Recent work has resulted in the recognition of an increasing number of Hemipteran families and scarcely any two authorities are in complete agreement as to a system of classification (Horvath, 1911a; Beier, 1938; Poisson, 1951; Pesson, 1951). The early catalogue of the Hemiptera of the world by Lethierry & Severin (1893–96), brought up to date by Bergroth (1908; 1913), is incomplete, dealing with only a part of the Heteroptera but another catalogue under the editorship of Horvath & Parshley (later China & Parshley) started publication in 1927 and parts are still continuing to appear. An admirable classified and annotated guide to much of the more important taxonomic and faunistic literature is provided by Oshanin (1916), and is indispensable to all who require a detailed acquaintance with the order. The same author's catalogue of the Palaearctic species (1906–10) and his later list (1912) are also valuable. Van Duzee (1917) has catalogued the N. America forms giving very full synonomy.

Suborder 1. HOMOPTERA

A very diverse assemblage. Head more or less deflexed, gular region small and membranous or wanting. Wings usually sloping over the sides of the body, the fore pair generally of uniform consistency throughout: apterous forms frequent. Base of rostrum extending between anterior coxae. Pronotum small. Tarsi with 1–3 segments. Metamorphosis usually incomplete, sometimes complete in male, more rarely so in female.

Series I. COLEORRHYNCHA

Short, 3-segmented antennae, concealed beneath head and without terminal arista. Base of rostrum partly ensheathed by propleura. Tarsi 3-segmented. A few small species with Tingid-like facies and discontinuous distribution in the Southern hemisphere.

Series II. AUCHENORRHYNCHA

Antennae very short with a terminal arista; rostrum plainly arising from the head. Tarsi 3-segmented. Active forms, capable of free locomotion.

Series III. STERNORRHYNCHA

Antennae well developed without conspicuous terminal arista, sometimes atrophied. Rostrum apparently arising between anterior coxae, or wanting, Tarsi 1 or 2-segmented. Species often inactive, or incapable of locomotion (in the female).

Suborder 1. HOMOPTERA

General accounts of the suborder are given by Beier (1938) and Pesson (1951) and its biology is discussed by Weber (1929–35; 1930). Taxonomic works are mentioned below under the appropriate group.

Series I. COLEORRHYNCHA

There is only one family, with characters as on p. 436.

FAM. PELORIDIIDAE.—This family includes about a dozen species with a peculiar discontinuous distribution, representatives occurring in S. America, Australia and New Zealand. Morphologically (Myers & China, 1929; J. W. Evans, 1938; 1939) they show many primitive features, suggesting them to be a remnant of a stock similar to that from which all other Hemiptera arose. They are found mostly in forests of *Nothofagus*, living in damp moss there, but the New Zealand *Oiphysa fuscata* is cavernicolous (Drake & Salmon, 1950). For their biology see Helmsing & China (1937) and Evans (1941).

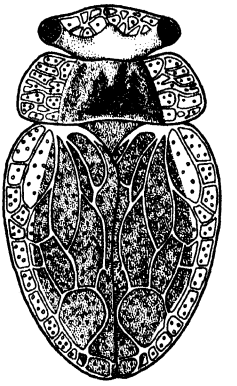


FIG. 344.—*Hemiodoecus fidelis* (Peloridiidae) (*after* Poisson & Pesson)

In section Homoptères of *Traité de Zoologie*, Vol. **10** (1951), under direction of P.-P. Grassé, Masson & Cie., Éditeurs.

Series II. AUCHENORRHYNCHA

The subdivision of this group presents one of the main problems in the taxonomy of the Homoptera. The older systems may be studied in Kirkaldy (1906; 1907) and Hansen (1900–03) should also be consulted. In the present work Kirkaldy's later subdivision (1907) into Cicadoidea and Fulgoroidea is adopted: the former group is separable into four easily recognizable families, but the Fulgoroidea, on the other hand, include a large assemblage of divergent forms (Muir, 1930). Although formerly regarded as a single family, the progress of later investigation shows that the group is far too heterogeneous to admit of such relatively simple treatment. Metcalfe (1945) has provided an extensive bibliography of all aspects of the group but there are few general taxonomic works. The Central and South American species are monographed by Distant (1880–1900) and Fowler (1894–1909) and the Indian ones by Distant (1902–18). For the fauna of N.W. Europe see Sahlberg (1871), Melichar (1896) and Haupt (1935).

Superfamily Cicadoidea

Tegulae absent; wings with ambient vein; 1A and 2A not forming Y-vein. Middle coxae short, articulations near together; hind coxae mobile. Antennal pedicel without sensilla, flagellum with sensory grooves.

Four families (sometimes given higher taxonomic status) may be distinguished by the following key, based on one by Muir:

1. 3 ocelli near together; anterior femora thickened and spined beneath; no empodia; male, except in a very few cases, with sound-producing organs at base of abdomen . . . . . CICADIDAE (p. 438)
–. 2 ocelli or none; empodia large 2
2. Posterior coxae short, conical, not laterally dilated; tibiae cylindrical; flagellum composed of a large subpyriform base and a very slender seta CERCOPIDAE (p. 438)
–. Posterior coxae transverse, dilated up to the lateral margins of the sterna; tibiae angular; flagellum composed of numerous segments 3
3. Genae more or less dilated; lorae generally conspicuous; frons, lorae and genae generally forming one curved surface; pronotum never prolonged backwards JASSIDAE (p. 440)

Genae not dilated; frons, lorae and genae not forming one curved surface; pronotum generally prolonged backwards into a process, sometimes of bizarre form . . . . . MEMBRACIDAE (p. 439)

FAM. CICADIDAE (Cicadas).—Their large size and sound-producing powers render these insects familiar objects in the warmer regions of the world. About 1,500 species are known, rather more than 100 being Palaearctic. The only British representative is *Cicadetta montana* which occurs in the New Forest and extends as far north as Finland. The capacity for sound-production (vide p. 117) is limited to the males and varies very greatly in note and degree of intensity in different species. The sound has been variously compared to a knife-grinder, scissor-grinder, and even a railway whistle. In the moist sub-Himalayan forest tracts of India the noise emitted by these insects is almost deafening, and extremely monotonous. Notwithstanding so many species being described, their biology has been little studied (Beamer, 1928; Myers, 1929). The nymphs so far known are subterranean, and the greatly enlarged and modified femora and tibiae of the fore legs are special adaptations to that mode of life. One of the best-known species of the family is the 'periodical Cicada' (*Magicicada septendecim*) of the United States (Figs. 345, 346), which appears in great numbers after long intervals of time. Its periodical appearance is due to the nymphs requiring thirteen (in the south) or seventeen years (in the north) for their development, and the fact that the adults of one generation appear about the same time in vast numbers. This insect has been intensively studied (e.g. Marlatt, 1907) and more than 20 distinct broods have been located in various parts of the country: the 17-year race has also been reared under field conditions from the egg. In many districts several broods of different ages are known to co-exist, thus explaining the appearance of swarms of the insect several times during the 17-year cycle. The female deposits her eggs in slits which she makes in the twigs of trees, and the young emerge in about six weeks. They fall to the ground and thereupon commence to lead a subterranean life, 12–18 inches below the surface, sucking the juices from the finer roots of various trees. In May of the 17th year they regain the surface and, leaving their nymphal exuviae attached to tree-trunks, etc., emerge as perfect insects. When very abundant the nymphs practically honeycomb the soil, but, considering their size and numbers, the injury occasioned does not appear to be great; at times, however, fruit growers experience a good deal of loss. Under certain circumstances the final-stage nymphs (often termed pupae) construct cones or chimneys (Fig. 346), about 4 inches high, of earthen particles wherein they live above ground for several weeks before emerging as adults. Several explanations have been offered as to the meaning of these structures and it may possibly be that in certain districts individuals prematurely reach the surface before they are prepared to become adults and construct cones as means of protection until they reach maturity. There appears to be a correlation between an unusually high local temperature and the occurrence of these cones; the latter are also stated to be prevalent over burned areas. Taxonomic works on the Cicadidae include those of Distant (1889–92; 1906; 1912–14) and Myers (1928) deals with their morphology.

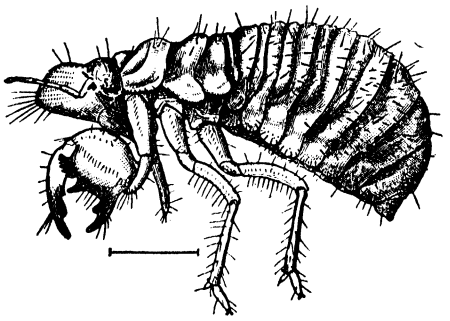


FIG. 345.—*Magicicada septendecim* nymph in 4th instar

After Marlatt, *U.S. Dept. Agr., Ent. Bull.* 71.

FAM. CERCOPIDAE (Frog-hoppers or Cuckoo-spit Insects).—Members of this family may usually be separated from the Jassidae by the characters of the tibiae as enumerated above. Only a very few genera are Palaearctic, and four thereof occur in Britain—*Cercopis*, *Aphrophora*, *Neophilaenus* and *Philaenus*. The nymphs of some genera are subterranean (e.g. *Cercopis*) while others are well-known objects from their habit of establishing themselves on plants and becoming enveloped in a frothy substance commonly termed 'cuckoo spit'. It has been generally regarded that they are in this way protected from predacious insects and other Arthropods, but, on the contrary, they are not infrequently seized from their spume by fossorial Hymenoptera and other enemies. Kirkaldy has observed that the froth serves to protect their soft bodies from the sun, and, when extracted from the spume and not allowed moisture, they speedily

shrivel and die; probably there is truth in both explanations and the function is twofold. In adaptation to this mode of life the nymphs have to a large extent lost that power of leaping which is so characteristic of the adults, and are also nearly devoid of coloration. *Philaenus leucophthalmus* is the common 'cuckoo spit' insect of Europe and N. America; the life-histories of this and other species of the family are described by Osborn (1916a) and Speers (1941). It affects a wide range of wild and cultivated plants other than grasses, while *Neophilaenus lineatus* occurs almost entirely on the latter hosts. The production of the froth has given rise to much speculation and has been studied by Sŭlc (1911) and Gahan (1918), whose conclusions are in close agreement. According to Gahan the tergites and pleurites of the 3rd to 9th abdominal segments, instead of ending as usual at the sides to form lateral edges, are curved beneath the abdomen as membranous extensions, which meet along the mid-ventral line. Between them and the true ventral surface of the abdomen there is thus formed a cavity into which the spiracles open. This chamber is closed anteriorly, but air can be admitted or expelled by means of a posterior V-shaped valve or slit. The frothing is the result of a fluid issuing from the anus (vide p. 162) forming a film across this valve and becoming blown into bubbles by means of air expelled from the latter.

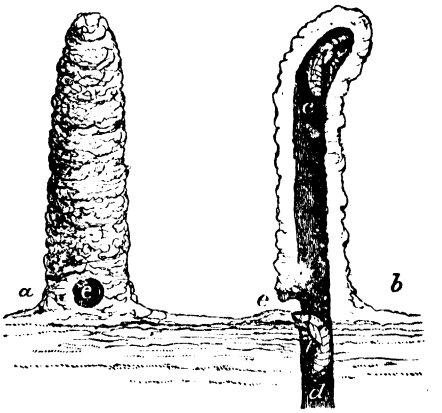


FIG. 346.—*Magicicada septendecim*, 'Earthen Chimneys'

a, front view; *b*, section; *c*, nymph in last instar awaiting time of change and at *d* ready for transformation; *e*, emergence hole. From Marlatt *after* Riley.

On the 7th and 8th abdominal segments are lateral glands which have been variously interpreted. Osborn states that they secrete a viscid material which, mixing with the discharge from the alimentary canal, enables the foam to maintain its coherence, even in wet weather. Sŭlc and others regard the secretion as being of a waxy nature which is acted upon by an enzyme in the anal discharge. He explains that the acid thus produced forms, with the alkali present, a substance which imparts to the froth the properties of a soap-solution. In Madagascar the nymphs of *Ptyelus goudoti* are stated to discharge clear water in such amounts as to resemble fine rain. Thus Goudot estimated that some 70 individuals could emit one quart in 1½ hours. The Oriental and Australian genus *Machaerota* has the scutellum prolonged backwards in the form of a relatively enormous spine thus simulating a Membracid in appearance. The nymphs of certain species of the genus are known to live in curious serpuliform tubes (about ½ inch long) attached to the branches of trees; their life-history is discussed by Lefroy (1909) and Evans (1940). For taxonomy, see Lallemand (1912; 1949) and Doering (1930).

FAM. MEMBRACIDAE (Tree-hoppers).—These insects (catalogued by Funkhouser, 1927) may almost always be easily recognized by the pronotum, which is prolonged backwards into a prominent elevated hood or process, lying over the abdomen, and often assuming the most bizarre forms (Fig. 347). The family, with over 2,000 species, is most nearly related to the Jassidae and reaches the zenith of its development in the Neotropical region. The Palaearctic fauna only includes three genera, two of which, *Centrotus* and *Gargara*, are British. Biological studies on the family have been made by Branch (1914), Funkhouser (1917) and Couturier (1938). The eggs are usually deposited in small groups arranged in two nearly parallel slits cut in the twigs of trees and shrubs. The nymphal stages differ from the adults in the absence, or only partial development, of the pronotal process; the tergites are often furnished with elongate filaments or spinose projections. Certain genera (*Telamona*, *Thelia*, etc.) are affected by parasites which induce 'castration parasitaire' noticeable in the reduction or other modification of the external genitalia (vide Kornhauser, 1919). The life-history of *Vanduzea arquata*, a widely distributed N. American species, has been studied by Funkhouser (1915). It abounds on *Robinia* and appears to pass through two generations in the year. Both the nymphs and adults are commonly attended by ants, as is usual whenever Membracids are present in large numbers.

The ants stroke the Membracids with their antennae, whereupon the latter insects exude a liquid from the retractile anal tube. The mutual relationships of the two groups of insects has attracted the attention of a number of observers (vide Lamborn *et al.*, 1913). A few species have been noted to exhibit maternal solicitude; although usually leaping away at the first alarm, they refuse to move if disturbed while guarding their offspring. Among taxonomic papers see Goding (1926–39), Evans (1948) and Funkhouser (1950).

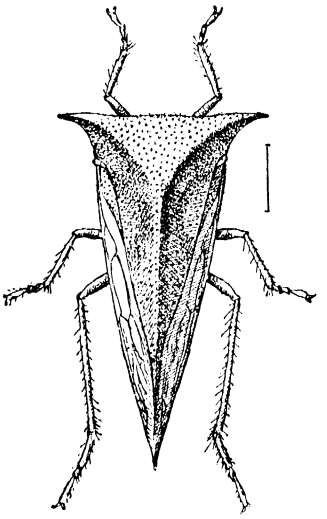


FIG. 347.—*Ceresa bubalus*, enlarged
After Marlatt, *Ins. Life*, 7.

FAM. JASSIDAE (Cicadellidae; Leaf-hoppers).—The members of this group have been divided into a number of families, but the lack of agreement between different authorities on their limits (Baker, 1923; Melichar, 1924–31; Haupt, 1929; Evans, 1946–47) makes it preferable here to follow Oman (1949) in treating them as a single family. Excepting the Aphididae, they are probably the most abundant of all Homoptera, and may be readily collected by sweeping grass, herbage and other foliage. They are slender, usually tapering posteriorly, and rest in a position ready for jumping. When disturbed they leap often several feet and readily take to the wing. Their slender form and the structure of the hind tibiae (Fig. 348) will enable most species to be distinguished from those of the Cercopidae. The metamorphoses of many are figured by Osborn (1916a), that of *Idiocerus* by Leonard (1915) and of *Nephotettix* by Misra (1920). The ovipositor of the female is adapted for lacerating plant-tissues; the eggs are usually elongate and are deposited in longitudinal rows on the stems, under the leaf-sheaths, or on the leaves of the food-plant. They pass through six instars, the wing-rudiments becoming noticeable in the 3rd instar.

The species have a decided limitation of food-plant during early life but feed more indiscriminately later; many are univoltine, others pass through two or three generations in a season. Their chief economic importance lies in their attacks upon cereal and fodder crops as well as fruit and forest trees. Thus the rice leaf-hoppers (*Nephotettix*) in 1914 were reported to have damaged 3,000,000 acres of paddy fields in one division only in the Central Provinces of India, entailing a loss of nearly £1,000,000 (Misra); similar heavy losses are recorded from the United States. Several species are vectors of virus diseases (Leach, 1940).

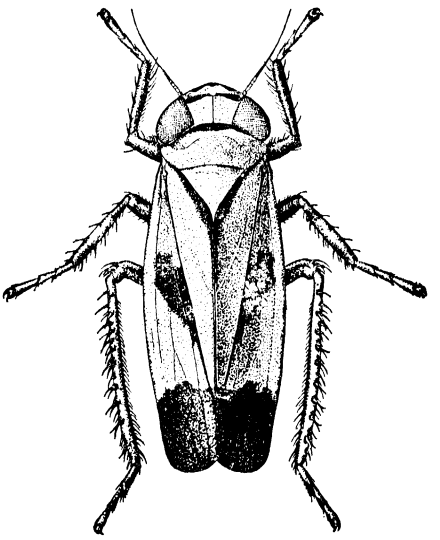


FIG. 348.—*Nephotettix apicalis* × 12
After Misra, *Mem. dep. Agric. India Entom. Ser.* 5.

Among the more important genera are *Empoasca* which includes the Apple Leaf-hopper (*E. mali*), *Typhlocyba* (ocelli absent), *Bythoscopus* and *Deltocephalus*. In addition to those cited above, there are important taxonomic works by Delong (1916; 1948), and Ribaut (1936; 1952).

Superfamily **Fulgoroidea**

Included herewith is a large assemblage of very diverse forms whose many dissimilarities of structure render it difficult to frame any comprehensive definition.

Tegulae are present; wings without ambient vein; 1A and 2A of fore wings unite to form a Y-vein. Middle coxae elongate and placed wide apart; hind coxae immobile. Antennal pedicel with numerous sensilla and a large sense-organ on basal segment of flagellum. Much morphological work is required before a satisfactory classification can be achieved, but the arrangement of Muir (1930) is followed here and the key below is based on his paper. Metcalfe (1938) and Fennah (1945) should be consulted on the taxonomy of American Fulgoroids.

1. Antennal flagellum segmented; ocelli not outside lateral carinae of head. TETTIGOMETRIDAE (p. 442)
–. Antennal flagellum not segmented; ocelli outside lateral carinae of head . 2

2. 2nd segment of hind tarsus not very small, its apex with row of small spines. 3
–. 2nd segment of hind tarsus small or very small, its apex without or with only two spines 11

3. One or both claval veins granulate; apical segment of labium much longer than wide . . . . . MEENOPLIDAE (p. 442)
–. Claval veins usually not granulate; if so, then apical segment of labium about as long as wide 4

4. 6th to 8th abdominal tergites with wax-secreting pores . KINNARIDAE (p. 442)
–. These tergites without pores 5

5. Anal area of hind wing reticulate . . . . . FULGORIDAE (p. 442)
–. Anal area of hind wing not reticulate 6

6. Apical segment of labium about as long as wide . . DERBIDAE (p. 442)
–. Apical segment of labium distinctly longer than wide 7

7. Claval vein extending to apex of clavus 8
–. Claval vein running into claval commissure before apex 9

8. Base of abdomen with 1 or 2 short appendages bearing 3 hemispheroidal depressions . . . . . ACHILIXIIDAE (p. 442)
–. Base of abdomen without appendages . . . . ACHILIDAE (p. 442)

9. Hind tibiae each with a mobile, apical spur . . . DELPHACIDAE (p. 442)
–. Hind tibiae without such spurs 10

10. Head usually markedly prolonged in front, or, if not so, then frons with 2 or 3 carinae or tegulae absent and claval suture obscure DICTYOPHARIDAE (p. 442)
—. Head not markedly produced in front; frons unkeeled or with median carina only; tegulae present and claval suture distinct . . . CIXIIDAE (p. 442)

11. 2nd segment of hind tarsus with spine on each side 12
—. 2nd segment of hind tarsus without spines 16

12. Posterior angle of mesonotum cut off by a groove or fine line . . . TROPIDUCHIDAE (p. 442)
—. Posterior angle of mesonotum not cut off in this way 13

13. Costal area with cross-veins; clavus without granules; clypeus usually with lateral carinae . . . . . NOGODINIDAE (p. 442)
—. Costal area usually without cross-veins; if cross-veins present, then clavus granulate or clypeus without lateral carinae 14

14. Clavus granulate or base of costa strongly curved . . FLATIDAE (p. 442)
—. Neither clavus granulate nor base of costa strongly curved . . . 15

15. Tegmina large, steeply tectiform; hind tibiae without spurs on the side . ACANALONIIDAE (p. 443)
—. Tegmina not so large and usually not so steeply tectiform; hind tibia with one or more spurs on the side . . . . . ISSIDAE (p. 443)

16. Hind trochanters directed ventrally; hind basitarsus short or very short . RICANIIDAE (p. 443)
—. Hind trochanters directed backwards; hind basitarsus long or very long . 17

17. Frons seldom as wide as long, nearly always with 1–3 longitudinal carinae. LOPHOPIDAE (p. 443)

—. Frons wider than long, without longitudinal carinae or only one obscure one. EURYBRACHIDAE (p. 443)

FAM. TETTIGOMETRIDAE.—The 70 or so species are superficially similar to Jassids; they include some myrmecophilous species and are found chiefly in Europe but also occur in the Ethiopian region while one species is known from Peru. (See Metcalfe, 1932; Fennah, 1952a.)

FAM. CIXIIDAE.—This is one of the largest Fulgoroid families, almost 800 species having been described from all parts of the world (Muir, 1925; Metcalfe, 1936). Very little is known of their biology, but the nymphs of *Oliarus felis* feed underground on the roots of grass in Australia and the same is probably true of the British species of *Cixius* (China, 1942).

FAM. DELPHACIDAE (Araeopidae).—One of the most characteristic features is the large mobile, serrulate apical spur on the hind tibiae; the costal cell is wanting and the clavus non-granulate. This family is the largest of the Fulgoroids with over 1,100 species (Muir, 1915; Metcalfe, 1943) and is well represented in Great Britain where there are about 70 species, the biology of some being described by Hassan (1939). The Sugar-cane Leaf-hopper *Perkinsiella saccharicida* (Fig. 349) is very destructive in Queensland and was formerly so in the Hawaiian Islands; owing to the habit of oviposition in cane stalks this and other species are liable to transportation.

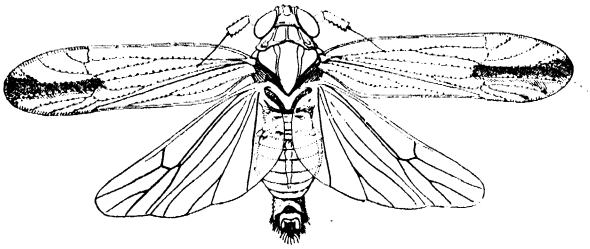


FIG. 349.—*Perkinsiella saccharicida*, male: magnified
After Kirkaldy, *Entom. Bull. Pt.* 9, *Hawaiian Sugar Planters' Assn.*

FAM. DERBIDAE.—Very delicate, usually long-winged insects of which over 700 species are known, mostly tropical (Muir, 1918; Metcalfe, 1945; Fennah, 1952). None are British and few Palaearctic but *Melenia* occurs in the Mediterranean region.

FAM. ACHILIXIIDAE.—A small family of 9 species (Fennah, 1947) related to the Cixiidae and with a wide distribution.

FAM. MEENOPLIDAE.—The 50 or so species are confined to the Eastern hemisphere. Muir (1925) gives a key to genera and Metcalfe (1945) a catalogue.

FAM. KINNARIDAE.—Another small family with 42 species (see Fennah, 1942; Metcalfe, 1945). *Bytrois nemoralis* feeds on leaves of cacao in Trinidad.

FAM. DICTYOPHARIDAE.—This family of about 500 species includes medium-sized Fulgoroids, often with strongly modified heads bearing a distinct process. They are widely distributed and many species are confined to arid and semi-arid areas. *Retiala viridis* is a minor pest of coffee. See Melichar (1912), Haupt (1929) and Metcalfe (1946) for taxonomy.

FAM. FULGORIDAE (Lantern Flies).—Principally characterized by the reticulated anal area of the wing. A tropical family including many brilliantly coloured insects, often of large size. In many genera the front of the head is greatly drawn out to form a huge hollow proboscis-like prolongation which was, at one time, believed to be luminous. Some species have the power of secreting quantities of a flocculent white wax which, in *Phenax*, streams behind as long filaments while the insect flies. The family has been catalogued by Metcalfe (1947).

FAM. ACHILIDAE.—A moderately large family (Metcalfe, 1948; Fennah, 1950) of world-wide distribution, especially in the tropical zone. The nymphs live under bark or in cavities in dead wood.

FAM. TROPIDUCHIDAE.—Melichar (1915a) recognizes 140 species in this family, mostly from the Indo-Malaysian and Neotropical regions; a very few occur in southern Europe.

FAM. NOGODINIDAE.—Over 90 species have been described from Africa, America and the Indo-Malaysian region (Melichar, 1923).

FAM. FLATIDAE.—Beautiful mothlike species, often with delicately pigmented

tegmina, inhabiting tropical regions. They can usually be recognized by the well-developed transversely-veined costal cell and the granulate clavus. Both nymphs and adults frequently rest gregariously and the former are largely covered with long, curled, waxy filaments (Fig. 350). The adults of some species occur in two conspicuously different colour forms and, in the case of an African species, observed by Gregory, the insects were clustered on a stem with green individuals occupying the upper portion and red individuals situated just below them. In this attitude they were curiously like a red flowered spike with green unopened buds above. In other dimorphic species the colour forms have been observed intermixed; for a discussion of this subject and the literature thereon vide Imms (1914). There is a generic monograph by Melichar (1923) who lists almost 700 species.

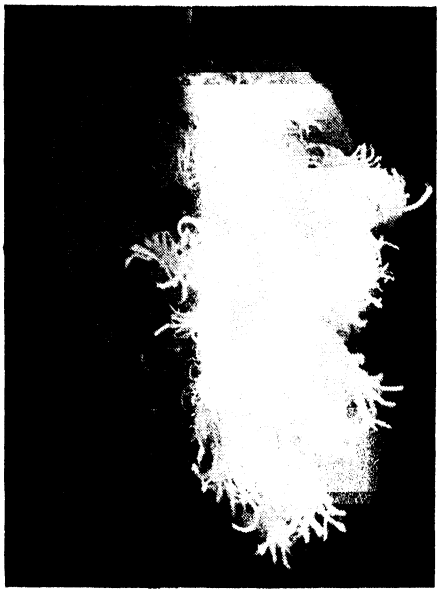


FIG. 350.—*Phromnia marginella*, India (Flatidae): a colony of nymphs on a leaf: about ⅔ actual size

FAM. ACANALONIIDAE.—This small family of about 40 species (Melichar, 1923) is represented in America, Africa and the Indo-Malaysian region.

FAM. ISSIDAE.—A large family with several European representatives (Melichar, 1906; Doering, 1938–41). Some of its members have a squat, beetle-like facies and *Augilia* and *Caliscelis* are unusual in possessing enlarged fore legs with foliaceous femora and tibiae.

FAM. RICANIIDAE.—Over 250 species are known, mostly from Africa and the Oriental region (Melichar, 1923).

FAM. LOPHOPIDAE.—Melichar (1915) recognized over 50 species, especially numerous in the Oriental region.

FAM. EURYBRACHIDAE.—Among the members of this family, *Eurybrachys tomentosa* is a pest of the sandal tree in S. India (Chatterjee, 1933). Its eggs—which are covered with a white, flocculent secretion—are laid in clusters; there are five nymphal instars and three overlapping generations per year.

The **Gengidae** (Fennah, 1949) and **Hypochthonellidae** (China & Fennah, 1952) are each represented by a single species and are not included in the key on p. 441.

Series III. STERNORRHYNCHA (Phytopthires)

Key to superfamilies

1. Tarsi 1-segmented with single claw. Females scale-like, gall-like or covered with waxy exudation; apterous and often devoid of legs. Males dipterous, mouthparts atrophied . . . . . COCCOIDEA (p. 452)
–. Tarsi 2-segmented, the basal segment sometimes reduced, with paired claws. Mouthparts present in both sexes. Wings, when present, 4 in number . 2

2. Femora thickened, antennae usually 10-segmented. Fore wings of rather harder consistency than hind pair . . . . . PSYLLOIDEA (p. 444)
–. Legs long, slender. Wings of equal consistency. Antennae 3- to 7-segmented. 3

3. Wings opaque, whitish, clouded or mottled with spots or bands. Antennae 7-segmented. Tarsi with 2 subequal segments and pad-like empodium or spine between claws . . . . . ALEYRODOIDEA (p. 445)
–. Wings transparent. Tarsi 2-segmented, the basal segment sometimes reduced. Paired dorsal processes usually present on 5th abdominal segment . . APHIDOIDEA (p. 446)

Superfamily **Psylloidea**

This group contains only 1 family:

FAM. PSYLLIDAE (Chermidae: Jumping Plant Lice).—Psyllids are small insects about the size of aphides and bear a resemblance to minute cicadas. They are usually very active, their rapid movements being a combination of leaping and flying, but are incapable of sustained flight. The act of leaping is performed with the aid of the hind legs which are larger and more muscular than the other pairs. The venation is simple and exhibits relatively few marked deviations among various genera. The most striking feature in the fore wing is the presence of a principal basal vein formed by the fusion of the stems of R, M and Cu (Fig. 351). In *Trioza* and its allies, this compound vein divides distally into its three components while in *Psylla* and related genera it is bifurcate, dividing into R and M + Cu_1, the latter again dividing into M

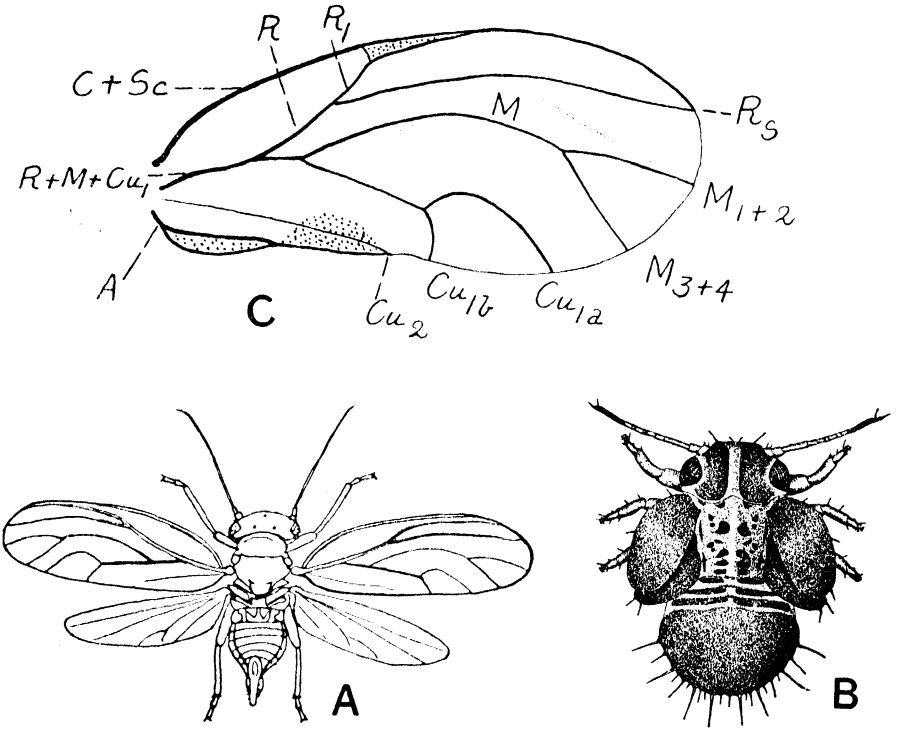


FIG. 351.—A, *Psylla mali* (*after* Carpenter). B, *Psylla pyricola*, nymph in last instar (*after* Slingerland). C, *Psylla pyricola*, venation of fore wing. All enlarged

and Cu. In the hind wing the venation is extremely simple; R is represented by Rs only, M is unforked and Cu divided into Cu_1 and Cu_2 as in the fore wing. Cross-veins are absent from both wings and A is vestigial or wanting. A general account of the external anatomy of Psyllids is given by Crawford (1914) and of the venation by Patch (1909). The chief source of information on the internal anatomy is a paper by Witlaczil (1885) and an account of the morphology of *Pachypsylla* is given by Stough (1910) and of the head and thorax of *Psylla* by Weber (1929). There is a bibliography by Zacher (1916) and important taxonomic works by Aulmann (1913), Crawford (1914), Caldwell (1938), Tuthill (1943) and Heslop-Harrison (1949). The species of N.W. Europe may be identified from Haupt (1935) and their biology is discussed by Lal (1934) and Schaefer (1949).

The life-history of the 'Apple Sucker' *Psylla mali* (vide Speyer, 1929) may be regarded as fairly typical (Fig. 351). It passes the winter in the egg, the latter being laid about the beginning of September on the spurs of the food plant, around leaf-scars and in cracks, etc., on the new wood. The nymphs hatch in April, and are flattened

objects with whitish waxen threads projecting from the extremity of the abdomen. Five nymphal instars occur, and the different stages may be recognized by the increasing number of antennal segments; thus these organs are 2-segmented in the 1st instar and 7-segmented in the 5th. Wing-pads are evident in the 3rd instar and during later development they extend laterally in a prominent manner so as to make the insect appear nearly as broad as long (Fig. 351, B). The imago appears in early summer and the species is univoltine. The nymphs are very injurious to the apple in Britain, damaging the blossoms and stunting the shoots; the imagines, on the other hand, cause little appreciable injury. The 'Pear Sucker' *P. pyricola* is very destructive in America and exhibits a different life-history. It is tri-voltine, hibernates as an imago and both nymphs and adults are injurious. The winter form of the imago differs from the summer type and was formerly regarded as a separate species. It is about one-third larger than the summer form and of much darker coloration, particularly with regard to the wing-veins. Certain species produce gall-like malformations on their food-plants; thus in Britain *Psylla buxi* causes the apical shoots of the box to become deformed into miniature cabbage-like growths, and *Livia juncorum* forms tassel-like galls on rushes. When Psyllids are abundant copious honey-dew is excreted by the nymphs on to the leaves and twigs. In *Psylla mali* a long waxen thread enclosing a central core of translucent liquid exudes through the anus and when the threads become broken up the fluid spreads over the leaves and twigs (Awati, 1915).

Superfamily **Aleyrodoidea**

Only one family is included here:

FAM. ALEYRODIDAE (Aleurodidae: White Flies).—The 'white flies' are a much neglected group related to the Psyllidae and probably the majority of the world's species are as yet unknown. For taxonomic accounts see Quaintance & Baker (1913–14; 1917) and Sampson (1943; 1947) and among other biological papers, see Trehan (1940). Both sexes are winged and are dusted with a characteristic mealy white powdery wax; all are small or minute with an average wing expanse of about 3 mm. *Trialeurodes vaporariorum* is the well known 'Greenhouse White Fly' which is particularly injurious to tomato and cucumber, the insect infesting the lower surface of the leaves in all its stages (Fig. 352), (Weber, 1931; 1935; and, for a related pest, Butler, 1938; 1938a). *Dialeurodes citri* is the 'Citrus White Fly' which is destructive to Citrus in the southern United States (Morrill & Back, 1911). The most characteristic organ of the Aleyrodidae is the *vasiform orifice* which opens on the dorsal surface of the last abdominal segment. It is a conspicuous opening provided with an *operculum*, and situated within the orifice and beneath the operculum is a tongue- or strap-shaped organ known as the *lingula*. The latter in some species is covered by the operculum and in others it projects beyond it. The anus opens within the orifice at the base of the lingula. Honey-dew is excreted in large quantities by the insect in all stages, particularly by the larvae. It issues through the anus accumulating on the lingula, and this fact probably gave rise to the view that the latter organ secretes the honey-dew. The vasiform orifice is present both in the larval and adult stages and, in the latter, affords characters of taxonomic value.

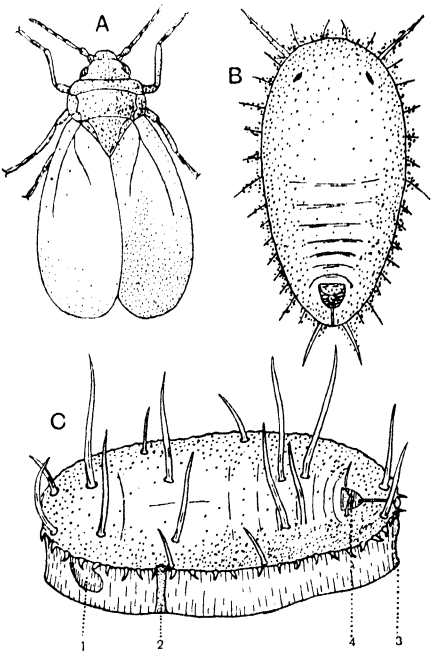


FIG. 352.—*Trialeurodes vaporariorum*

A, imago × 50; B, larva in first instar × 150; C, puparium × 65. 1, adult eye; 2, thoracic breathing fold; 3, caudal breathing fold; 4, vasiform orifice. *After* Lloyd, *Ann. App. Biol.*, 9.

The venation shows closest affinity with the Psyllidae (*Trioza*); it is always much reduced and exhibits evident signs of degeneration (Fig. 352). The most primitive condition is seen in *Udamoselis*; in other genera C and Sc are more or less fused, R_1 often disappears, and either M or Cu may be present but are usually not coexistent. With the exception of R the veins are unbranched and, in the most modified forms, practically the only remaining vein is Rs.

Parthenogenesis is a common phenomenon in several species and probably occurs in many others, but the subject needs thorough investigation. Morrill & Back (1911) observe that virgin females of *D. citri* produce males. According to Schrader (1926) in *T. vaporariorum* there are two parthenogenetic races, one of which produces males and the other females; the fertilized females give rise to individuals of both sexes.

The eggs are very characteristic, being provided with a pedicel which, in some cases, exceeds the length of the egg itself. According to Cary (1903), at the time of fertilization the lumen of the pedicel is filled with protoplasm. The spermatozoan moves through the latter until it meets the female pronucleus which migrates until it comes to lie at the entrance to the pedicel. After fertilization the contents of the pedicel shrivel up. The eggs are attached to the leaves of the food-plant by means of this stalk, and are generally laid in a circle or arc of a circle, one or more rows deep. Three larval instars are present and a so-called pupal stage (Weber, 1934). The larvae are ovoid and greatly flattened and, after the first moult, the legs and antennae degenerate; towards the end of the 3rd instar the imaginal organs become visible. The so-called pupal stage is only imperfectly understood: it is similar in general shape to the larva, but differs very much in appearance, being thicker and more opaque and, frequently, adorned with conspicuous rods or filaments of wax. During the first part of this instar the insect feeds after the manner of the larvae. Towards the end of the period it becomes inactive, remaining anchored to the leaf by means of its stylets, and exhibits the characters of a rudimentary pupa with the imaginal appendages enclosed in their sheaths clearly visible within the outer case. The imago emerges by means of a T-shaped rupture of the dorsal wall of the latter.

Superfamily **Aphidoidea**

The three families recognized here may be distinguished by the following key:

1. Fore wings, when present, with separate R_5. Sexual females oviparous; parthenogenetic females viviparous . . . . . APHIDIDAE (p. 446)
   Fore wings, when present, without separate R_5. Sexual and parthenogenetic females oviparous 2

2. Wings at rest held roof-like over abdomen; fore wings with Cu arising separately from A. Apterous parthenogenetic females covered with flocculent wax. Confined to conifers . . . . . ADELGIDAE (p. 451)
   Wings at rest held flat; fore wings with Cu and A arising on common stalk. Wax of apterous parthenogenetic females, if present, not flocculent . . . PHYLLOXERIDAE (p. 450)

FAM. APHIDIDAE (Greenfly; Plant-lice).—These familiar insects, as a rule, pass their life on the young shoots and foliage of plants. A few species, however, live below ground on roots (e.g. *Trama*), some others occur on the branches of woody trees and shrubs (e.g. *Lachnus*) and a certain number are gall-formers (e.g. *Pemphigus*, *Hormaphis*). A few such as *Eriosoma lanigerum* live both on the leaves, or shoots, and roots. The apterous generations of aphides, more especially when of flattened form (as in *Hormaphis*), are liable to confusion with the nymphs of other Sternorrhyncha. Usually they may be distinguished therefrom by the following combination of characters, viz.—the 2-segmented tarsi with paired claws, the long several-jointed rostrum, the frequent presence of compound eyes and cornicles, and 9 pairs of lateral spiracles. Perhaps the most characteristic morphological features associated with these insects are the cornicles or 'honey tubes'; the latter organs, however, are greatly reduced in *Eriosoma* and some other genera. Réaumur believed their function to be excretory but later observers concluded that they secreted the sweet substance known as 'honey-dew'. It is now known that they are the secretory channels belonging to glands producing a waxy fluid which acts as a protection against predacious enemies (Hottes, 1928). Honey-dew is emitted through the anus (Broadbent, 1951). Many aphides also secrete a white waxy substance, either in the form of a powder dusted over the surface of the

body (e.g. *Hyalopterus*), or in flocculent threads (*Eriosoma*); in either case it is the product of dermal glands (vide p. 169).

The venation of aphides has been studied in detail by Patch (1909); both the tracheae C and Sc are absent in all forms examined and the costal area of the adult wing is strengthened by a stout vein-like structure expanding distally into a stigma. This vein channel is interpreted as representing the fusion of the main stems of all the principal veins.

Aphides are remarkable on account of their peculiar mode of development and the polymorphism exhibited in different generations of the same species. The associated phenomena concerning reproduction are—(1) parthenogenesis; (2) oviparity and viviparity; (3) the occurrence of generations in which the sexes are very unequally represented, males often being wanting and frequently rare. With regard to structure the phenomena are—(1) the production of totally different types of individual of the same sex either in the same or different generations; (2) the production of individuals with perfect and also atrophied mouthparts; (3) the production of individuals of the same sex but differing as to the gonads. Associated with habits are—(1) migration to totally different plant hosts (host alternation); (2) different modes of life of the same species on the same host; (3) different habits of individuals of the same generation (Parallel series).

In extreme cases almost all the above phenomena may occur associated with the annual cycle of an individual species. The most usual life-history of an aphid is as follows (Fig. 353). The winter is passed as eggs which are laid during the previous autumn by sexual females. With the advent of spring they hatch and give rise to apterous parthenogenetic viviparous females. The latter produce a new generation of similar forms among which a few winged females may occur. A variable number of generations of this kind are produced throughout the summer and winged viviparous females often become common. The latter are concerned with the migration and dispersal of the species and are produced in varying numbers in different generations. At times these winged females appear in such swarms as to darken the sky and cover the vegetation. Those individuals which are fortunate enough to find plant hosts of the right species similarly reproduce on their own account. Towards the end of summer or in the autumn their progeny, and also those of the apterous forms which remained on the original plant, give rise to sexual males and females. These latter pair and the females are oviparous, their eggs overwintering on the food-plant, and the same cycle is repeated annually. In non-migratory aphides the whole life-cycle is spent on the same plant or on individuals of the same species. If any migration to other species of host does occur it is inconsiderable and an alternation of hosts is not essential to the life of the species. Among migratory forms well-known species are—*Pemphigus bursarius* which occurs on poplar and flies to the roots of various Compositae, returning to poplar in autumn; *Myzus persicae*, the primary (winter) host of which is peach and which occurs on a number of secondary host species; *Aphis fabae* which is found in autumn on the Spindle Tree (*Euonymus*), where it overwinters as the egg and which, in May and June flies to beans, sugar-beet, dock, poppies, etc., returning to the spindle tree in October (Jones, 1942). Mordvilko (1928; 1934) considers that all aphides were originally polyphagous and that existing migrations are remnants of that habit. He divides these insects into three groups. (*a*) Those in which migration is absent but the species are widely polyphagous. (*b*) Species in which there is facultative migration, two hosts may be utilized and polyphagy is more restricted. Thus, a species may complete its life-cycle on one host but, on the other hand, it is capable of utilizing an alternative host for a portion of its development. (*c*) Species in which migration is obligatory and which are only slightly polyphagous.

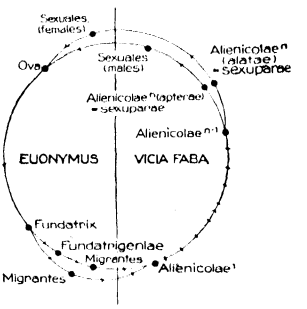


FIG. 353.—Diagram of the life-cycle of *Aphis fabae* (based on observations by J. Davidson, at Rothamsted)

The following types of individuals, arranged in sequence, are present in the life-cycle of migratory aphides (Figs. 353, 354). (1) The *Fundatrices*; apterous, viviparous, parthenogenetic females which emerge in spring from the overwintered eggs. The sense organs, legs and antennae are not so well developed as in succeeding apterous generations, the antennae, for example, being shorter and may comprise a smaller number of segments. The reduction of the parts is apparently correlated with increased

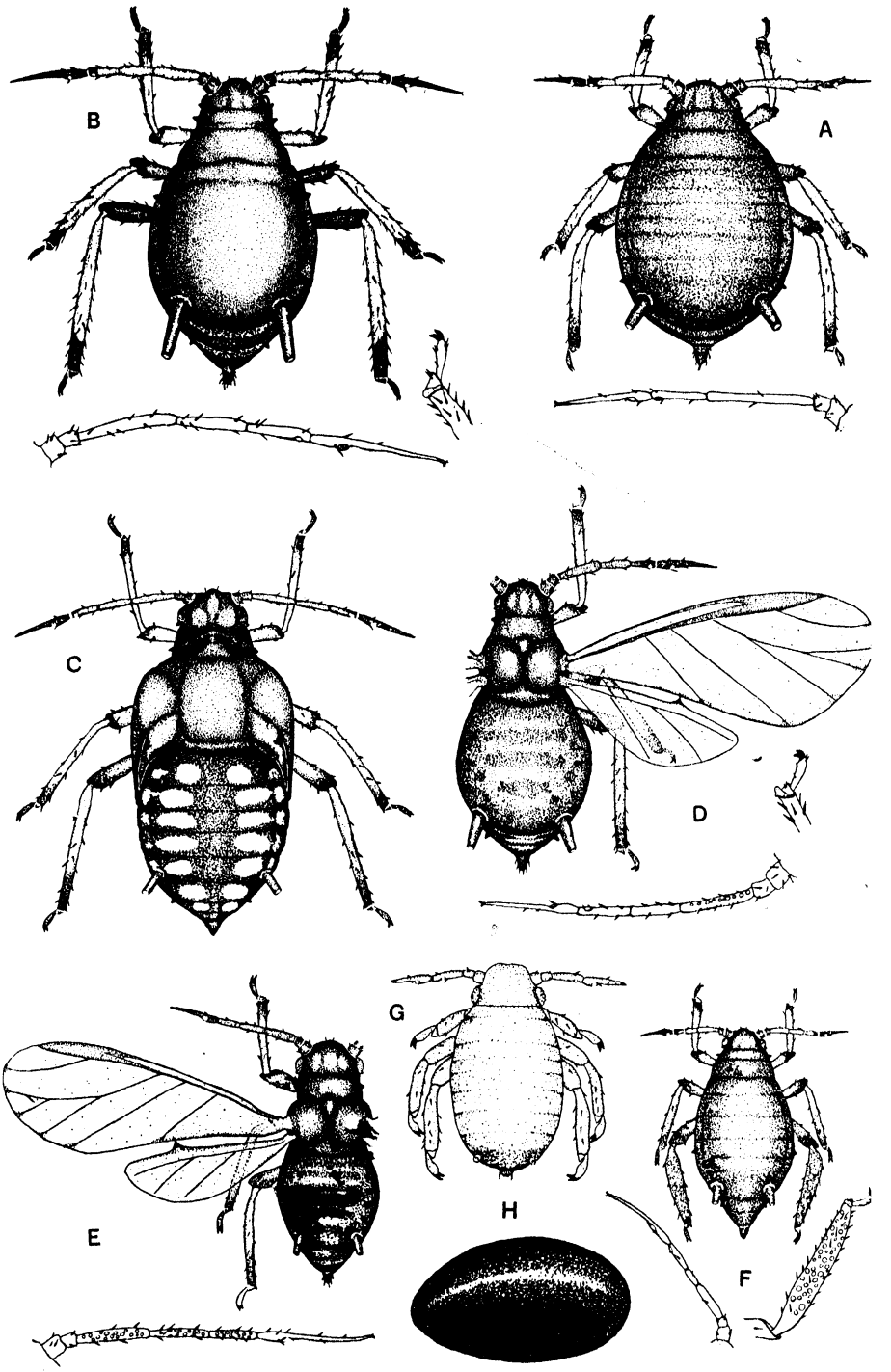


FIG. 354.—*Aphis fabae*

A, fundatrix; B, apterous viviparous female; C, nymph of winged viviparous female; D, winged viviparous female; E, male; F, oviparous female; G, fundatrix, 1st instar; H, egg. The antennae are also shown under higher magnification, together with the tarsus in B and D and the hind tibia and tarsus in F. (From original drawings by J. Davidson.)

reproductive capacity. The eyes are often smaller, or consist of fewer facets than in the succeeding generations, and there may be differences in the cornicles. In *Drepanosiphon platanoidis* the fundatrices are exceptional in being winged. (2) *Fundatrigeniae*; apterous, parthenogenetic, viviparous females which are the progeny of the fundatrices and live on the primary host. (3) *Migrantes*; these usually develop in the second, third or later generations of fundatrigeniae and consist of winged parthenogenetic viviparous females. They develop on the primary host and subsequently fly to the secondary host. In *Drepanosiphon platanoidis* all the viviparous females are winged and consequently fundatrigeniae are wanting. (4) *Alienicolae*; parthenogenetic, viviparous females developing for the most part on the secondary host. They often differ markedly from the fundatrices and migrantes; many generations may be produced comprising both apterous and winged forms. (5) *Sexuparae*; parthenogenetic viviparous females which usually develop on the secondary host, the alate forms migrating to the primary host at the end of the summer. The sexuparae terminate the generations of alienicolae by giving rise to the sexuales. (6) *Sexuales*; usually appear but once in the life-cycle and consist of sexually reproducing males and females, the latter being oviparous. The females with rare exceptions (*Neophyllaphis*, *Tamalia*, *Cervaphis*) are apterous, and distinguishable from the apterous viviparous generations of the same sex by the thickened tibiae of the hind legs, and the greater body length. The males are either winged or apterous, and in *Chaitophorus populeti* both types are produced. Intermediates between alate and apterous forms also occur. The sexuales exhibit various types of specialization among different genera, which reach their culminating point in *Eriosoma* and its allies. In these instances both sexes are apterous, there are no functional mouthparts, the digestive system is degenerate, and the female lays only a single very large egg produced in a single ovary, the counterpart of the latter having atrophied (Baker, 1915). The eggs are laid on the primary host and in this stage the vast majority of species hibernate. Apterous parthenogenetic viviparous females may overwinter in several species, e.g. *Brevicoryne brassicae* and *Myzus persicae*.

With non-migratory species the terms migrantes and alienicolae are not applicable. In these cases the winged and wingless viviparous females are more conveniently referred to as fundatrigeniae alatae or apterae as the case may be, and either one or the other may give rise to the sexuparae.

A high degree of specialization is met with in *Hormaphis* and the allied genera *Hamamelistes* and *Cerataphis*. They are gall-formers not only on the primary host, but often on the secondary one also; cornicles are vestigial or wanting and the sexuales are usually small and apterous. The alienicolae are flattened and scale-like, often with a marginal fringe of wax glands, which imparts to them a close resemblance to an Aleyrodid. The life-history may become greatly abbreviated, and both the intermediate host and the aleyrodiform generations thereon eliminated, as in *Hormaphis hamamelidis*. According to Morgan & Shull (1910), in the vicinity of New York this species has only fundatrices, sexuparae and sexuales generations.

The physiological mechanisms underlying host-alternation and polymorphism are obscure, but these changes are probably, at least in part, the result of alterations in the physiology of the growing host-plant. Work by Kennedy and his colleagues (1950; 1951) on *Aphis fabae* and *Myzus persicae* shows that the aphides' readiness to feed and their rate of reproduction depend not only on the host species but also on the age and physiological condition of its leaves, actively growing and senescing leaves being preferred to mature or dying ones. The normal association of each seasonal form with its respective primary winter host and secondary summer host is therefore not obligatory but is due to the normal inaccessibility of the summer host to fundatrigeniae and to the normal unsuitability (due to maturity) of the winter host when winged alienicolae are about. Under the appropriate conditions, a reversal of normal relations was observed: fundatrigeniae of *A. fabae* colonized very young sugar-beet leaves and winged alienicolae started colonies on actively growing shoots of *Euonymus*.

So far as polymorphism is concerned, A. C. Evans (1938) has shown for *Brevicoryne brassicae* that the proportion of alate forms produced on different cabbage plants is inversely related to the latter's protein content. On the other hand, Schaefer (1938) and others consider that the water-balance of the developing insect is an important determining factor, a low water-content—such as results when aphids are partially starved through overcrowding—leading to the production of alates. Shull (1942 and earlier papers) appears to believe from experiments on *Macrosiphum solanifolii* that the parental generation is caused to produce apterous progeny under the direct influence of high temperatures and continuous light while alates result at

lower temperatures and in intermittent light. Unfortunately he did not investigate chemical changes in the host-plant or the aphides.

The remarkable reproductive powers of these insects has already been referred to (p. 420) and the capacity of different species in this respect varies within very wide limits. Numerical evidence of the fecundity of *Sappaphis crataegifoliae* is afforded by Baker & Turner (1916). The fundatrix produces on an average 71 young. From 5 to 7 generations of spring forms occur and consist at first exclusively of fundatrigeniae, but migrantes appear in increasing numbers in each generation. The average number of young produced by the fundatrigeniae was 121 per female: the later generations were rather less prolific. The migrantes yielded on an average 18 young per female, the alienicolae 65, sexuparae 7, and the sexuales produced an average of 6 eggs per female. It can be readily imagined that if this numerous progeny survived, the available supply of plant life would speedily become exhausted. This result is avoided, owing to the fact that aphides are destroyed by very numerous parasitic Hymenoptera, they also form the food supply for the progeny of many Aculeata and are further preyed upon by great numbers of Coccinellidae and larval Syrphidae and Neuroptera. In addition to the above enemies, vast numbers are washed away by rains, and many migratory forms probably perish through failing to reach suitable hosts. In spite of all these and other controlling agencies, sufficient numbers survive to render many species pests of prime importance to the agriculturist and fruit-grower.

The literature on the family is very extensive. Theobald's (1926–29) monograph on the British species has now been supplemented by the works of Ris Lambers (1933–34) and Stroyan (1950), while Ris Lambers (1938–49) has partially monographed the European species and Börner (1952) surveys the C. European forms. General taxonomic works include the older papers by Kaltenbach (1843), Koch (1854–57) and Tullgren (1909) and recent ones by Baker (1920), Börner (1930; 1938) and Oestlund (1942). Among papers on the N. American fauna, see Hottes & Frison (1931) and Gillette & Palmer (1931–36). For lists of species and their host-plants, see Davidson (1925), Patch (1938) and Averill (1945), while Börner & Schilder (1932) survey the species of economic importance. Anatomical information is given by Witlaczil (1882), Mordvilko (1895), Davidson (1913; 1914), Baker (1915) and Weber (1928). General biological accounts are due to Mordvilko (1907; 1909) and Weber (1929–35) and the life-history and biology of individual species is dealt with by, among others, the following: Davis (1914; 1915), Patch (1912), Baker & Turner (1916; 1919), Matheson (1919), Jones & Gillette (1918), Marchal (1928; 1933), Smith (1936) and Jones (1942).

FAM. PHYLLOXERIDAE.—This relatively small family includes such forms as *Phylloxera*, occurring on oaks, and *Viteus vitifolii*, the notorious Vine Phylloxera. The life-history attains a high degree of complexity among Phylloxerids and in *Phylloxera quercus* Lichtenstein states that no less than twenty-one forms occur in the life-cycle. In *V. vitifolii* of the vine the life-history, in a summarized form, is as follows according to Grassi (1915). The fundatrices are seldom met with on the European vine, and their fate on that plant has not been definitely settled. Grassi states that they usually perish, while those on the American vine produce leaf-galls; in no case do they develop on the roots as was formerly maintained. Given a suitable race of vine the fundatrices, therefore, are *gallicolae* or leaf-gall formers. They lay a large number of eggs and their progeny, or fundatrigeniae, are dimorphic when newly hatched. Grassi recognizes *neogallicolae-gallicolae* or those which will become gallicolae and *neogallicolae-radicicolae* or those which pass to the roots and become *radicicolae*. The neogallicolae-gallicolae pass through several generations producing in each case both gallicolae and radicicolae. The former appear in greater numbers when the vine is in active growth and never develop on the roots. The radicicolae are produced from the later eggs when the season is advanced. They may continue as radicicolae and hibernate as nymphs, or produce sexuparae. The latter are winged and fly to the aerial parts of the vine to lay their eggs, which are of two kinds—the larger being female-producing and the smaller giving rise to males. The sexuales are small and apterous; the females each lay a single large overwintering egg, on the bark of the trunk and branches, which hatches the following year into a fundatrix. The actual details of the life-cycle on the European vine in southern Europe has been productive of much discussion, but it seems probable, from Grassi's account, that the radicicolae are the principal form of the species on that host, and that gallicolae are seldom met with. When, however, European vines are in contact with heavily galled American plants, it is stated that they are sometimes infested with neogallicolae-gallicolae derived from the latter.

FAM. ADELGIDAE (Chermesidae).—This family includes such genera as *Adelges* and *Pineus* and all its members are confined to conifers. Two hosts are normally required for the complete life-cycle which extends over two years; the primary hosts are species of *Picea* (Spruce) and the secondary host may be *Larix*, *Pseudotsuga*, *Tsuga*, *Pinus* or *Abies*, according to the species of Adelgid concerned. In a few cases the life-cycle is confined to either the primary or the secondary host. The life-history (e.g. Cholodkovsky, 1907; Börner, 1909; Marchal, 1913; Chrystal, 1922; Speyer, 1923; Cameron, 1936) is complex and has proved difficult to elucidate, especially as some species are difficult to distinguish anatomically. In a typical life-cycle, however, the following forms may be recognized (Marchal's terminology): (1) The apterous *sexuales* are produced on the primary host and the eggs which the females lay hatch in the autumn, giving rise to nymphs of (2) the apterous *fundatrices*.

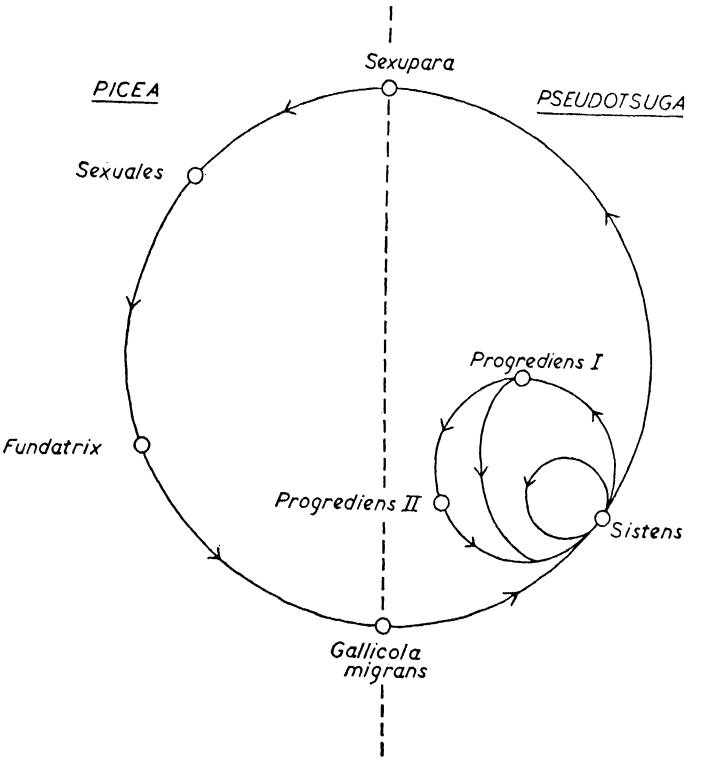


FIG. 355.—Life-cycle of *Adelges cooleyi* in Scotland (based on Cameron, 1936)

These nymphs overwinter and mature in the following spring when they lay parthenogenetic eggs from which hatch (3) the young *gallicolae*. The members of this stage immediately settle at the base of the spruce needles and produce a characteristic gall. Within the gall some of these young nymphs develop into apterous *gallicolae nonmigrantes* which remain on the spruce and produce further fundatrices parthenogenetically while others develop into alate *gallicolae migrantes* which fly to the secondary host. Here they give rise parthenogenetically to (4) the apterous *exsules*. In *Pineus* the exsules are all alike, but in *Adelges* the first generation of exsules are known as *sistentes* and give rise parthenogenetically (after overwintering as a young nymph—the neosistens) to alate *sexuparae* and to apterous *progredientes*. The latter produce a number of generations, progrediens usually alternating with sistens; the sexuparae fly to the primary host where they lay parthenogenetic eggs from which develop the sexuales. The life-history of *Adelges cooleyi* is shown diagrammatically in Fig. 355. For the taxonomy of Adelgids, see especially Cholodkovsky (1895–96), Börner (1908) and Annand (1928).

Superfamily **Coccoidea**

Modern workers regard this group as composed of several families which, in spite of their great diversity in habits and structure, are all characterized by the more or

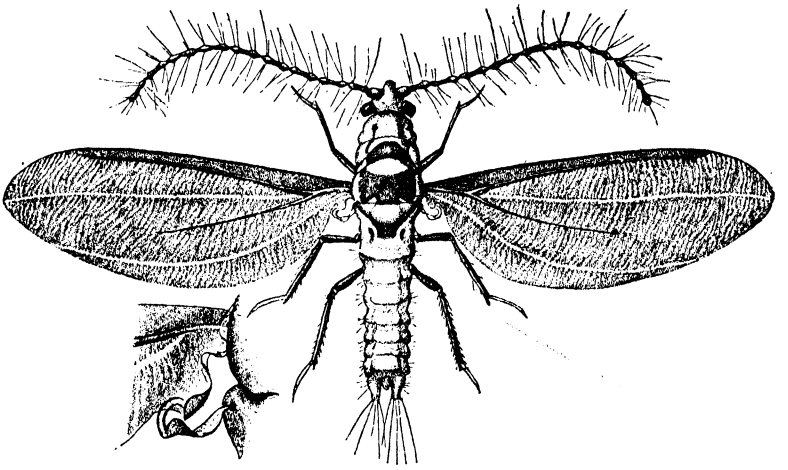


FIG. 356.—*Icerya purchasi*, male, enlarged; on left, wing pocket and hooks more highly magnified

After Riley, *Ins. Life*, 1.

less degenerate females (Fig. 357) which are apterous, obscurely segmented and may be scale-like, gall-like or with a waxy or powdery coating. Their legs and antennae are often atrophied, the tarsi, when present, are 1-segmented with a single claw and the rostrum is short. The early male instars usually resemble the females but adult males (Fig. 356) are more normal in appearance, recalling the Aleyrodidae in general facies but with the hind wings reduced to haltere-like structures or completely apterous and with the mouthparts atrophied. The fore wing, when present, has a greatly reduced venation (Fig. 356. See Patch, 1909). In *Pseudococcus*, for example, R is unbranched and only a spur-like rudiment of Sc and a part of M are present. The hind wings in those species where they are developed are represented by a pair of halteres which develop from the metathoracic wing-buds (Witlaczil); each is furnished with one or more hooklets which engage in a basal pocket of the corresponding fore wing. Taxonomic works on this group are mentioned below; its general biology is dealt with by Balachowsky (1939) and Bodenheimer (1935).

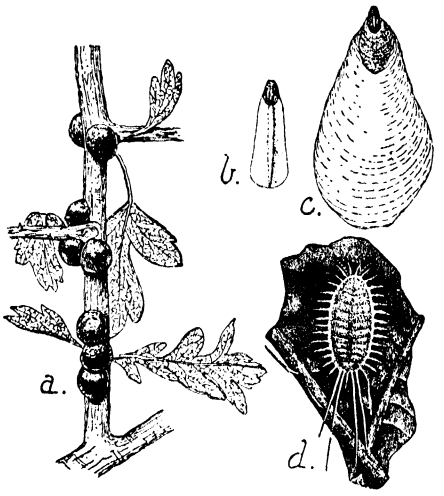


FIG. 357.—A, *Eulecanium coryli* on *Crataegus* (original); B, male and C, female scales of *Chionaspis salicis* (*after* Green); D, *Pseudococcus* female (*after* Comstock)

The form most usually encountered is the female and consequently such expressions as 'scale insect' or 'mealy bug' refer particularly to that sex. The plant-hosts are extremely numerous and probably include representatives of all orders of Phanerogams. It is therefore not surprising that the group includes important pests of cultivated plants, especially in tropical and subtropical areas and under glasshouse cultivation elsewhere. The San José Scale (*Quadraspidiotus perniciosus*) of deciduous

fruits and the Red Scales of Citrus (*Aonidiella aurantii* and *Chrysomphalus ficus*) may serve as examples. The food-habits of the Coccoidea are variable, some species being monophagous (e.g. *Cryptococcus fagi* on *Fagus sylvaticus* and *Physokermes abietis* on *Abies excelsa*) while others feed on a wide variety of plants. *Lepidosaphes ulmi*, for example, is known to infest about 130 widely separate species and species of *Pseudococcus* occur on a variety of plants grown under glass. The facility with which the living insects can be transported over long distances on their hosts has resulted in many becoming almost cosmopolitan and even strict quarantine measures are not wholly successful in preventing their dispersal by man.

The life-history has been fully studied in only a few cases. Reproduction may be bisexual or, in some cases, parthenogenetic and oviparous, ovoviviparous and viviparous forms are known, while *Icerya purchasi* is a functional hermaphrodite (p. 193). The eggs are protected in various ways, sometimes being enclosed in an ovisac of felted waxen threads (e.g. *Pseudococcus*) or, as in the Diaspididae, enclosed beneath the scale-like covering of the female, or between wax plates secreted from the end of the abdomen (*Orthezia*) or beneath the body of the female (*Eulecanium*). The first-stage nymphs ('crawlers') are provided with functional legs and their mobility ensures the dispersal of the species. Subsequent nymphal instars and the adult females are stationary, being attached by their mouthparts to the host, and though Pseudococcid nymphs always possess legs, one or more apodous instars occur in the life-cycles of other families. Females have one less instar than males, indicating that they are neotenous. The males, when winged, develop wing-pads in the last two instars which are commonly known as prepupal and pupal stages because of some resemblance to the corresponding stages of Endopterygote insects (Fig. 358, B). Mäkel (1942) gives a detailed account of the metamorphosis of a male coccid.

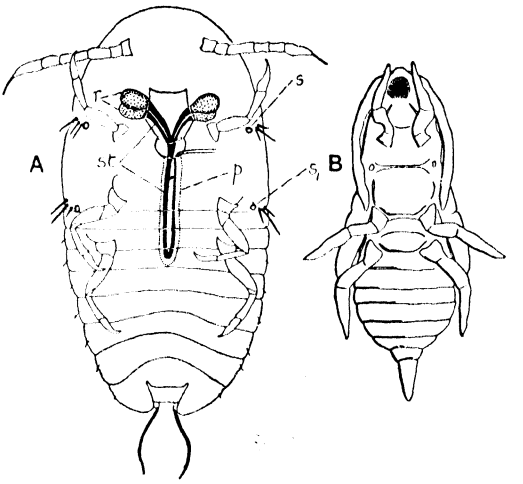


FIG. 358.—A, larva of *Coccus hesperidum*, ventral view × 110

p, stylet sheath; *r*, retort-shaped organs; *s*, s_1, spiracles; *st*, stylets.

B, male pupa of *Lepidosaphes fulva*, ventral view × 48

Adapted from Berlese, *Riv. di. Pat. Veg.*, 1893–95.

Like the aphides, many Coccoidea secrete honey-dew, which renders them attractive to ants and in some cases, e.g. *Pseudococcus kenyae*, tended by the ant *Pheidole punctulata*, the multiplication of the coccid colonies is greatly increased when ants are present (see Nixon, 1951, for a review of this subject).

The group is now considered to consist of over a dozen families, opinions differing on the exact number recognized and their precise limits. The taxonomy of the Coccoidea is still in an unsatisfactory state and is based almost entirely on characters provided by the adult female. Among older general taxonomic works are those of Lindinger (1912), Leonardi (1920) and MacGillivray (1921) while more recently there have appeared accounts by Ferris (1937–51) and Balachowsky (1942) which maintain a much higher standard of description. Green (1927–28) has extended Newstead's (1901–03) earlier work on the British species and has monographed the species from Ceylon (Green, 1896–1922). Other taxonomic monographs are cited below, while for general biological accounts see Pflugfelder (1939) and Balachowsky (1937–50).

The following key, which refers to adult females only, will help in identification:

1. Abdominal spiracles present; if, rarely, absent, then fore legs stout, enlarged and fossorial 2
–. Abdominal spiracles absent; fore legs when present not modified thus . 3

2. Setigerous anal ring present . . . . . ORTHEZIIDAE (p. 454)
–. Setigerous anal ring absent . . . . . MARGARODIDAE (p. 454)

3. Pygidium present, i.e. terminal abdominal segments more or less fused and distinct from anterior ones; body usually covered by thin, shield-like scale . . 4
–. Pygidium absent 5

4. Pygidial segments less completely fused; legs present CONCHASPIDIDAE (p. 455)
–. Pygidium quite distinct from anterior abdominal segments; legs absent or, rarely, vestigial . . . . . DIASPIDIDAE (p. 455)

5. Posterior end of body cleft; openings of wax-glands rarely 8-shaped . . 6
–. Posterior end not cleft; if apparently so, then some of wax-gland openings 8-shaped 7

6. Anus covered by 1 dorsal plate . . . . . ACLERDIDAE (p. 455)
–. Anus covered by 2 dorsal plates, rarely none . . . COCCIDAE (p. 455)

7. Abdomen narrowed apically or produced into anal tube; gallicolous or enclosed in resinous cell 8
–. Abdomen and habit not thus 9

8. Enclosed in dense resinous cell; legs absent . . LACCIFERIDAE (p. 454)
–. Gallicolous; at least 1 pair of legs . . . . APIOMORPHIDAE (p. 455)

9. Anal opening at level of 1st abdominal segment in centre of dorsal surface of body . . . . . STICTOCOCCIDAE (p. 455)
–. Anal opening at end of body 10

10. Wax-gland openings 8-shaped, usually in rows . ASTEROLECANIIDAE (p. 455)
—. Wax-gland openings otherwise 11

11. Antennae 11-segmented . . . . PHENACOLEACHIIDAE (p. 455)
—. Antennae with 9 or fewer segments, often reduced or absent . . . 12

12. Anal ring present 13
—. Anal ring absent 14

13. Anal ring with 4 or more setae, often cellular . . PSEUDOCOCCIDAE (p. 455)
—. Anal ring with 2 setae, never cellular . . . DIASPIDIDAE part (p. 455)

14. Body elongate, cylindrical; hind legs, when present, 2–3 times as long as others CYLINDROCOCCIDAE (p. 455)
—. Not thus; legs, when present, subequal 15

15. Ducts of wax glands minute, arising from centre of cluster of sessile pores. DACTYLOPIIDAE (p. 455)
—. Ducts not arising in this way; confined to oaks . . KERMIDAE (p. 455)

FAM. MARGARODIDAE.—The females of this family possess rather distinctly segmented bodies, often covered with a waxy secretion. In *Monophlebus* this takes the form of a mealy coating while the bodies of the subterranean *Margarodes* are covered with pearl-like waxy scales and form the 'ground-pearls' which are collected and strung into necklaces in S. Africa and the Bahamas. *Margarodes* females are capable of undergoing prolonged quiescence ('encystment') accompanied by histolysis. The legs and antennae of Margarodids are usually well-developed and simple eyes are often found. The adult male is usually winged, has simple 10-segmented antennae and normally possesses compound eyes, *Steingelia* being an exception to the latter rule. *Icerya purchasi* (see Dingler, 1930) is injurious to citrus trees but has been controlled in California by the introduction of the predacious Coccinellid beetle *Rodolia cardinalis*. The family has been monographed by Morrison (1928).

FAM. ORTHEZIIDAE.—A small group native to America and the Palaearctic region though *Orthezia insignis* is a widely distributed pest of many glasshouse crops. Females of this family show rather distinct segmentation of the body which is covered with white waxy plates. They have normal legs and antennae and simple eyes. The males have compound eyes. For a taxonomic treatment, see Morrison (1952).

FAM. LACCIFERIDAE (Lac Insects).—This family is largely confined to the tropics and subtropics (Chamberlin, 1923–25). Its females are highly degenerate with vestigial antennae, no legs and an irregularly globular body enclosed in a dense resinous cell. The Indian Lac-insect, *Laccifer lacca* (Fig. 359) is of great commercial importance since its secretion provides the stick-lac from which shellac is prepared. Its biology has been studied by Imms & Chatterjee (1915) who report its occurrence

on many species of trees where it undergoes two generations annually and has dimorphic males—the first generation includes both alate and apterous forms, the second consists solely of wingless ones. *Gascardia*, of Madagascar, yields an inferior type of lac ('gum-lac') containing much wax.

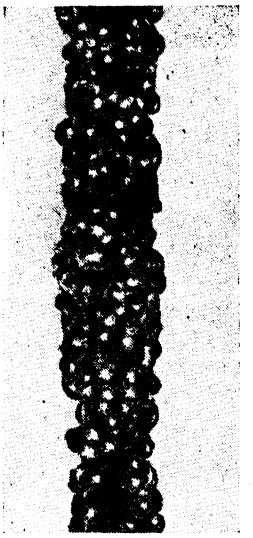


FIG. 359.—Portion of a twig of *Butea frondosa* encrusted by *Laccifer lacca* (actual size). India

FAM. PSEUDOCOCCIDAE.—The familiar and distinctive 'mealy-bugs' belong here (Ferris, 1937–53). They are typified by the large genus *Pseudococcus* with many species injurious to tropical and glasshouse crops: *P. njalensis* is a vector of a serious virus disease of cacao ('swollen shoot'). The females are usually elongate-oval with distinct segmentation and generally covered with a mealy or filamentous waxy secretion which may be extended into lateral or terminal filaments. Legs are well-developed, antennae less so. *Ripersia* is subterranean and *Ericoccus devoniensis* causes galls on *Erica*.

FAM. KERMIDAE.—As here defined, this family includes only *Kermes*, the species of which are confined to oaks where the adult female has a spheroidal, gall-like form with a strongly sclerotized integument. It may be noted that Ferris (1937) associates *Kermes* with many Pseudococcidae (Eriococcinae) in his family Kermidae.

FAM. DACTYLOPIIDAE.—As restricted by Ferris (1937) this group includes only *Dactylopius*, *D. coccus*—a native of Mexico, living on various Cactaceae—producing the dyestuff cochineal which is extracted from the bodies of the females and used for colouring foodstuffs and cosmetics. The females are elongate-oval, convex and have small legs and antennae (Fig. 357).

FAM. COCCIDAE (Lecaniidae).—This is one of the most important families and its members display considerable diversity of form. The segmentation of the female is obscure and the integument may be naked or covered with wax while the degree of development of antennae and legs varies considerably. Species of *Saissetia* are injurious to many cultivated plants (e.g. Smith, 1944) while *Ericerus pe-la* and *Ceroplastes ceriferus*, both Oriental, yield wax on a small commercial scale (see also Blumberg, 1935).

FAM. ACLERDIDAE.—Contains only the subterranean *Aclerda*.

FAM. ASTEROLECANIIDAE.—These scales are of variable form with reduced antennae and legs vestigial or absent. In the American *Cerococcus quercus*, the female is completely embedded in a mass of yellow wax, while in *Asterolecanium variolosum* from the Holarctic region the females lie in pits on the twigs of oak and olive (see also Habib, 1943).

FAM. PHENACOLEACHIIDAE.—Contains only one species (*P. zelandica*) on *Fagus*, *Cupressus* and *Podocarpus* in New Zealand.

FAM. STICTOCOCCIDAE.—Includes only *Stictococcus*, the female of which is circular, flattened and with a wax-impregnated integument. The first instar shows unusually marked sexual dimorphism.

FAM. APIOMORPHIDAE.—Sometimes known from the shape of the female as 'pegtop coccids', these are confined to Australia and New Zealand where they form galls on *Eucalyptus*.

FAM. CYLINDROCOCCIDAE.—The members of this small family are restricted to the Southern hemisphere.

FAM. CONCHASPIDIDAE.—These include a few tropical genera resembling the Diaspididae in the presence of a shield-like scale which covers the female, but differing from them in that the nymphal exuviae are not incorporated into the scale.

FAM. DIASPIDIDAE.—A large family, the N. American species having been monographed by Ferris (1937–53). The adult females are specialized by the absence or vestigial nature of the antennae and the loss of legs and are covered by a hard waxy scale responsible for their common name of 'armoured scales'. Representatives of the family occur in all regions and include many injurious species such as the Red Scales of citrus (*Aonidiella aurantii* and *Chrysomphalus ficus*) and the San José Scale (*Quadraspidiotus perniciosus*) which attacks deciduous fruit trees. *Lepidosaphes ulmi*, the Mussel Scale, also belongs here.

Suborder 2. HETEROPTERA

The classification of this suborder has been discussed by Reuter (1910) who reviewed the various earlier systems and criticized the values of the characters utilized. In addition to this work the reader should also consult Schiödte (1870), who lays great stress on the method of articulation of the hind coxae, the tentative paper by Kirkaldy (1908), and others by Reuter (1912), Ekblom (1929), China (1933), Börner (1934) and Leston *et al.* (1954). The arrangement of families here adopted retains the time-honoured division into Gymnocerata and Cryptocerata which is based on obvious antennal characters and, broadly speaking, separates the truly aquatic forms from those which are either terrestrial or live only on the surface of water. Much further morphological work is required before relationships within the Heteroptera can be clearly defined, and though some of the described superfamilies are evidently natural, opinions differ widely about others. For this reason, the present account gives no formal subdivision of the Heteroptera into superfamilies.

The very extensive taxonomic literature on the Heteroptera is partly accessible through the works cited on p. 436. In addition the following accounts of the fauna of restricted areas may be mentioned:

Europe: Fieber (1861), Stål (1870–76), Puton (1878–81), Reuter (1878–96), Stichel (1925–38), Hedicke (1935) and Gulde & Jordan (1933–38); Saunders (1892) on the British fauna is out of date, but the British water-bugs are dealt with by Macan (1941; 1941a). **N. America:** van Duzee (1917), Britton et al. (1923), Parshley (1925), Blatchley (1926), Torre-Bueno (1939–46). **Central and S. America:** Distant (1880–1900), Champion (1897–1901). **Africa:** Stål (1864–66). **India:** Distant (1902–1918).

General accounts of the Heteroptera are given by Beier (1938) and Poisson (1951) while Weber (1929–35; 1930) deals with their biology and Butler (1923) describes systematically the biology of the British species. Various aspects of the biology of aquatic Heteroptera are discussed by Hungerford (1919), Poisson (1924), Jordan (1928), Karny (1934) and Jaczewski (1937).

Key to families of Heteroptera

The following key to the families of Heteroptera is based mainly on Reuter (1912) but the families recognized are almost exactly those given by China (1933). The key is not entirely satisfactory and difficulty may be experienced in trying to identify brachypterous specimens or members of a few annectent genera.

1. Antennae shorter than head, usually concealed; eyes present . . . 2
–. Antennae usually much longer than head; if shorter, then eyes absent . . 10

2. Front tarsi spatulate, 1-segmented; rostrum 1- or 2-segmented . . . CORIXIDAE (p. 467)
–. Front tarsi not spatulate, rarely 1-segmented; rostrum 3- or 4-segmented . 3

3. Head completely fused with prothorax, the boundary indicated by a shallow impression . . . . . HELOTREPHIDAE (p. 467)
–. Head free or at most partially fused with prothorax 4

4. Ocelli present 5
–. Ocelli absent 6

5. Fore legs raptorial; antennae concealed . . . GELASTOCORIDAE (p. 465)
–. Fore legs normal; antennae free . . . . OCHTERIDAE (p. 465)

6. Fore coxae inserted at front of prosternum; hind tarsi with distinct claws . 7
–. Fore coxae inserted at back of prosternum; hind tarsi without claws . . 9

7. Membrane without veins . . . . . NAUCORIDAE (p. 465)
–. Membrane with reticulate venation 8

8. Hind tibiae flattened and fringed for swimming; respiratory funnel short . BELOSTOMATIDAE (p. 466)
–. Hind tibiae simple; respiratory funnel usually long . . NEPIDAE (p. 466)

9. Rostrum 4-segmented; abdomen with ventral furrow in which lies median carina . . . . . NOTONECTIDAE (p. 466)
–. Rostrum 3-segmented; abdomen without furrow or carina PLEIDAE (p. 467)

10. Eyes present 11
—. Eyes absent 49

11. Pulvilli usually absent; if present then either meso- and metapleura divided or clavus membranous or hemelytra reticulate or base of membrane densely reticulo-punctate; tibiae simple apically 12
—. Pulvilli usually present; if absent then tibiae with apical membranous lobe; meso- and metapleura simple; hemelytra with coriaceous clavus, never reticulate or with reticulo-punctate membrane 37

12. Hemelytra of macropterous forms with clavus which meets that of opposite side behind scutellum to form distinct claval commissure 13
—. Clavus of macropterous forms not exceeding scutellum to form commissure; body flattened, with head produced and bearing pointed antennal tubercles . 36

13. First two antennal segments very short, last two long and pilose, 3rd segment swollen basally 14
—. 2nd antennal segment usually equal to or longer than 3rd which is never swollen basally 15

14. Head directed backwards between fore coxae . . SCHIZOPTERIDAE (p. 461)
—. Head more or less porrect . . . . CRYPTOSTEMMATIDAE (p. 461)

15. Meso- and metapleura divided or if, rarely, simple then clypeus triangular, broader apically; cuneus present in macropterous forms 16
—. Meso- and metapleura simple 20

16. Clypeus with parallel or sub-parallel sides 17
—. Clypeus broadened apically; ocelli absent; micropterous . CIMICIDAE (p. 462)

17. Ocelli absent in both sexes; tarsi usually 3-segmented . MIRIDAE (p. 461)
—. Ocelli present in males, sometimes absent in females, in which case these are micropterous with swollen abdomen and 2-segmented tarsi . . . 18

18. Tarsi 3-segmented . . . . . ANTHOCORIDAE (p. 461)
—. Tarsi 2-segmented 19

19. Membrane with divided semicircular basal cell; male genitalia asymmetrical; female with 8th sternite entire . . . . ISOMETOPIDAE (p. 461)
—. Membrane with one rectangular basal cell; male genitalia symmetrical; females with swollen abdomen and divided 8th sternite . MICROPHYSIDAE (p. 462)

20. Hind coxae hinged; rostrum 3-segmented 21
—. Hind coxae rotatory 25

21. Ocelli absent; eyes small; hemelytra reduced . . . AEPOPHILIDAE (p. 459)
—. Ocelli present; eyes large and projecting. 22

22. Cuneus present . . . . . VELOCIPEDIDAE (p. 459)
—. Cuneus absent 23

23. Fore tarsi 1-segmented, middle and hind tarsi 2-segmented . . . LEOTICHIIDAE (p. 459)
—. All tarsi 3-segmented 24

24. Ocelli on pedunculate tubercle . . . . LEPTOPODIDAE (p. 459)
—. Ocelli not on pedunculate tubercle . . . SALDIDAE (p. 459)

25. Claws ante-apical; hemelytra homogeneous 26
—. Claws apical 27

26. Middle femora markedly exceeding end of abdomen; vertex without longitudinal groove . . . . . GERRIDIDAE (p. 460)
—. Middle femora scarcely, if at all, exceeding end of abdomen; vertex with longitudinal groove . . . . . VELIIDAE (p. 460)

27. Pulvilli absent, rarely with membranous appendage between claws, in which case clavus and membrane confluent 28
—. Pulvilli present; tarsi 2-segmented. 35

28. Prosternum without stridulatory groove 29
—. Prosternum with stridulatory groove 34

29. Ocelli absent; body linear with long, apically dilated head HYDROMETRIDAE (p. 461)
—. Ocelli usually present, if absent then head not dilated apically . . . 30

30. Head constricted basally and behind eyes; hemelytra entirely membranous . ENICOCEPHALIDAE (p. 460)
—. Head not thus constricted; hemelytra not entirely membranous . . . 31

31. Clavus membranous or sub-membranous and confluent with veinless membrane 32
—. Clavus coriaceous and distinct 33

32. Rostrum 4-segmented; antennae usually 5-segmented . HEBRIDAE (p. 461)
—. Rostrum 3-segmented; antennae 4-segmented . MESOVELIIDAE (p. 461)

33. Tarsi 2-segmented . . . . . JOPPEICIDAE (p. 463)
—. Tarsi 3-segmented . . . . . NABIDIDAE (p. 459)

34. Antennae filiform, often apically slender, geniculate . REDUVIIDAE (p. 459)
—. Last antennal segment clavate or fusiform; fore legs stoutly raptorial. . PHYMATIDAE (p. 460)

35. Head bifid anteriorly; ocelli present in macropterous forms PIESMIDAE (p. 464)
—. Head not bifid anteriorly; ocelli absent; body and hemelytra densely reticulate TINGIDAE (p. 464)

36. Head widened posteriorly and enclosing eyes; trochanters distinct . . DYSODIIDAE (p. 462)
—. Head not widened behind prominent eyes; trochanters fused with femora . ARADIDAE (p. 462)

37. Membrane usually with 5 or fewer veins; if veins numerous and branching then ocelli absent; scutellum normal 38
—. Membrane with many veins and ocelli present; if otherwise scutellum unusually large 43

38. Pulvilli absent; tibiae with apical membranous lobe . . . . . THAUMASTOTHERIIDAE (p. 463)
—. Pulvilli present; tibiae without lobe 39

39. Ocelli absent . . . . . PYRRHOCORIDAE (p. 463)
—. Ocelli present 40

40. Membrane without distinct veins; elongate forms with long antennae. . COLOBATHRISTIDAE (p. 463)
—. Membrane with distinct veins 41

41. Antennae geniculate; head constricted in front of eyes . BERYTIDAE (p. 463)
—. Antennae not geniculate; head not thus constricted 42

42. Membrane with 4 veins which form 3 large preapical cells then branch . HYOCEPHALIDAE (p. 464)
—. Membrane usually with 4 or 5 veins which never form preapical cells . . LYGAEIDAE (p. 463)

43. Scutellum smaller, never reaching membrane; antennae 4-segmented. . COREIDAE (p. 463)
—. Scutellum larger, rarely not reaching membrane, in which case antennae 5-segmented 44

44. Hemelytra about twice as long as abdomen, folded beneath enlarged scutellum at rest; tarsi 2-segmented . . . . . PLATASPIDIDAE (p. 465)
—. Hemelytra usually normal; if elongate then tarsi 3-segmented . . . 45

45. Connexivia of 6 abdominal tergites visible; tibiae spinose CYDNIDAE (p. 465)
—. Connexivia of 7 abdominal tergites visible; tibiae rarely spinose. . . 46

46. Head and body with lamellate lateral expansions; antennae 3-segmented . PHLOEIDAE (p. 465)
—. Lamellate lateral expansions absent; antennae 4- or 5-segmented . . 47

47. Base of antenna concealed by side-margins of head 48
—. Base of antenna not concealed . . . . . UROLABIDAE (p. 465)

48. Body concave ventrally; base of corium not reaching sides of body to form epipleura . . . . . APHYLIDAE (p. 465)
—. Body flat or convex ventrally; base of corium reaching sides of body and forming epipleura . . . . . PENTATOMIDAE (p. 464)

49. Broadly oval, flat, apterous forms resembling woodlice and living in termites' nests . . . . . TERMITAPHIDIDAE (p. 463)
—. Oblong forms with vestigial hemelytra parasitic on bats POLYCTENIDAE (p. 462)

GYMNOCERATA

FAM. SALDIDAE (Acanthiidae).—*Head short and broad; eyes very large and prominent; ocelli present. Rostrum 3-segmented, not applied against ventral surface of head. Metathorax without scent-glands. Coxae hinged; tarsi 2-segmented.* Most of the 150 or so described species (Drake & Hoberlandt, 1952a) frequent borders of streams and marshy places, especially near the coast, and are predominantly Holarctic. They usually inhabit mud, moss or salt-marsh plants and fly and run rapidly. *Saldula orthochila* occurs in dry places while, at the other extreme, *S. pallipes* can withstand submergence by tides (Brown, 1948). So far as is known they are predacious. For the biology of *Salda littoralis*, see Jordan & Wendt (1938).

FAM. LEPTOPODIDAE.—This small family resembles the Saldidae in structure and habits and is represented mainly in the Oriental region (Horvath, 1911; Drake & Hoberlandt, 1952).

FAM. LEOTICHIIDAE.—This group is allied to the two preceding families and includes only *Leotichius*, with two species from S.E. Asia (China, 1933).

FAM. AEPOPHILIDAE.—A family including a single species *Aepophilus bonnairei*. This insect has vestigial hemelytra and lives beneath stones, etc., some distance below high-tide mark on the coasts of Ireland, South England and neighbouring countries of Europe. Its biology has been studied by Lienhart (1913).

FAM. VELOCIPEDIDAE.—*Medium-sized oval insects with prominent eyes; ocelli present. Antennae long and thin. Rostrum 3-segmented, the 2nd segment very long. Metapleura with small scent-gland orifices. Cuneus present.* This family, of uncertain affinities, includes only a few Oriental species of *Velocipeda*. It is perhaps to be regarded as a subfamily of the Nabididae.

FAM. NABIDIDAE.—*Thin antennae with 4 or 5 segments. Rostrum 4-segmented. Coxae rotatory. Prosternal stridulatory groove absent. Scent-gland openings present on metapleura. Fore legs somewhat raptorial; tarsi 3-segmented.* The Nabididae, partly monographed by Reuter & Poppius (1909), includes about 300 species from all regions, especially the tropics. Its members are all predacious and commonly encountered on herbage where they attack the smaller phytophagous insects and lay their eggs in plant stems (see, e.g., Mundinger, 1922). The males of some species have a stridulatory organ at the apex of the abdomen and, according to Carayon (1950), fertilization in *Prostemma* and *Alloeorrhynchus* involves the passage of spermatozoa into the haemocoele in a fashion recalling the remarkable mechanism known to exist in *Cimex* (p. 434). For this and other reasons they are therefore perhaps closer to the Cimicoid families than to the Reduvioid ones. Harris (1928) describes the N. American species.

FAM. REDUVIIDAE.—*Allied to the Nabididae but prosternal stridulatory groove present, metathoracic scent-glands absent and rostrum 3-segmented. Antennae filiform.* This extensive family exhibits an extremely wide range of variation in form among various genera, such dissimilarity being scarcely paralleled in any other family of insects. Upwards of 3,000 species are known and are grouped by Usinger (1943) in 20 subfamilies, of which the largest is the Harpactorinae. The biology of many species is described by Readio (1927). A large number is predacious and they are sometimes known as 'Assassin Bugs'. Although usually living on the blood of other insects they occasionally attack the higher animals, including man. Species of *Triatoma* and *Rhodnius prolixus* are the main carriers of *Trypanosoma cruzi*, the causal agent of a fatal form of human trypanosomiasis in South America (Usinger, 1944). *Triatoma*

rubrofasciata also extends into Madagascar and South Asia; its nymphs are common in houses, where they are partially concealed with floor debris. There are numerous records of violent reactions to Triatomine bites but cases of severe illness lasting several days appear to be anaphylactic reactions on the part of hypersensitive individuals, others experiencing no ill effects. *Reduvius personatus* (Fig. 360) also frequents houses, normally preying upon *Cimex* and other insects; it is known to attack man, inflicting severe pain. Although uncommon in Britain it is widely distributed in Europe and has been introduced into North America. Certain members of the large genus *Acanthaspis* are also capable of inflicting painful punctures. Among the more exceptional members of the family is the genus *Afrodecius* in which the 3rd segment of the rostrum is apposable to a process on the 2nd segment, suggesting an organ of prehension. The insect is African and resembles *Lycus* (Coleoptera) in form and coloration. *Rhaphidosoma* is apterous and greatly attenuated, resembling Phasmids. *Arilus cristatus* is the 'Wheel Bug' of North America, which frequents fruit-trees, preying upon various soft-bodied larvae. *Harpactor costalis* preys upon *Dysdercus cingulatus* in India, closely resembling it in coloration (Lefroy).

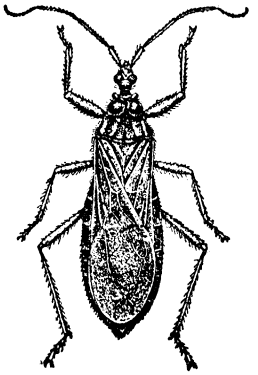


FIG. 360.—*Reduvius personatus* (enlarged)
After Howard.

FAM. PHYMATIDAE (Macrocephalidae).—*Related to the Reduviidae but apical antennal segments swollen and front femora enormously dilated with chelate tibiae.* The 100 or so members of this tropical family (Handlirsch, 1897; Evans, 1931) are predacious, with the fore legs adapted for grasping. Some of the species have the habit of secreting themselves in flowers for the purpose of securing prey which may come within reach. In the oriental genus *Carcinocoris* the whole body is margined with fine spines and the front tibia is articulated to the femur in such a manner as to form a pair of pincers. The prey of these insects consists of small members of other orders and also Tenthredinid larvae. Balduf (1941) describes the biology of *Phymata pennsylvanica*.

FAM. ENICOCEPHALIDAE.—*Reduvioid insects with 4-segmented rostrum; prosternum without stridulatory groove; head constricted basally and behind eyes. Hemelytra entirely membranous.* A small (*c.* 50 spp.) but widely distributed family, the members of which occasionally appear in swarms like midges; such swarms have been observed in South America, Tasmania and Ceylon. In *Aenictopechys alluaudi* (Africa) the rostrum projects forwards in a manner quite different from other Hemiptera, and its apex is bifid. For taxonomy, see Usinger (1945) and Jeannel (1942).

FAM. GERRIDIDAE (Pond-skaters).—*Moderately large, usually slender insects. Rostrum 4-segmented. Small median scent-gland opening on metathorax. Hemelytra, when present, homogeneous. Coxae rotatory; middle and hind legs usually elongate; tarsi 2-segmented with ante-apical claws.* This and the four succeeding families make up the group Gerroidea (Horvath, 1915; China & Usinger, 1949). They are sometimes considered as a separate series (the Amphibicorisae) equivalent to the Cryptocerata and the remaining Gymnocerata. All five families are semi-aquatic, living on the surface of still or running water where they feed mainly on dead insects or those floating there accidentally. The body is covered ventrally with a dense, hydrofuge hair-pile and the wings are frequently reduced. The Gerrididae include over 200 species from all regions, a number of genera being marine. *Gerris*, the common pond-skater, is cosmopolitan, laying its eggs in a group surrounded by a kind of mucilage and attached to submerged plants (Mitis, 1937). *Halobates* and its allies are apterous and frequent the tropical and subtropical oceans, often occurring many hundreds of miles from land. They have been observed running over the surface of the sea in calm weather and feed upon dead, floating marine animals (White, 1883; Usinger, 1938; Barber, 1943). See Drake & Harris (1934) for an account of the Gerridinae of the W. hemisphere.

FAM. VELIIDAE.—*Resemble Gerrididae but stoutly built with 3-segmented rostrum; middle and hind legs not elongate.* The Veliidae include about 200 species from all regions, especially the Neotropical and Oriental. *Velia* affects streams and is often gregarious; macropterous forms are rare and the hemelytra, when present, are entirely membranous. *Rhagovelia* swims against the current of swift streams. The last tarsal segment of its middle pair of legs has a fan-like arrangement of hairs which spreads

out and functions very much after the manner of the webbed feet of water-fowl. The classification of the family is discussed by China & Usinger (1949) and the biology of *Microvelia capitata* from C. America by Frick (1949).

FAM. HYDROMETRIDAE.—*Delicate rod-like insects with long head, 4- or 5-segmented antennae and 3-segmented rostrum. Thoracic gland openings absent. Legs thin and stilt-like. Tarsi 3-segmented; claws apical.* There are about 70 species, mostly tropical, typified by *Hydrometra* (Fig. 361) which is found crawling slowly over the surface of stagnant water. There is a monograph by Hungerford & Evans (1934).

FAM. MESOVELIIDAE.—*Small forms with large head and eyes and long, delicate legs. Antennae 4-segmented; rostrum 3-segmented; claws terminal.* This small family (*c.* 20 species) is widely distributed (Horvath, 1915; 1929). *Mesovelia* frequents the leaves of water-plants, in the stems of which its eggs are embedded (Hungerford, 1917). The New Guinea *Phrynovelia papua* is terrestrial, living among fallen leaves in forests.

FAM. HEBRIDAE (Naeogaeidae).—*Very small, stoutly built forms. Antennae usually 5-segmented; rostrum 4-segmented. Clavus membranous and confluent with membrane.* A small family of minute semi-aquatic species found among *Sphagnum*, *Lemna*, etc. in marshes and other wet localities. *Hebrus* is widely distributed with two British species.

FAM. CRYPTOSTEMMATIDAE (Dipsocoridae, Ceratocombidae).—*Small, delicate insects; head more or less porrect, eyes usually small; ocelli present. Antennae with 2 small basal segments, 3rd and 4th segments long and pilose, 3rd swollen basally. Rostrum 3-segmented. Metathorax without scent-glands. Coxae hinged. Cuneus usually present. Tarsi 3-segmented.* A small but widely distributed family living among moss, dead leaves, etc. (Reuter, 1891; McAtee & Malloch, 1925).

The **Schizopteridae** are often regarded as a subfamily of the Cryptostemmatidae which they closely resemble but have the head strongly bent backwards, with large eyes.

FAM. ISOMETOPIDAE.—*Small, oval insects with ocelli and large eyes. Rostrum 4-segmented. Pronotum strongly transverse. Cuneus present. Tarsi 3-segmented.* This and the five succeeding families constitute the Cimicoidea (China & Myers, 1929). Less than 20 species of Isometopids are known, mostly Holarctic. They live mainly on the bark and dry branches of trees and *Letaba bedfordi* preys on the coccid citrus pest *Aonidiella aurantii* in S. Africa (Hesse, 1947).

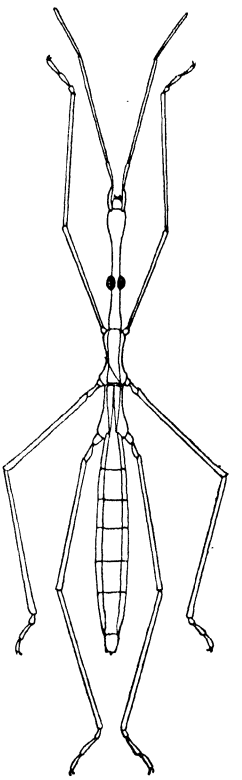


FIG. 361.—*Hydrometra stagnorum* × 8·5. Britain

FAM. MIRIDAE (Capsidae).—*Medium or small, usually delicate insects. Ocelli absent. Rostrum 4-segmented. Cuneus usually present, embolium indistinct. Tarsi almost invariably 3-segmented.* A very large family of *c.* 5,000 species whose taxonomy presents many difficulties (Reuter, 1910; Knight, 1941). It constitutes the largest Palaearctic family of Heteroptera, Oshanin (1912) listing 1,066 species from that region; over 180 occur in Britain and much information on the biology of the Swedish forms is given by Kullenberg (1944). Though the majority live on plant juices, some prey on small arthropods—e.g. *Blepharidopterus angulatus* is an important predator of the Fruit Tree Red Spider Mite, *Metatetranychus ulmi* (Collyer, 1952). Other Mirids do considerable damage to cultivated plants. Thus, *Plesiocoris rugicollis* (Fig. 186), the original host of which was *Salix*, now attacks apple, black- and red-currants (Petherbridge & Husain, 1918) while *Lygus pabulinus* (the Tarnished Plant-bug) is an almost cosmopolitan pest with many named varieties (Crosby & Leonard, 1914). *Helopeltis theivora* is very destructive to tea in Assam.

FAM. ANTHOCORIDAE.—*Small, elongate-oval, flattened insects. Ocelli present. Rostrum 3-segmented. Metathorax with scent-gland openings. Cuneus and embolium present. Tarsi 3-segmented.* This family of about 300 species (Reuter, 1885) is represented in all regions, its members being predacious on small arthropods and occurring mainly on foliage and flowers, under bark or among fallen leaves. *Orius insidiosus* is a major predator on larvae of the corn pest *Heliothis obsoleta* in the U.S.A. (Barber, 1936). *Lyctocoris campestris* occurs in association with human habitations (granaries,

thatched roofs, etc.) and it and some other species (e.g. *Anthocoris kingi*) are known to bite man occasionally. Some Anthocorids are myrmecophiles; some others live in birds' nests.

FAM. MICROPHYSIDAE.—*Allied to the Anthocoridae but rostrum 4-segmented and tarsi 2-segmented. Females usually brachypterous with swollen abdomen and no ocelli.* About 20 species are known, mostly Palaearctic. Some are myrmecophiles, others found among fallen leaves, moss, lichens, etc. They are predacious.

FAM. CIMICIDAE (Acanthiidae: Bed-bugs).—*Oval flattened insects with very short hemelytra; rostrum lying in a ventral groove, ocelli absent, tarsi 3-jointed. Parasites of mammals and birds.* A small but well-defined family of blood-sucking ectoparasites. The bed-bugs (Fig. 362A) belong to the genus *Cimex* and the two common species are *C. lectularius*, which is prevalent throughout Europe and N. America and is almost cosmopolitan, and *C. rotundatus* (= *hemipterus*) which abounds in southern Asia and also in Africa. They are particularly prevalent in dirty houses, especially in large cities, and are nocturnal in habits, hiding by day in any convenient crevices about the walls, floors or furniture of rooms. Man is the host for both species, and the effect of their punctures varies very much with the individual person: with some people swelling and irritation may last for several days. With others the effects are but slight. Pathologists have suspected the bed-bug of transmitting various diseases from infected to healthy persons, but definite confirmatory evidence has not been forthcoming. The eggs of bed-bugs (Fig. 362B) are laid in crevices, etc., of wooden bedsteads and other objects and, under favourable laboratory conditions, hatch in about eight days and the life-cycle is completed in seven weeks. Under normal conditions, however, the latter period may occupy six months and over. A fuller account of the structure and biology of these insects is given in papers by Puri (1924), Mellanby (1935) and Johnson (1942). Other members of the genus are parasites of birds and bats; *Oeciacus hirundinis* lives in martins' nests and *Haematosiphon inodorus*, which occurs in North and Central America, is a pest of poultry and has a greatly elongated rostrum.

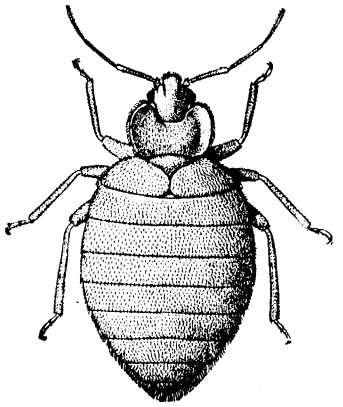


FIG. 362A.—*Cimex lectularius*, male, × 10. Europe, N. America, etc.

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FIG. 362B. — *Cimex rotundatus*, egg, after eclosion of nymph, showing operculum: × *c.* 30

FAM. POLYCTENIDAE.—*Insects parasitic upon bats and provided with ctenidia. Rostrum 3-segmented, antennae and tarsi 4-segmented, eyes wanting; hemelytra short, of uniform consistency and devoid of a membrane.* Eighteen species are known (Ferris & Usinger, 1939; Usinger, 1946), all obligate parasites living deep in the fur of tropical bats belonging mainly to the genera *Molossus*, *Megaderma*, *Taphozous* and *Cynopterus*. The Polyctenids are characterized by the possession of one or more combs (ctenidia) of short flat spines—an armature which they share with *Platypsylla*, the Nycteribiidae and Siphonaptera. They are viviparous, the embryos remaining in the ovarioles where they gradually mature. The young are born at an advanced stage but differ very considerably from the adults (Hagan, 1931) and two postnatal nymphal instars occur.

FAM. ARADIDAE.—*Broad, flattened insects. Head not widened behind eyes. Ocelli absent. Rostrum 4-segmented, 1st segment very short. Metathoracic gland-openings inconspicuous. Coxae rotatory; trochanters fused with femora; tarsi 2-segmented.* This and the succeeding family, which are often united, together comprise about 400 species from all regions. They occur usually beneath bark, in chinks of dead trees, among fungi, etc. Little is known of their biology but they appear to be mycetophagous and the feeding stylets are very long, being coiled within the head when retracted. The eggs are laid externally. *Aradus* is a large, cosmopolitan genus.

The **Dysodiidae** resemble the Aradidae in habits and structure but their head is broad behind the eyes and the trochanters are free.

FAM. TERMITAPHIDIDAE.—*Flat, blind, apterous, broadly-oval insects resembling woodlice. Antennae 4-segmented, concealed beneath head; rostrum 4-segmented, tarsi 2-segmented.* Usinger (1942) recognizes nine species in this tropicopolitan family; all occur in termite galleries. The long stylets, coiled within the head when retracted, have suggested Aradoid affinities, but the resemblance may be the result of convergent adaptation to similar mycetophagous habits (China, 1931).

FAM. THAUMASTOTHERIIDAE (Thaumastocoridae).—*Small insects with broad head. Ocelli present. Rostrum short, 3-segmented. Thoracic scent-glands absent. Coxae rotatory, widely separated. Tibiae usually with membranous apical appendage.* Three species from N. America and Australia.

FAM. JOPPEICIDAE.—*Small; rostrum 4-segmented, the 1st segment short. Membrane large, with 4 free veins. Coxae rotatory; tarsi 2-segmented; pulvilli absent.* Contains only one Mediterranean species of uncertain affinities.

FAM. LYGAEIDAE (Myodochidae).—*Small, dark or brightly coloured forms. Ocelli almost always present. Antennae inserted well down on sides of head. Rostrum 4-segmented. Thoracic gland openings present. Membrane with 4–5 veins. Coxae rotatory; tarsi 3-segmented; pulvilli present.* A large family with *c.* 2,000 species from all regions, about 70 being British (Fig. 363). For the N. American species, see Torre-Bueno (1946). Most are plant-feeders and occur usually in moss, surface rubbish, beneath stones or low plants, but a few may be taken by sweeping. *Blissus leucopterus* is the American 'Chinch Bug', which is very destructive to grasses and cereals; *Oxycarenus hyalinipennis* is the Egyptian 'cotton stainer' and *Nysius vinitor* is stated to be most destructive to fruit trees in Australia. Among the predacious Lygaeids, *Geocoris punctipes* is a common enemy of the mite *Tetranychus telarius* on cotton in the U.S.A. (McGregor & McDonough, 1917).

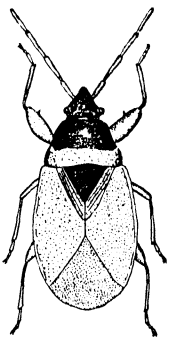


FIG. 363.—*Gastrodes grossipes* × 5. Britain

FAM. COLOBATHRISTIDAE.—*Moderate-sized insects with long legs and basally constricted abdomen. Ocelli present. Rostrum 4-segmented. Metathoracic gland-openings present. Tarsi 3-segmented; pulvilli present.* Over 60 species are referred to this family, mainly from the Indo-Malaysian and Neotropical regions (Horvath, 1904).

FAM. BERYTIDAE (Neididae).—*Elongate insects structurally resembling the Lygaeidae but with geniculate antennae and long, slender legs with apically clavate femora.* These are delicately formed insects, never very common, and sometimes known as 'stilt bugs'. In habits they are sluggish, frequenting undergrowth and meadows. Although they are probably universally distributed, their small size and fragility have caused them to be overlooked, and the tropical forms have been very little collected. Nine species occur in Britain. McAtee (1919) deals with the Nearctic species.

FAM. PYRRHOCORIDAE.—*Moderately sized, usually brightly-coloured insects. Ocelli absent. Rostrum 4-segmented. Metathoracic gland-openings present. Membrane with 4 veins which branch and anastomose. Coxae rotatory; tarsi 3-segmented; pulvilli present.* A small family whose members exhibit strongly contrasting red and black coloration and include the well-known 'cotton stainers' (*Dysdercus*). The latter comprise many species, widely distributed in warm countries (Fig. 331). The name 'cotton stainer' is derived from their habits of piercing the bolls and thereby contaminating them with the fungus *Nematospora* which stains the fibres (Frazer, 1944). *D. cingulatus* is a serious cotton pest in India and *D. sulphurellus* is prevalent in N. America. The widely distributed *Pyrrhocoris apterus* is the only British representative of the family, and is remarkable on account of its alary dimorphism. Kershaw & Kirkaldy (1908a) have followed the life-history of *Dindymus sanguineus* which is carnivorous, feeding on flies; the nymphs, however, apparently prefer termites. The oriental *Lohita grandis* attains a length of over 2 in. and is sexually dimorphic, the male having the antennae and abdomen greatly elongated.

FAM. COREIDAE (incl. **Corizidae** and **Alydidae**).—*Medium to large insects. Ocelli present. Antennae inserted well up on sides of head. Rostrum 4-segmented. Metathoracic gland openings usually present. Membrane with richly branched venation. Tarsi 3-segmented, pulvilli present.* The 2,000 or so species are usually dull in colour but *Serinetha* and a few others are brightly coloured. They are represented best in India, Africa and South America, are all phytophagous and include some pests of cultivated plants. The 'Squash Bug' (*Anasa tristis*) attacks Curcurbitaceae in N. America (Beard,

1940) and *Leptocorisa varicornis* is an Oriental pest of rice and millet. Coreids are usually capable of producing penetrating nauseous odours and many genera exhibit extraordinary dilations of the antennae and tibiae, the functions of which are unknown.

FAM. HYOCEPHALIDAE.—*Medium-sized forms with ocelli. Rostrum 4-segmented. Membrane with 4 veins forming 3 ante-apical cells then branching. Tarsi 3-segmented; pulvilli present.* Includes only the monotypic *Hyocephalus* (Australian).

FAM. PIESMIDAE.—*Small, elongate-oval insects. Ocelli present in macropterous forms. Rostrum 4-segmented. Mandibular plates produced into a pair of horn-like structures at front of head. Scutellum visible. Fore wing reticulo-punctate. Coxae rotatory; tarsi 2-segmented; pulvilli present. Piesma* (McAtee, 1919) includes about 25 species, the majority Palaearctic and all phytophagous, especially on Chenopodiaceae. Wille (1929) describes the biology of *P. quadrata*.

FAM. TINGIDAE (Lace-bugs).—*Perhaps allied to Piesmidae but scutellum concealed by pronotum and ocelli absent. Body and hemelytra densely reticulate.* About 700 species are known, very many from the Mediterranean region. They exhibit great variety of form, the prothorax often being produced into laminate outgrowths, or the whole body may be margined with closely set spines. In some genera there are crest-like modifications of the pronotum suggestive of the Membracidae. All species are plant feeders and sometimes occur in sufficient numbers to constitute minor pests. The eggs are frequently inserted upright in the plant tissue, and are invested with a brown viscid substance which hardens to form a cone-like elevation on the surface of the leaf. The immature stages are very different from the adults, the characteristic ornamentation of the latter not appearing until after the last moult. *Stephanitis pyri* attacks pear and apple in Europe, badly infested leaves dying and *S. rhododendri* is a minor pest of rhododendrons (Johnson, 1936). Species of *Copium* are known to form galls on *Teucrium* and, according to Houard, castration of the floral generative organs results. For the biology of some N. American species see Bailey (1951).

FAM. PENTATOMIDAE.—*Moderate or large insects. Head with lateral margins concealing bases of antennae. Ocelli almost always present. Antennae usually 5-segmented. Rostrum 4-segmented. Scutellum always large, often enormous. Metathoracic gland openings present. Tarsi with 2 or 3 segments; pulvilli present. Abdomen with 7 connexivia visible dorsally.* This and the following five families make up the Pentatomoidea (Shield-bugs). The Pentatomidae, of which Kirkaldy (1909) lists over 3,400 species, occur in all regions, especially Africa, S. America and the Indo-Australian region (Fig. 364).

The vast majority are vegetable feeders but members of the subfamily Asopinae are chiefly predacious, particularly upon lepidopterous larvae (Dupuis, 1949). Nymphs of *Zicrona caerulea* are recorded by Kershaw & Kirkaldy (1908) in China to pray upon larvae of *Haltica caerulea* while the adults attack the beetle of that species. Others (e.g. *Picromerus bidens*) appear to live on either plant or animal tissue. In temperate regions the species appear to be mainly single-brooded, the nymphs occurring in spring or early summer and the adults later—many of the latter hibernate. The eggs (Esselbaugh, 1947) are usually barrel-shaped and deposited in compactly arranged masses. The nymphs are flattened and rounded in outline, their coloration is often striking and usually different from that of the adults; for observations on the biology of the family see Morrill (1910), Tischler (1938; 1939) and Esselbaugh (1949). The life-history of *Chrysocoris stollii* in S. China has been briefly described by Kershaw and Kirkaldy (1908). That of the oriental *Tessaratoma papillosa* has also been followed by Kershaw (1907); the early stages are found on 'logan' and 'lichee' fruit trees which they apparently injure. Both sexes have the property of stridulation (p. 428) and are also able to eject an obnoxious fluid to a distance of 6–12 inches (Muir, 1907). In the later nymphs there are four pairs of dorsal abdominal odoriferous glands which atrophy in the adult, and are replaced by the usual ventral thoracic glands. Maternal instinct is exhibited in *Tectocoris lineola*, the parent resting in a brooding attitude over the eggs, and subsequently remaining for a while in close proximity to the newly hatched young (Dodd, 1904). In *Elasmostethus interstinctus* which occurs on birch in England, etc., the female likewise manifests parental care for the eggs and young.

Certain exotic genera (*Ceratocoris* and *Elapheozygum*) exhibit a remarkable sexual dimorphism, the males having the head greatly produced in front of the eyes, forming prominent horn-like projections. Only a few members of the family occur in the British Isles and are found on various trees and shrubs. Notwithstanding their abundance, Pentatomids are rarely major pests of crops. *Murgantia histrionica*, the 'Harlequin Cabbage Bug' of the United States and Central America, is one of the

best known and is especially partial to Cruciferae. *Chlorochroa ligata* is the 'Conchuela' of N. America which is injurious to various plants (Fig. 364). *Nezara viridula* (see, e.g., Kamal, 1938) is remarkable in that it is almost world-wide in distribution.

For a generic monograph of some subfamilies, see Schouteden (1904–13). The catalogue of Kirkaldy (1909) gives full bibliographical references including habits and food-plants.

The **Urolabidae** (Urostylidae) resemble the Pentatomidae but the head has no definite lateral margins. The antennae are 5-segmented, the tarsi 3-segmented and ocelli are often absent. About 50 species occur in Asia and Australia. The **Phloeidae** (Leston, 1953) are large, flat insects with lamellate lateral extensions of the head and body. The antennae and tarsi are 3-segmented and the 3 Neotropical species occur on the bark of trees where their form and colour-pattern help to conceal them.

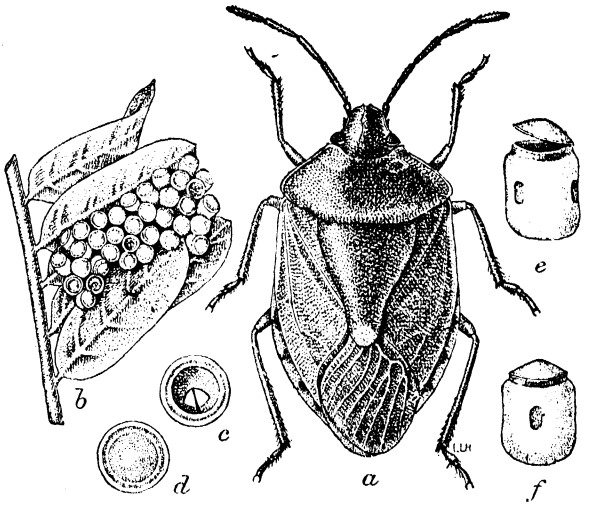


FIG. 364.—*Chlorochroa ligata*

a, imago; *b*, egg-mass; *c*, egg after hatching with operculum removed showing egg-burster; *d*, egg before hatching, from above; *ef*, lateral views of egg showing operculum. All magnified. *After* Morrill, *U.S. Ent. Bull.* 64, Pt. 1 (reduced).

FAM. CYDNIDAE (inc. **Thyreocoridae**).—*Abdomen with 6 connexivia visible dorsally. Scutellum normal or enlarged to cover hemelytra and abdomen. Tibiae strongly spinose. Antennae 5-segmented. Tarsi 3-segmented.* This rather large family is represented in all regions by dark-coloured insects which live under stones and dead leaves or at the base of plants. Some are myrmecophilous. Taxonomic papers include those of Signoret (1881–84) and McAtee & Malloch (1933) while Southwood & Hine (1950) deal with the biology of *Sehirus bicolor*.

The **Plataspididae** (Coptosomatidae) comprise about 400 species from the Old World. The antennae are 4- or 5-segmented and the very long hemelytra fold transversely beneath the enormous scutellum. The **Aphylidae** contains only the Australian *Aphylum* which is small, convex dorsally and concave ventrally with the scutellum covering the abdomen. The antennae are 5-segmented and the tarsi 3-segmented.

CRYPTOCERATA

FAM. OCHTERIDAE (**Pelogonidae**).—*Small, oval insects with ocelli and large eyes. Antennae 4-segmented, short but not concealed. Rostrum long, 4-segmented. Membrane with 2 series of cells. Legs similar, tarsi with 1–3 segments.* About 20 species are known from all regions (Jaczewski, 1934; Schell, 1943). They are predacious, live at the margins of ponds or streams and can fly and jump actively.

FAM. GELASTOCORIDAE (**Mononychidae**: Toad-bugs).—*Allied to the Ochteridae and of similar habits but with concealed, 3- or 4-segmented antennae, raptorial fore legs and short rostrum.* Over 70 species are known and the biology of *Gelastocoris* is described by Hungerford (1922a).

FAM. NAUCORIDAE.—*Small or medium, broadly oval, flattened insects. Antennae 4-segmented, simple. Rostrum strong, 3-segmented. Membrane without veins. Coxae hinged. Fore legs usually strongly raptorial; hind legs fringed with swimming-hairs.* About 150 species, mostly tropical, make up this family (Usinger, 1941). They are mostly predacious insects frequenting both fresh and stagnant water. In the oriental genus *Cheirochela* the fore legs are very powerful and chelate. They mostly haunt aquatic vegetation, among which they creep, coming to the surface to replenish their supply of air which is retained between the somewhat concave dorsum of the abdomen

and the wings. *Aphelocheirus*, however, exhibits plastron respiration and is therefore independent of atmospheric oxygen (Thorpe & Crisp, 1947). The two British species belong respectively to the genera *Ilyocoris* and *Aphelocheirus*. Among biological papers may be mentioned Kramer (1935), Larsén (1927; 1931a) and Usinger (1946a).

FAM. BELOSTOMATIDAE (Giant Water Bugs).—*Antennae 4-segmented; posterior legs adapted for swimming, the tibiae flattened and fringed with hairs. Membrane reticulate; abdomen with 2 retractile apical appendages.* In this family are included the largest members of the Heteroptera and, in fact, of almost all insects, *Lethocerus grandis* exceeding 4 inches (109 mm.) in length. The 100 or so species are unrepresented in Britain, but prevalent in N. America, S. Africa and India. See De Carlo (1938), Cummings (1934).

In habits they are very rapacious, feeding upon small fish, tadpoles, young frogs and insects. *Lethocerus* flies readily from one piece of water to another, is often attracted to lights and met with far away from water. The antennae in this genus are placed in ear-like pockets on the ventral surface of the head and not readily detected when in repose; the 2nd to 4th segments are provided with curious outgrowths whose significance is unknown. For the biology of *L. americanus* see Rankin (1935).

The life-history of *Zaitha flumineum* has been followed by Bueno (1906), and the average time taken from time of oviposition to full development is 50 days. Its favourite haunts are muddy-bottomed pools, where it lurks among the weeds. Both nymphs and adults obtain their air supply by piercing the surface film with the apex of the abdomen. The retractile appendages, when opposed, form a tube leading to the spiracles of the 6th abdominal segment (Bueno). The dorsum of the abdomen in this family is somewhat concave, forming a reservoir under the wings which is ordinarily stored with air. In *Sphaerodema* and some other genera, the eggs are usually borne on the elytra of the males, being cemented thereto by means of a waterproof secretion. According to Slater they are forcibly attached to the male by the female.

FAM. NEPIDAE (Water Scorpions).—*Antennae 3-segmented; anterior legs strongly prehensile, posterior pair adapted for walking; tarsi 1-segmented, anterior pair clawless. Abdomen with an apical breathing tube.* This family includes about 150 species, with only a few in the Holarctic and Australasian regions. The life-history of *Ranatra quadridentata* (N. America) has been followed by Bueno (1906) (see also Larsén, 1937). It occupies about 70 days from the time of oviposition to the adult stage, and the insect hibernates in the latter condition. The female is provided with a pointed toothed ovipositor, and the eggs in this genus are laid in notches cut in the petioles of water plants, each egg being provided with a pair of apical filaments. Both nymph and adults are capable of stridulation (Bueno, 1905). The respiratory tube is the most striking character of the family and consists of two elongate spine-like processes, each of which is grooved to form a demi-canal. Bueno finds that *Ranatra* can move the two halves of the tube at will when beneath the water, and states that they are locked together by numerous hook-like bristles. When the insect is submerged the tube penetrates the surface film and air is conducted to a pair of spiracles placed at its base. Marshall and Severin found that the insect suffered no apparent ill-effects or inconvenience after the tube had been amputated. In the immature stages the latter organ is short and is wanting in the newly hatched individual.

Nepa differs in several important characters from *Ranatra*: the respiratory tube is short and among other features the eggs in (*N. cinerea*) are deposited in chains, the ova adhering to one another by means of seven long filaments radiating from one extremity. Three pairs of 'false spiracles', situated respectively on the 3rd, 4th and 5th ventral abdominal segments, are present in both *Ranatra* and *Nepa*. They are sieve-like structures with the perforations occluded by a delicate membrane, and they are also provided with sensory setae. Baunacke (1912) made a detailed study of their histology and regarded them as exercising a static function, and Thorpe & Crisp (1947) confirmed that they function by detecting relative differences in hydrostatic pressure between different spiracles. The general structure of *N. cinerea* has been studied by Hamilton (1931), but that of *Ranatra* needs further investigation.

FAM. NOTONECTIDAE (Backswimmers).—*Body convex dorsally; head inserted into prothorax, rostrum 3- or 4-segmented, antennae 4-segmented. Tarsi 2-segmented, anterior pair not flattened, posterior pair devoid of claws.* These insects differ from other aquatic Hemiptera in their habit of swimming on the back, which is shaped like the bottom of a boat. They are usually observed floating on the surface of the water with the long oar-like hind legs outstretched. They dive readily when alarmed, carrying a supply of air beneath the wings; they can also leap into the air and take to flight. Care

is needed in handling them, as they are able to inflict painful punctures. *Notonecta* is almost universally distributed and markedly predacious, attacking small fish, tadpoles, etc., when kept in an aquarium. In *N. glauca* and its allies (Fig. 365) the female is provided with a piercing ovipositor with which it makes incisions in the stems of water plants, partially burying an egg in each notch; certain other species merely attach their eggs to the plants or other supports (Walton, 1936). The abdomen is keeled down the middle, and arising therefrom is a longitudinal row of outwardly directed hairs on either side. These meet a corresponding series of similar hairs arising from near the pleura. In this manner there is formed a channel on either side of the abdomen, which is filled with air and enables the insect to respire when submerged. Larsén (1930) describes the biology of some species of *Notonecta*.

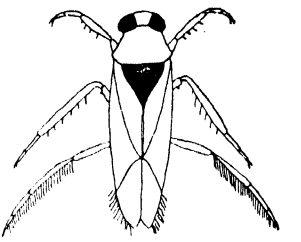


FIG. 365.—*Notonecta glauca* (enlarged). Britain

FAM. PLEIDAE.—*Small, stout insects, strongly convex dorsally. Rostrum and antennae* 3*-segmented. Fore wing uniformly coriaceous, hind wing reduced. Hind tibiae and tarsi without conspicuous swimming-hairs. Tarsi* 2- *or* 3*-segmented.* Over 20 species have been described from all regions. The biology and external structure of the European *Plea leachi* is described by Wefelscheid (1912).

FAM. HELOTREPHIDAE.—*Small forms. Head and thorax fused. Antennae* 1- *or* 2*-segmented. Rostrum* 4*-segmented. Scutellum large. Clavus and corium usually fused. Hind wings usually absent or rudimentary.* The 15 or so species of this widely distributed family (Esaki & China, 1928; China, 1935; 1936) occur in still water with abundant vegetation (Usinger, 1937).

FAM. CORIXIDAE (Water Boatmen).—*Body flattened dorsally; head not inserted into the prothorax; rostrum concealed and* 1- *or* 2*-segmented; antennae* 3- *or* 4*-segmented. Anterior legs greatly shortened, fore and hind tarsi clawless, the latter* 2*-segmented.* With over 200 species this is evidently the dominant family of aquatic Hemiptera. The genus *Corixa* (Fig. 366) is nearly world-wide and includes 26 British species.

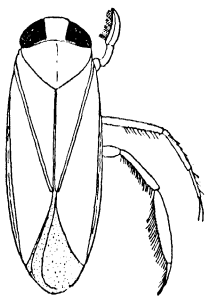


FIG. 366.—*Corixa* (enlarged). Britain

As a rule these insects remain at the bottom of the water, holding fast by the middle legs to various objects; now and again they ascend to the surface, swiftly propelled by the hind limbs. The dorsum of the abdomen is somewhat concave, forming a reservoir beneath the wings which serves to retain a supply of air. The feeding habits of the family are unusual in that its members are microphagous, consuming diatoms, the contents of algal cells, etc. *C. punctata* attaches its eggs to the stems and leaves of pond weeds by means of a glutinous substance. They are more or less onion-shaped, with one extremity prolonged into a blunt point. In some species the eggs are very numerous and closely grouped together; thus those of *Arctocorixa abdominalis* and *mercenaria* form very considerable masses which are used as food by the Mexican Indians. Bundles of reeds are placed in the water and collected at suitable intervals, and the eggs are detached therefrom by beating the reeds. The adult insects are also used as food in Mexico and Egypt. Hagemann (1910) has contributed some observations on the respiration of *Corixa* at successive stages in its life and on the structure of the spiracles. He also describes a tympanal organ in association with the 2nd pair of the latter, which may possibly serve for the perception of stridulatory sounds produced by the male.

The minute *Micronecta* (= *Sigara*) lives in *Spongilla* and among water weeds and, like other members of the family, is able to stridulate, but this faculty is much less developed in the female than the male. The stridulatory organs of *Corixa* consist of the pedal organs mentioned on p. 428. There is no evidence that the strigil is used to produce sounds except in *Micronecta*. Among the numerous papers on this group, see Griffith (1945) on morphology, Hutchinson (1929) and Hungerford (1945) on taxonomy and Macan (1938; 1954) and Popham (1943; 1947) on biology.

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Order 20. **THYSANOPTERA** (**Physopoda:** Thrips)

Small or minute slender-bodied insects with short 6- *to* 10-*segmented antennae and asymmetrical piercing mouthparts: maxillary and labial palpi present. Prothorax well developed, free: tarsi* 1- *or* 2-*segmented, each with a terminal protrusible vesicle. Wings when present very narrow with greatly reduced venation and long marginal setae. Cerci absent. Metamorphosis accompanied by one or two inactive pupal instars.*

The insects comprised in this order are commonly known as 'thrips'. The majority vary in length from $\frac{1}{50}$ to $\frac{1}{3}$ of an inch, the smaller forms being by far the most prevalent. They are mostly yellow, yellowish-brown or black in colour and are found among all kinds of growing vegetation, both on the flowers and about the foliage: others are subcortical or frequent moist decaying plant remains, particularly wood and fungi. Some species are predacious, or at least occasionally so, and suck the body-fluids of aphids, mites and other small insects. When disturbed different species exhibit certain differences of movement: some crawl in a leisurely fashion, others run quickly or leap, and a large number are able to fly but they often do not readily resort to this means of locomotion. Many exhibit the habit of curving the apex of the abdomen upwards and, in the case of winged individuals, this movement is generally preparatory to flight: it appears to be for the purpose of drawing the lateral comb-like setae of the abdomen through the marginal fringes of the wings. The latter organs when in repose are laid in a more or less parallel manner along the back.

The vast majority of species derive their nutriment by penetrating the living tissues of plants by means of their piercing mouthparts, and imbibing the sap. It is, therefore, not surprising that certain members of the order are recognized by economic entomologists as pests, especially the Pear Thrips (*Taeniothrips inconsequens*), the Onion Thrips (*Thrips tabaci*), the Grass Thrips (*Anaphothrips striatus*), the Greenhouse Thrips (*Heliothrips haemorrhoidalis*) and several others. In addition to the particular plants with which their names are associated, these, and other species, affect a wide range of hosts, and several are polyphagous. On the other hand, a number of species have so far only been obtained from single plant species. The primary injury to vegetation is caused by the extraction of the sap and, when severe, a whole crop may be ruined. The effects of the injuries are very variable in different cases; in apple blossoms, for example, thrips have been known to prevent the formation of fruit, and when *A. striatus* feeds upon the spikelets of oats it produces sterility. *Thrips tabaci* is able to transmit the virus causing spotted wilt of tomatoes. It is true, however, that thrips play a part in the fertilizing of beet, and many other plants, but their value in this direction does not compensate for their injurious feeding habits. Some species, notably the Corn Thrips (*Limothrips cerealium*), are well known to be capable of

sustained flight and migration: in such instances they fly in large numbers, particularly during sultry weather.

Parthenogenesis is of frequent occurrence throughout the order, and in several species (*H. haemorrhoidalis*, *T. inconsequens*, etc.) males are either unknown or extremely rare: in others the eggs are capable of developing parthenogenetically, although males are quite common.

Approximately 1,500 species of the order have been described, and about 150 have been found in the British Isles. The most important general works on the order are those of Uzel (1895) and Priesner (1928; 1949). The British forms may be identified by the key of Morison (1949).

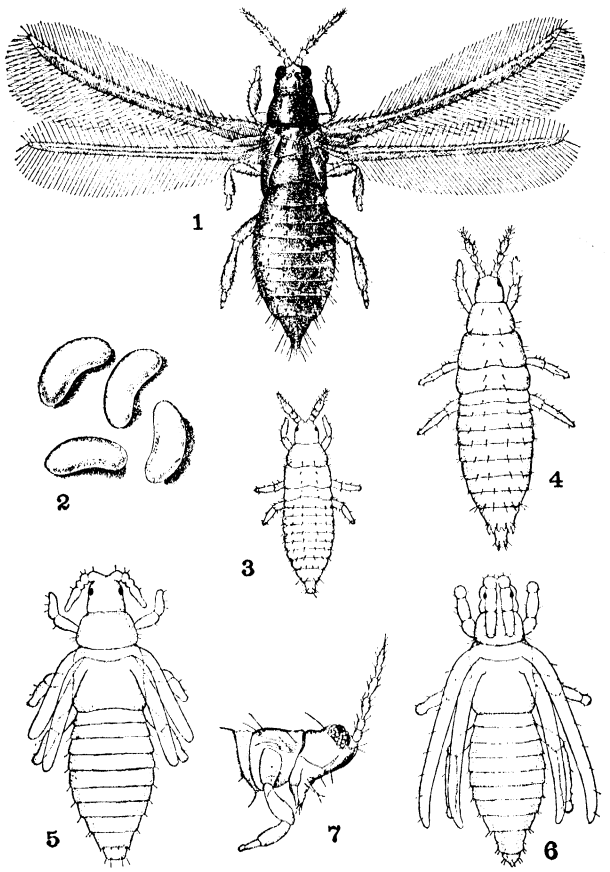


FIG. 367.—The Pear Thrips (*Taeniothrips inconsequens*)

1, Imago; 2, eggs; 3, 1st instar nymph; 4, fully-grown nymph; 5, prepupa; 6, pupa; 7, lateral view of head of imago. Reduced from Foster and Jones, *U.S. Dept. Agric. Bull.*, 173.

External Anatomy.—Melis (1934; 1936; 1939), Doeksen (1941) and Jones (1954) have given good general accounts of the external morphology of several species. The head (Fig. 368) is generally somewhat quadrangular in form with a pair of small but prominent compound eyes: the facets of the latter are relatively large and convex, assuming a rounded instead of the usual hexagonal form. Three ocelli are present on the vertex of winged forms but are absent from apterous ones. Nearly all the head sclerites are intimately fused, almost all traces of sutures being lost and the tentorium is greatly reduced. The antennae are 6- to 10-segmented, and are inserted close together in a very forward position. The mouthparts are adapted for piercing and suction, certain of the organs being modified as stylets which are enclosed in a short cone, or rostrum, projecting downwards from the ventral surface of the head (Fig. 368). Reyne (1926) has made a detailed study of the structure and development of the mouthparts and his interpretation is followed here. The mouth-cone is formed by the labrum and clypeus above, and the labium below, while the actual piercing organs are protruded through the short tubular base thus formed. Among the Terebrantia the mandibles of the two sides are

totally unlike: the left organ is a strong sclerotized stylet while the right one is absent in all postembryonic stages. The maxillae consist of a pair of palpus-bearing plates with associated stylets. The plates (which probably represent stipites) may be either symmetrical or unlike and they form the side walls of the mouth-cone already alluded to. The palpi are composed of a variable number of segments which range from 2 to 8 among different genera. Each stylet consists of a small basal piece articulating with the palpus-bearing plate of its side, and a long piercing organ which is usually divided into a proximal and a distal element. The labium forms the trough-like floor of the mouth-cone and is divisible into a mentum and submentum.

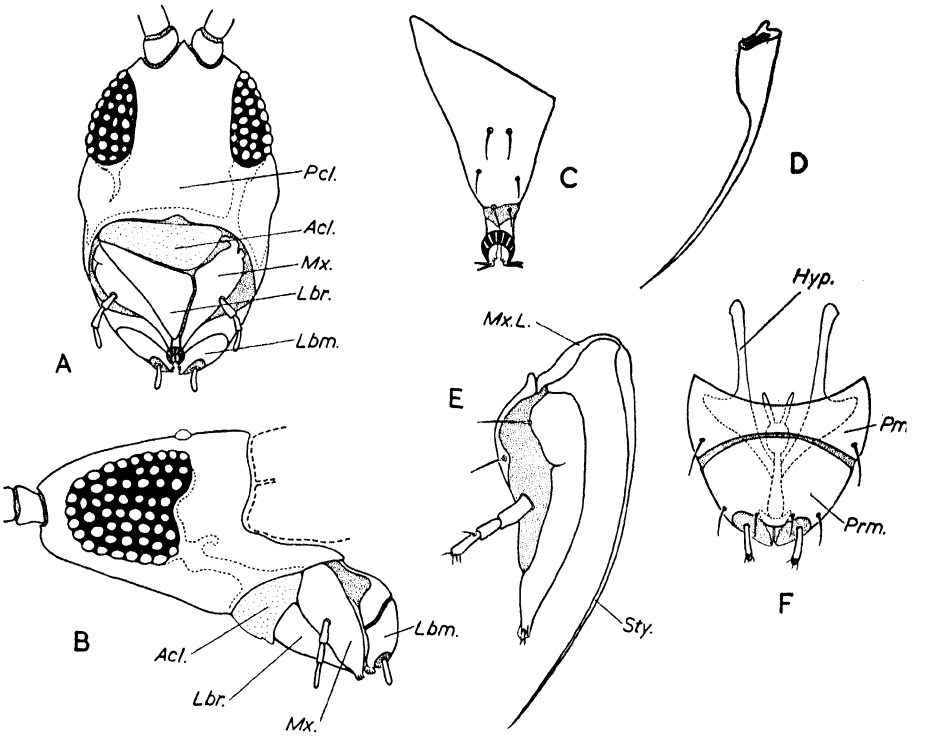


FIG. 368.—Head and mouthparts of *Chirothrips hamatus* (*after* Jones, 1954). A. Frontal view of head. B. Lateral view of head. C. Labrum. D. Left mandible. E. Maxilla. F. Labium and hypopharynx

Acl, anteclypeus; *Hyp*, hypopharynx; *Lbm*, labium; *Lbr*, labrum; *Mx*, maxilla; *Mx.L*, maxillary lever; *Pcl*, postclypeus; *Pm*, postmentum; *Prm*, prementum. (N.B. *Pm* and *Prm* correspond to the submentum and mentum of other authors.)

The membranous apex of the mentum is more or less bilobed and carries a pair of short labial palpi which are 1- to 4-segmented. A small hypopharynx is present. Among the Tubulifera certain differences in the mouthparts are noticeable. The mandible has come to articulate with the palpus-bearing plate of its side; the two maxillary stylets are very long and have acquired separate, and more posterior, articulations with the head-capsule. These are secondary differences, however, since the mouthparts of the Tubuliferan nymphs are similar to those of the Terebrantia.

When a thrips feeds the apex of the mouth-cone is applied to the surface of the plant, and the stylets are driven into the tissues. The laceration of the latter causes a minute wound through which the sap escapes. The

apex of the mouth-cone is applied to the puncture, and the juices of the plant are pumped up into the gut by means of the action of the cibarial sucking pump.

The prothorax is free and distinct, with a broad tergum, while the meso- and metathorax are compactly united. The legs are composed of the usual parts and only the tarsi present special features. The latter are 1- or 2-segmented, and the claws may be either single or paired. A remarkable protrusible vesicle is associated with the extremity of the tarsus, and it is to the presence of this organ the alternative ordinal name Physopoda is due. When at rest, the vesicle is retracted and invisible, but when the insect is walking it appears to be exerted by means of blood pressure and enables the insect to walk upon almost any kind of surface. The wings are membranous, very narrow, and strap-shaped: they have very few or no veins, and only rarely possess cross-veins. They are fringed with long setae and some species bear spines along the veins or along the former courses of the latter. The wings of a side are interlocked by means of several hooked spines near the base of the hind wing which engage a membranous fold on the anal area of the fore wing. The imagines of many species exhibit striking variations in the degree of development of the wings. The adults of a single species (e.g., *Chirothrips manicatus*) may have fully developed wings, reduced functionless wings, or be completely apterous. In other species both sexes may be winged or one winged and the other apterous: one or both sexes may be brachypterous or both may be wingless. When brachypterous forms occur among normally winged individuals the phenomenon is especially evident towards autumn.

The abdomen is elongate, tapering posteriorly and composed of 11 segments, though the first is reduced and the terminal ones may be modified in connexion with the external genitalia. The Tubulifera lack an ovipositor but in the Terebrantia it is a conspicuous serrated structure formed of a pair of appendages from both the 8th and 9th abdominal segments. In the Terebrantian male, according to de Gryse & Treherne (1924), the enlarged 9th sternum bears a pair of laterally placed appendages and conceals a complex median aedeagus. The Tubuliferan male lacks external genitalia.

Internal Anatomy.—Most of what is known concerning the internal structure of Thysanoptera is due to Jordan (1888), Uzel (1895), Klocke (1926) and Sharga (1933). The digestive system is characterized by a cibarial sucking pump provided with radial muscles, a small crop, an extensive mid intestine and four Malpighian tubes. The mid intestine forms the largest portion of the alimentary canal and is divided into a capacious anterior chamber followed by a tubular coiled posterior region. The hind intestine forms a straight passage to the anus and four rectal papillae are usually present. Two pairs of *salivary glands* are commonly present and are located in the thorax and abdomen: their ducts unite to form a common canal opening into the front of the oesophagus. According to Uzel three pairs of salivary glands are found in the thorax of *Trichothrips*. The *nervous system* is highly concentrated: the brain is well developed, the suboesophageal and prothoracic ganglia are fused while the meso- and metathoracic ganglia remain separate. A median nerve-cord passes down the abdomen, but the ganglia have shifted forward and are concentrated into a single centre which is located in the first segment of that region. The *circulatory organ* consists of a very short contractile heart lying in the 8th abdominal segment and continued forwards as a long aorta. In the *female reproductive* organs the ovaries each consist of four short panoistic ovarioles: a receptaculum seminis is present but accessory glands do not

always seem to occur. The *male reproductive organs* consist of a pair of fusiform testes which communicate by means of rather short vasa deferentia with an ejaculatory duct. The latter is somewhat swollen proximally, forming an ampulla-like enlargement. At this point it receives the ducts of one or two pairs of relatively large accessory glands which considerably exceed the testes in size. The tracheal system is well developed and usually opens to the exterior by means of four pairs of spiracles. There is a pair on the mesothorax, another on the metathorax (small and easily overlooked in the Terebrantia) and a pair on the 1st and 8th abdominal segments.

Life-History and Metamorphoses (Fig. 367).—The eggs of the Terebrantia are more or less reniform, while those of the Tubulifera are commonly elongate-oval. In the first-mentioned suborder the female cuts a slit with her saw-like ovipositor, laying the eggs singly in the tissues of the host plant. The Tubulifera lay their eggs externally, either singly or in groups, upon leaves, stems, under bark, etc. The newly hatched nymphs resemble the adults in general facies and feeding habits but are less strongly sclerotized, without wing-pads and with fewer antennal segments. This stage is followed by a very similar second instar then, in the Terebrantia, by a prepupa and a pupa. The Tubulifera, however, have an additional pupal instar. The prepupa and pupa have conspicuous wing-pads but do not feed and their pretarsi lack the characteristic protrusible vesicles of the adults and first two nymphal stages. They differ in that the antennae of the pupa are bent back over the thorax. The pupa is inactive but capable of slow movement when stimulated, and though *Heliothrips haemorrhoidalis* and a few other species pupate on the host-plant, most Thysanoptera do so among debris or under the ground in an earthen cell. Müller (1926) has shown that the cells of the mid gut undergo histolysis and replacement in the pupa but no complete study of internal metamorphosis has been made. The occurrence of a pupal stage superficially similar to that of Endopterygotes does not indicate a close relationship between them and the Thysanoptera. The number of generations passed through in the year differs in various species: many, such as *Taeniothrips inconsequens*, are univoltine, while on the other hand *Heliothrips fasciatus* is known to have 7 to 9 generations in a season in the United States. Hibernation may take place in the nymphal, pupal or imaginal stage.

Classification.—In the following classification, after Karny (1921) and Priesner (1928), European families are indicated thus *.

Suborder I. TEREBRANTIA

Ovipositor saw-like, apex of abdomen conical in female, bluntly rounded in male; fore wings with at least one longitudinal vein reaching to apex.

1. Antennae 9-segmented; fore wings broad, with rounded apices; ovipositor curved upwards; body not flattened . . . . . AEOLOTHRIPIDAE*
–. Antennae 6- to 10-segmented; fore wings narrow with apices more pointed; ovipositor curved downwards; body more or less flattened 2

2. Prothorax without sutures; wing-surface pubescent 3
–. Prothorax with longitudinal dorsal sutures; wing-surface smooth; antennae moniliform, 8-segmented, without apical style, 3rd and 4th segments without sense-cones, each with a tympanum-like sense area on apex; abdomen blunt, ovipositor very weak . . . . . MEROTHRIPIDAE

3. Antennae 9- or 10-segmented, without apical style 4
–. Antennae 6- to 8-segmented, usually with a 1- or 2-segmented apical style; 3rd and 4th segments not conical, with sense-cones; fore tarsus never with claw-like appendage at base of 2nd segment . . . . . THRIPIDAE*

4. 3rd antennal segment cylindrical, not conical . . . . HEMITHRIPIDAE
–. 3rd and 4th antennal segments enlarged, conical, without sense-cones, rarely with a sensory band at apex; fore tarsus with claw-like appendage at base of 2nd segment . . . . . HETEROTHRIPIDAE

Suborder II. TUBULIFERA

Ovipositor absent; apex of abdomen in both sexes usually tubular, fore wings with venation almost absent.

1. Maxillary palps 2-segmented; antennae 8-segmented, seldom 7-segmented; middle coxae wider apart than fore and hind pairs; 9th abdominal segment not or rarely longer than 8th; terminal abdominal setae seldom much longer than the tube 2
–. Maxillary palp 1-segmented; antennae 4- to 7-segmented; hind coxae further apart than remaining pairs; 9th abdominal segment longer than 8th; abdominal setae markedly longer than the tube . . . . . UROTHRIPIDAE*

2. Last abdominal segment not tubular, greatly swollen, parabolic in outline from above; 2nd to 9th abdominal terga transversely linear . . PYGOTHRIPIDAE
–. Last abdominal segment slender, cylindrical or tubular, comprising the tube; 2nd to 9th abdominal terga not transversely linear 3

3. 8th abdominal segment without peg-like projections on hind margin . . 4
–. 8th abdominal segment with long peg-like projections on posterior margin; antennae and tube unusually short and thick . . . . CHIROTHRIPOIDIDAE

4. Tube much shorter than remaining abdominal segments taken together . 5
–. Tube about as long as remaining abdominal segments taken together . . HYSTRICOTHRIPIDAE*

5. 3rd antennal segment with a distal ring of very prominent sensory rods. . ECACANTHOTHRIPIDAE
–. Sensory rods on 3rd antennal segment not more strongly developed than on other segments 6

6. Antennal sense-cones extraordinarily long and sharp; eyes unusually large, touching each other; mouth-cone sharply pointed . . . EUPATHITHRIPIDAE
–. Antennal sense-cones not unusually developed; eyes seldom touching each other PHLOEOTHRIPIDAE*

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Order 21. **NEUROPTERA** (Alder Flies, Lacewings, Ant Lions, etc.)

Small to rather large soft-bodied insects with usually elongate antennae. Mouthparts adapted for biting: ligula undivided or bilobed or often atrophied. Two pairs of very similar membranous wings, generally disposed in a roof-like manner over the abdomen when at rest. Venation primitive but with many accessory veins: costal veinlets numerous: Rs often pectinately branched. Abdomen without cerci. Larvae carnivorous, of a modified campodeiform type with biting or suctorial mouthparts: the aquatic forms usually with abdominal gills. Pupae exarate: wings with complete tracheation.

The heterogeneous group which formed the Neuroptera of Linnaeus is now divided into at least eight or nine well-defined orders, the original name being confined to the Megaloptera and Planipennia as enumerated below. The group thus restricted is still further dismembered by some authorities into two or three separate orders. This course, however, is very doubtfully warranted owing to the difficulty of separating such orders on the basis of any constant differences. It is evident, however, that the Neuroptera exhibit at least three lines of evolution with marked divergence also in their metamorphoses. These several lines appear, however, to be derivable from a common ancestral type. The species are rarely abundant in individuals, and all exhibit weak powers of flight. They feed upon soft-bodied insects and liquid matter, such as honey-dew.

With the exception of the Coniopterygidae, the Neuroptera are separable from the Mecoptera by the venational features enumerated above. The mouthparts are well developed with biting mandibles, the maxillary palpi are 5-segmented, the labial palpi 3-segmented, and the ligula is reduced to the condition of a median and sometimes slightly bilobed process, or is totally atrophied. The wing-coupling apparatus is of the jugo-frenate type, though usually much reduced and without bristles; a frenulum, however, is present in many Hemerobiidae. The tarsi have five segments and the abdomen ten. The morphology of the male genitalia (Killington, 1936) is still not fully understood. True appendages are probably not present. An aedeagus may be present (Hemerobiidae), or absent (Osmylidae), or even present or absent in one family (Coniopterygidae). In the first-named family it is associated with sternite 10. Clasping organs may be developed from tergite 10 (Hemerobiidae) or from sternite 10 (Sisyridae). In both sexes, tergite 10 commonly bears a group of trichobothria on each side. In the female, the genital aperture is behind sternite 8 which is rather reduced and may bear a pair of gonapophyses. Sternite 9 is more or less divided and may function as an ovipositor and its lobes may, indeed, be the coxites of an appendage. This seems even more probable in *Dilar* and *Raphidia* which have long ovipositors (Bo Tjeder, 1937; but cf. Ferris & Pennebaker, 1939). The

internal anatomy of the order has been very inadequately investigated. There are two pairs of thoracic and eight pairs of abdominal spiracles, and the ventral nerve-cord consists of three thoracic and generally seven abdominal ganglia. The digestive system is provided with a median dorsal food-reservoir, a peritrophic membrane is present, and the usual number of Malpighian tubes is eight: the ovaries consist of a variable number of usually polytrophic ovarioles.

The larvae exhibit great diversity of structure and mode of life, but are, in all cases, carnivorous; in a considerable proportion of the species they are aquatic. The latter forms are interesting from the fact that they usually carry segmentally arranged, and often jointed, abdominal processes.

The Neuroptera are divided in the present work into the suborders Megaloptera and Planipennia, which are treated separately below. The British species number 54, and for information concerning them see Killington (1936–37). Stitz (1927) deals with the C. European species and about 4,300 species of the order have been described.

Suborder I. **MEGALOPTERA** (Alder Flies and Snake Flies)

Branches of the veins usually without a conspicuous tendency to bifurcate at the margins of the wings. Larvae with biting mouthparts.

The Megaloptera fall very naturally into two superfamilies—the Sialoidea or 'alder flies' and the Raphidioidea or 'snake flies'. These two divisions are regarded by Handlirsch as being sufficiently distinct to warrant their separation into orders of their own. They include a small number of archaic types not very closely related among themselves. The British forms are described by Killington (1930).

The suborder is classified as follows:

A (B). Prothorax quadrate: an exserted ovipositor wanting: wings without pterostigma. Larvae aquatic . . . . . **Sialoidea**

1. Wing-expanse 45–100 mm.: 3 ocelli present: 4th tarsal segment simple. Larvae with 8 pairs of abdominal gills and no terminal filament . CORYDALIDAE

2. Wing-expanse 20–40 mm.: ocelli absent: 4th tarsal segment bilobed. Larvae with 7 pairs of abdominal gills and a terminal filament . SIALIDAE

B (A). Prothorax elongate: an exserted ovipositor present: wings with a pterostigma. Larvae terrestrial . . . . . **Raphidioidea**

3. A single family . . . . . RAPHIDIIDAE

The **Sialoidea** are of special interest both on account of the large size and striking appearance assumed by certain of the species, and because the group includes the most generalized representatives of the Neuroptera. Similarly to other primitive groups, the Sialoidea only include a small number of genera and species, but they exhibit an almost world-wide although discontinuous distribution. They differ from other Neuroptera in the hind-wings being broad at their bases with the anal area folded fanwise when at rest (Fig. 370).

The eggs of these insects are laid upon leaves, stones and other objects, usually not far from water. They are deposited regularly in compact masses: in *Sialis* each mass contains 200 to 500 eggs and in *Corydalis* the number amounts to two or three thousand. The eggs are cylindrical with rounded ends and dark brown in colour: at its free extremity each is provided with a conspicuous micropylar apparatus varying somewhat in form among different genera. The young larvae, after eclosion, make their way to the water:

those of *Sialis* are found in the muddy bottoms of ponds, canals and slow-moving streams, while the larvae of *Corydalis* lurk under stones in rapidly flowing water. All the larvae of the Sialoidea are actively predacious, devouring other insect larvae, small worms, etc. The mouth-parts resemble those of a Carabid larva, the mandibles being powerful and sharply toothed, while the maxillae exhibit the typical parts and the labium consists of a mentum, a dentate ligula and 3-segmented palpi. The antennae are prominent 4-segmented appendages, and the legs are well developed, terminating in paired claws. The larva of *Sialis* (Fig. 369) is provided with seven pairs of 5-segmented, lateral, segmentally arranged abdominal filaments or tracheal gills. Each of the latter is supplied by a tracheal branch and contains blood. On the 9th abdominal segment there is a terminal filament of a similar nature. In *Corydalis* and *Chauliodes* there are eight pairs of unjointed or imperfectly jointed filaments: in the former genus, and in *Neuromus*, each of the first seven abdominal segments also bears ventral, spongy tufts of accessory tracheal gills. The body in these three genera is terminated by a pair of hooked anal feet, without the gill-like filament of *Sialis*. According to Davis (1903), there are eight pairs of small abdominal spiracles in *Sialis*, while in *Corydalis* and *Chauliodes* thoracic spiracles are also present. Pupation occurs in the soil or in moss, etc., sometimes at a depth of several inches. The pupae are exarate and are able to work their way to the surface to allow of the emergence of the imagines. In the common European *Sialis lutaria* the whole life-cycle occupies about a year. This species and *S. fuliginosa* are the only British members of the superfamily. *Corydalis* is North American and Asiatic and the male has enormously elongate sickle-like mandibles and a wing-expanse ranging up to 150 mm. For a general account of the biology of the Sialoidea vide Davis (1903). Some account of the anatomy of *Sialis* is given by Dufour (1841), and by Loew (1848).

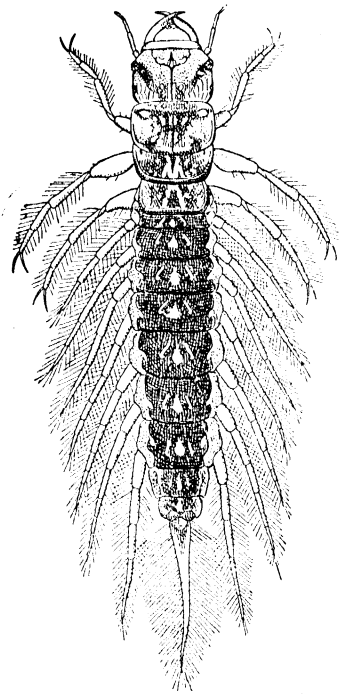


FIG. 369.—Larva of *Sialis lutaria*, enlarged
After Lestage.

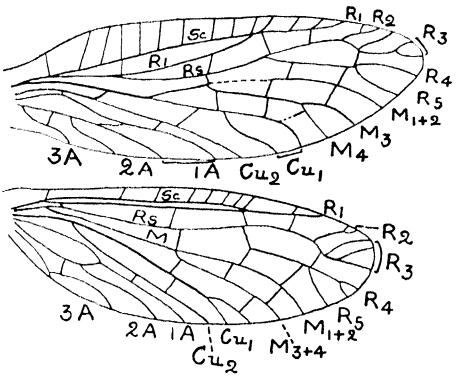


FIG. 370.—Right wings of *Sialis lutaria*

The **Raphidioidea** include the most specialized members of the Megaloptera and are entirely terrestrial in habits. The group occurs on all continents with the exception of Australia, and most of the species are included

in the genera *Raphidia* (Fig. 371) and *Inocellia*. The imagines are remarkable for the elongated prothorax which, together with the narrowed posterior region of the head, forms a kind of 'neck': unlike the Sialoidea, they possess an elongate setiform ovipositor. More than eighty species of the group are known, of which four, belonging to the genera *Raphidia* and *Agulla*, have

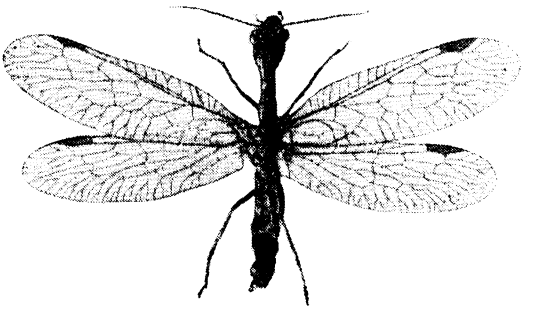


FIG. 371.—*Raphidia notata*, Britain × 2½

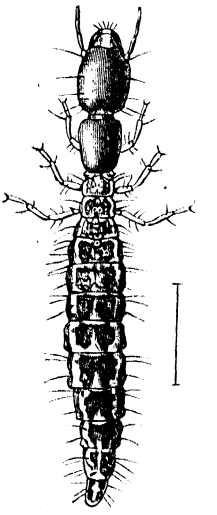


FIG. 372.—*Raphidia notata*, larva
After Sharp, *Camb. Nat. Hist.*

been recorded from Britain. They occur in wooded regions and are met with among rank herbage, on flowers or tree-trunks, etc. The eggs are inserted by means of the long ovipositor in slits in the bark: they are elongate-cylindrical with a small appendage at one extremity. The larvae occur under loose bark, particularly of conifers, and are very voracious, preying upon small soft-bodied insects which frequent similar situations. The larva of *Raphidia* (Fig. 372) is elongate and slender with a well sclerotized head and prothorax. The thoracic legs are long, the abdomen carries no processes or appendages, and the mouthparts resemble those of the imago. The pupa is more primitive than in any other of the Endopterygota and closely resembles the adult insect in its essential structural characters. Although first enclosed in a kind of cell the pupa emerges after a lapse of some time and, becoming active, crawls about until it finds a suitable place, where it remains until the eclosion of the imago.

The Raphidioidea have been monographed by Esben-Petersen (1913) and the N. American species by Carpenter (1936).

Suborder II. **PLANIPENNIA** (Lacewings, Ant Lions, etc.)

Branches of the veins usually conspicuously bifurcated at the margins of the wings. Larvae with suctorial mouthparts.

The Planipennia include the majority of the Neuroptera and their various families exhibit an exceptional wealth of venational specialization. Different as many of the families are in their imaginal characters, the group is well defined as a whole owing to the universal occurrence of suctorial piercing mouthparts in the larvae. Nearly all the Planipennia are terrestrial insects, a small number are more or less amphibious in their larval stages, and one or two genera have truly aquatic larvae. The most generalized family is the Ithonidae, which, to some extent, serves as a connecting link between the two suborders of Neuroptera.

The larvae of the Planipennia are universally predacious and are of considerable importance as destroyers of aphides and other injurious insects. The head is often large and very freely articulated with the prothorax. The mandibles and maxillae are long and exserted, being thereby adapted for seizing the prey (Meinert, 1889). The first-mentioned appendages are usually sickle-shaped and, in some families, armed with teeth. They are grooved along their ventral surfaces, and the lacinia of the maxillae, which closely resembles them in size and shape, fits one into each groove: in this manner the two sets of appendages form a pair of imperfect suctorial tubes. The combined organs are deeply inserted into the prey and its juices are imbibed by means of the pumping action of the pharynx. At the base of each maxilla there is usually a pair of small sclerites—the cardo and stipes—but, as a rule, maxillary palpi are absent. The labium is greatly reduced, and its palpi, although sometimes aborted, are very variable in different families. The antennae are filiform and often rather long. The prothorax is divided into three more or less distinct subsegments, but the meso- and metathorax are sometimes merged into the trunk and not sharply demarcated. The legs are long and slender and allow of activity of movement; their tarsi are of one segment. The abdomen consists of ten segments and is devoid of cerci. The larvae usually pass through three instars, except in *Ithone* where there are five: when about to pupate, they construct oval or spherical cocoons either of silk or of foreign particles bound together with that material. The pupae possess strong mandibles which are utilized in cutting through the cocoons to allow of the emergence of the imagines. The diet of the larvae consists solely of animal juices, and there is no through passage from the mid intestine to the anus. The Malpighian tubes are usually eight in number and, of these, six have acquired a secondary attachment by their distal extremities to the wall of the hind intestine. The tubes thus modified function as silk-producing organs in the last instar, the silken thread being emitted by means of an anal spinneret (Anthony, 1902). The respiratory system opens by nine pairs of spiracles, the 1st pair being prothoracic and the remainder abdominal in position.

The Planipennia may be classified according to the following key: only five of the undermentioned families (marked*) are represented in the British fauna, and useful accounts of their structure and biology have been contributed by Killington (1936–37), and by Withycombe (1925). The external anatomy of *Plega* (Mantispidae) is fully described by Ferris (1940).

1. Venation greatly reduced: small species covered by whitish powdery exudation . . . . . *CONIOPTERYGIDAE (p. 495)
–. Venation more complete. Insects without whitish exudation . . . 2

2. Fore legs raptorial . . . . . MANTISPIDAE (p. 498)
–. Fore legs not raptorial 3

3. Hind wings greatly elongated and ribbon-like . . NEMOPTERIDAE (p. 500)
–. Hind wings not as above 4

4. Antennae thickened distally or sharply clavate. 5
–. Antennae not thickened distally 6

5. Antennae not half as long as fore wing; wings with a very elongate hypostigmatic cell extending beyond the fusion of Sc with R_1 . MYRMELEONTIDAE (p. 502)
–. Antennae more than half as long as fore wing; an elongate hypostigmatic cell wanting . . . . . ASCALAPHIDAE (p. 502)

6. Large moth-like insects, wings elongate; head small and closely applied to the thorax . . . . . ITHONIDAE (p. 495)
–. Insects without these characters 7

7. Two or more branches of Rs in fore wing arising from fused stems of R_1 and Rs 8
–. All branches of Rs arising from latter vein after it has diverged from R_1 . 9
8. Antennae moniliform; cross-veins fewer; female with no ovipositor . . *HEMEROBIIDAE (p. 497)
–. Antennae coarsely pectinate in male; cross-veins more numerous; ovipositor exserted . . . . . DILARIDAE (p. 496)
9. Sc not joined at its apex to R_1 10
–. Sc joined at its apex to R_1 11
10. Body and wings not hairy . . . . . *CHRYSOPIDAE (p. 499)
—. Body and wings densely hairy . . . . . BEROTHIDAE part (p. 496)
11. Wings rounded with a prominent 'mid-rib' formed by Sc, R_1 and Rs. . PSYCHOPSIDAE (p. 498)
—. Wings more elongate and without any prominent 'mid-rib' 12
12. Cross-veins numerous . . . . . *OSMYLIDAE (p. 498)
—. Cross-veins few 13
13. Costal veinlets branched in fore wing; scales present on some part of wing in the female . . . . . BEROTHIDAE part (p. 496)
—. Costal veinlets unbranched in fore wing; wing-scales absent *SISYRIDAE (p. 496)

1. Superfamily **Ithonoidea**

Large, moth-like insects with unspecialized venation. The head small and closely applied to the prothorax. The larva subterranean and resembling that of a scarabaeid.

FAM. ITHONIDAE.—This family is the most nearly related to the Megaloptera of all the Planipennia. Its members are large and rather stout-bodied insects, with a wing-expanse of about 40 to 70 mm. Three genera and about half a dozen species are known: they frequent sandy localities in Australia and Tasmania (Tillyard, 1919b; 1922). Ithonidae are active runners taking refuge in dark crevices, etc., and when their wings are closed they bear a certain superficial resemblance to cockroaches. The eggs of *Ithone* are laid in sand which adheres to them owing to a sticky secretion with which they are covered: the larva is soft, whitish, and blind, with small mandibles and maxillae: it normally preys upon scarabaeid larvae.

2. Superfamily **Coniopterygoidea**

Small insects with mealy wings; Rs with two branches, veins not bifurcating near margins.

FAM. CONIOPTERYGIDAE.—This family includes about 50 species which are the smallest and most aberrant of the Neuroptera. They are extremely fragile insects bearing a general resemblance to aphides, with the body and wings covered with a whitish powdery exudation. The antennae are filiform and the segments vary between about 16 and 43 in number: the eyes are rather large and there are no ocelli. The mouth-parts do not differ in any important features from those of other Planipennia. The venation is greatly simplified by reduction, and there are but few cross-veins (Fig. 373). The strongest claims

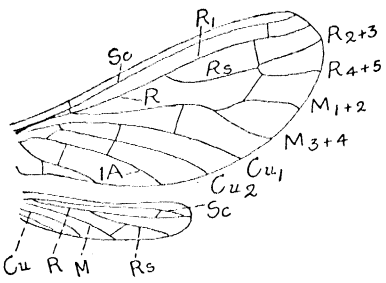


FIG. 373.—*Conwentzia psociformis*, right wings × 12

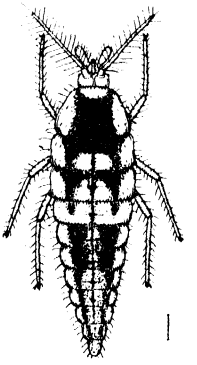


FIG. 374. — *Conwentzia psociformis*, larva
After Withycombe, *Trans. Ent. Soc.*, 1922

these insects have to be regarded as Planipennia rests on the structural characters of their larvae. So far as known the eggs are laid upon various trees frequented by Aphididae, Coccidae or Acarina, and the resulting larvae prey upon those organisms. The larvae are more or less pyriform, tapering sharply towards the hinder extremity, and the legs are long and slender (Fig. 374). The antennae are few-segmented and fringed with rather long hairs: the mandibles and maxillae are short and stout piercing organs, and the labial palpi are conspicuous clavate appendages projecting in front of the head. When about to pupate a cocoon is spun of silk emitted from the anus as in other Planipennia. According to Arrow (1917) the first generation of *Conwentzia psociformis* spins its cocoons on oak-leaves, while the second generation overwinters as larvae, which lie up in cocoons spun upon the trunk of that tree. The family has been monographed by Enderlein (1906): although its members are not rare they need carefully looking for and, up to the present, only seven species have been found in Britain. Anatomically the larvae differ from other Planipennia in possessing only six Malpighian tubes and in the greatly concentrated abdominal nerve-cord.

3. Superfamily **Hemerobioidea**

Antennae monili- or filiform. Larvae fusiform, body without dolichasters, mandibles not stout, straight or curved, without internal teeth.

FAM. DILARIDAE.—A very small family recognizable from its allies by the strongly pectinated antennae of the male and the exserted ovipositor of the female. Its affinities lie with the Hemerobiidae and Ithonidae, but nothing is known concerning its biology. *Dilar* occurs in N. America and Japan.

FAM. BEROTHIDAE.—The Berothidae are rather small, somewhat slenderly built insects with variably shaped wings. The latter are hairy, especially along their posterior margins, and peculiar scales of a seed-like form may be present in the females, either on the posterior fringe or on some of the principal veins. The limits of the family, however, are ill defined: thus in some species Sc is distally joined with R_1, while in *Berotha* there appears to be no such union owing to the distal atrophy of Sc. These two veins remain separate in the Australian genera *Trichoma* and *Stenobiella*, which are narrow-winged, densely hairy insects: they are regarded by Tillyard (1916b) as constituting a family of their own—the Trichomatidae. The eggs of *Spermophorella* are very similar to those of *Chrysopa* and are elevated upon long pedicels. The newly hatched larva is figured by Tillyard: it has an elongate narrow head with straight and rather short mandibles with broadened bases. The family is widely distributed and known from India, the United States and Australia.

The **Polystoechotidae** is a small N. American family allied to the Berothidae.

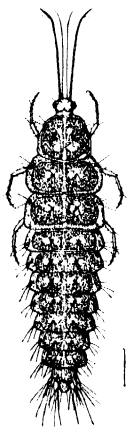


FIG. 375.—*Sisyra fuscata*, larva *After* Withycombe, *Trans. Ent. Soc.*, 1922.

FAM. SISYRIDAE.—These insects are to be regarded as an offshoot of the Osmylidae with which they agree in the distal fusion of Sc and R_1 and in the characters of Rs. On the other hand, the cross-veins are reduced in number and definitely specialized: the costal area, also, has no recurrent veinlet or branched transverse veinlets (Fig. 375). The larvae of *Sisyra* and *Climacia* are aquatic, living in association with fresh-water sponges (*Spongilla* and *Ephydatia*). The life-history of *Sisyra* has been followed by Anthony (1902) and by Withycombe. The eggs are very small, resembling those of *Hemerobius*: they are laid in small clusters on leaves, piles, and other objects standing in or overhanging water. The female covers each batch with a silken web as in the Psocoptera. The larva clings to the surface of the sponge or descends into the open osteoles, piercing the sponge-tissue with its mouthparts. It is yellowish green or brownish, hairy, resembling that of a Chrysopid in general form (Fig. 375); it bears seven pairs of segmentally arranged, several-jointed abdominal gills, each supplied by tracheal branches. The antennae are long and setiform, while the mandibles and maxillae form a pair of almost equally elongate bristle-like stylets. Labial palpi are wanting and the legs are single-clawed. Pupation takes place above water in a finely-woven double cocoon. Three species of the genus occur in Britain, *S. fuscata* being common.

FAM. HEMEROBIIDAE (Brown Lacewings).—This family was originally held to include all Neuropterous insects whose larvae possess suctorial mouthparts and whose imagines have a closely reticulated wing-venation. The growth of further knowledge, and more particularly the work of Handlirsch and of Tillyard, has made it evident that the group thus constituted really forms a complex of a number of separate families. The Hemerobiidae, as now restricted, are rather small delicate insects with moniliform antennae and no ocelli. Their principal venational feature is the fusion of R_1 and Rs, two or more of the branches of the latter vein arising from the common stem thus formed. The costal area is crossed by numerous branched veinlets, true cross-veins are few and of a specialized character (Fig. 377). A further character is afforded by Sc, which does not unite at its apex with any other vein. A wing-coupling apparatus of the jugo-frenate type is commonly present, and, although the jugal bristles are wanting, those of the frenulum are evident.

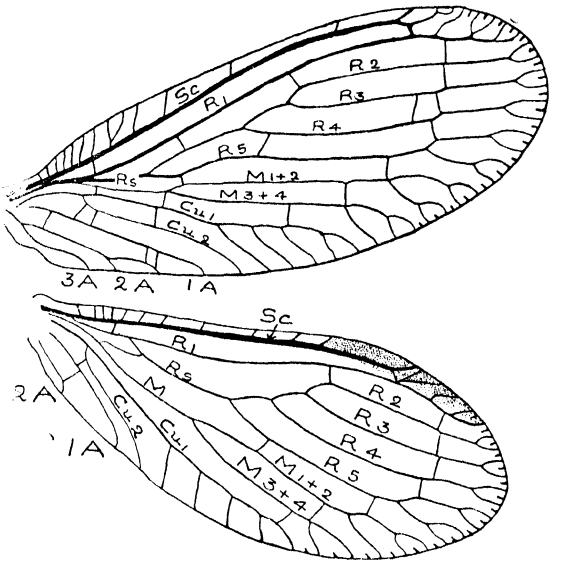


FIG. 376.—Right wings of *Sisyra flavicornis*
After Comstock, *Wings of Insects.*

The eggs, unlike those of the Chrysopidae, are devoid of pedicels and have a knob-like micropylar apparatus. Hemerobiid larvae (Fig. 378) are fusiform and smooth without tubercles of any kind, and the body hairs are simple. The mouthparts are rather stout and only slightly curved. A reduced padlike empodium

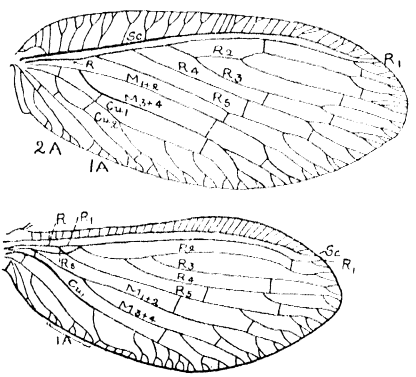


FIG. 377.—Right wings of *Hemerobius*

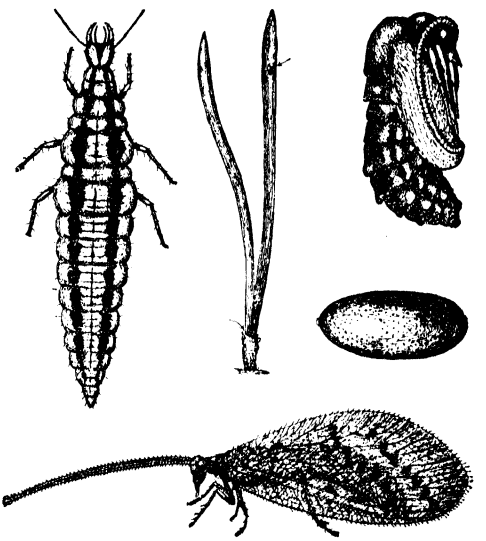


FIG. 378.—*Hemerobius stigma*
1, leaves of pine, the arrows indicate positions where eggs are laid; 2, egg × 30; 3, larva × 6; 4, pupa × 6; 5, imago × 4. *After* Withycombe, *Entom.*, 1922.

is present between the tarsal claws, but in the first instar it is trumpet-shaped. In colour the larvae are commonly creamy white with markings of some shade of brown. They roam about vegetation infested with aphids and other Homoptera, acari, etc., which serve as their food. They are naked, and the often repeated statement that they are

concealed by skins of their victims which they transfer, along with other debris, to their backs, refers to Chrysopids. Hemerobiidae are a widely distributed family, and rather less than 30 species occur in the British Isles.

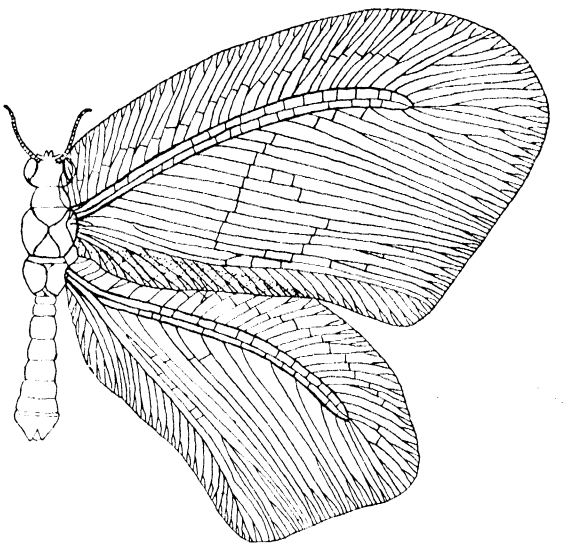


FIG. 379.—*Psychopsis gracilis*, male × 3
Adapted from Tillyard, *Proc. Linn. Soc. N.S.W.*, 43.

FAM. PSYCHOPSIDAE. — Although formerly regarded as a component part of the Hemerobiidae, this family is separable therefrom by its markedly different venational characters and the shortened antennae. The costal area of the wings is exceptionally deep and the three veins Sc, R_1 and Rs exhibit increased sclerotization and assume a parallel course as far as their terminal anastomosis (Fig. 379): they form, in this manner, a kind of broad mid-rib which renders these insects easily recognizable. The biology of the Australian *Psychopsis elegans* has been followed by Tillyard (1919a) and the life-cycle occupies about a year. The eggs are laid in January or February upon the bark of trees, especially Eucalypti: they are oval and each is provided with a small micropylar projection. The larva is characterized by the great size of the mandibles, which are sickle-like and devoid of teeth: the head is also large and its broad base is closely connected with the prothorax without any visible 'neck'. In their habits these larvae are arboreal, living beneath bark: they probably only emerge from their hiding-places to seize the insects which come to feed upon the gum which exudes from the trees. There are three larval instars: about November they construct silken cocoons in crevices of the bark and the pupal stage lasts about three weeks. Psychopsidae are rare insects of nocturnal habits: 18 species (Kimmins, 1939) occur in Australia, S. Africa, Tibet, China and Burma.

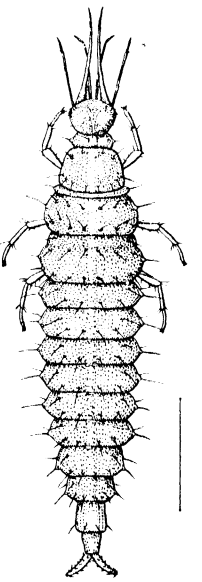


FIG. 380. — *Osmylus fulvicephalus*, larva
After Withycombe, *Trans. Ent. Soc.*, 1922.

FAM. OSMYLIDAE.—This family is closely allied to the Sisyridae and Berothidae and is separable from the Chrysopidae by the distal union of Sc and R_1, and by the presence of three ocelli near the frons. The very large number of cross-veins is also a characteristic of the family. The Osmylidae are a considerable assemblage of beautiful insects, often with maculated wings, and *Osmylus fulvicephalus* is the largest British Neuropteron. This species occurs locally along the borders of clear streams where there is a dense growth of bushes, etc. Its larvae (Fig. 380) lurks under stones or about moss, etc., either in or near the water. It is easily recognized by its long slender stylet-like mandibles and maxillae, which are only slightly curved upwards. Unlike the aquatic larva of *Sisyra* there are no gills and it breathes by means of thoracic and abdominal spiracles. According to Withycombe its natural food consists of Dipterous larvae.

FAM. MANTISPIDAE.—The members of this family are easily recognized by the elongate prothorax and the large raptorial anterior legs. The latter appendages are formed very much the same as in the Mantidae (vide p. 362) and fulfil similar functions. Each femur is armed with powerful spines and the tibia is adapted to fold closely on to it, the two parts forming a very effective prehensile organ for seizing the prey. The

family occurs in most of the warm regions of the world and a few species occur in S. Europe. The life-history of *Mantispa styriaca* has been followed by Brauer (1869). The eggs are borne on long pedicels as in *Chrysopa* and the newly-hatched larvae are elongate and campodeiform but are devoid of cerci. They pass into hibernation almost immediately and in the following spring they seek out the egg-cocoons of the spider *Lycosa*. Only a single *Mantispa* larva enters each cocoon and it preys upon the young spiders, piercing them with the pointed mouthparts and imbibing their body-fluids. Feeding in this manner leads to an expansion of the larva which becomes so swollen as to resemble that of a miniature cockchafer. It subsequently undergoes ecdysis, and becomes transformed into an eruciform larva with a minute head, and small thoracic legs. It becomes mature a few days later, and spins a cocoon around itself, amidst the dried remains of its victims, within the original egg-bag of the spider. Pupation occurs within the last larval skin and the imago consequently has to pierce the latter and its own cocoon, and that of the spider, before it emerges into the open. The parent spider watches over her cocoon without hostility to the presence of the parasite. The life-history of *Mantispa*, it will be observed, affords an example of hypermetamorphosis. Some species, however, are associated with Aculeate Hymenoptera.

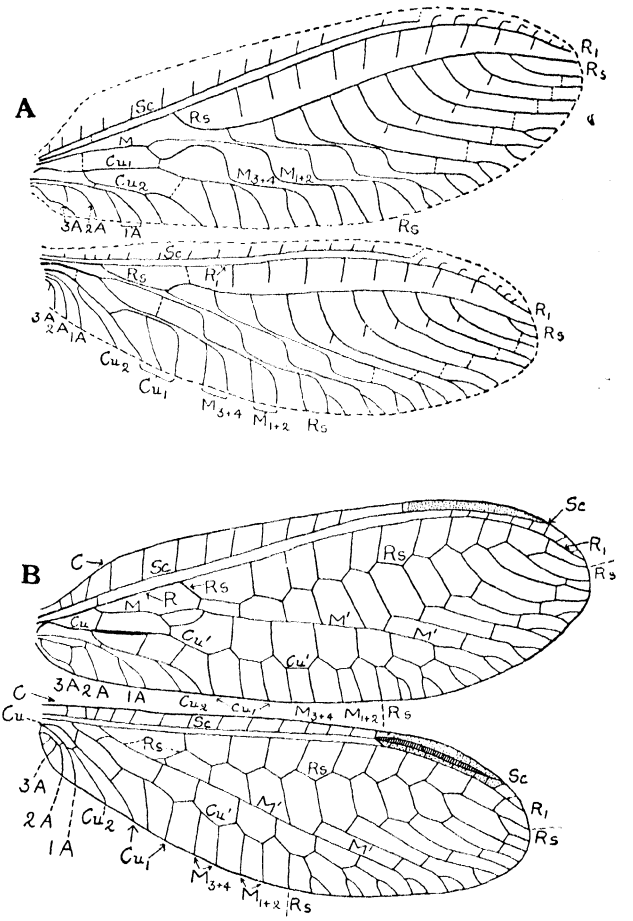


FIG. 381.—*Chrysopa signata*. A, diagram of wing-tracheation. B, wing-venation

Cu', pseudocubitus; M', pseudomedia. *After* Tillyard, *Proc. Linn. Soc. N.S.W.*, 41.

FAM. CHRYSOPIDAE (Green Lacewings).—This family includes a large number of closely related species popularly known as 'green lacewings' or 'golden eyes'. Many have bright green bodies and appendages, with the wing-veins similarly coloured, and the eyes exhibit a burnished metallic lustre. Certain of the species emit a disagreeable odour when handled from a pair of prothoracic glands, and have earned for the group the alternative name of 'stink flies'. The antennae of the Chrysopidae are filiform, and longer than they are in the Hemerobiidae, the segments being less distinctly demarcated. The venation (Tillyard, 1916a) is characterized (Fig. 381) by Rs arising from the main stem separately from R_1 which does not fuse distally with Sc and by the formation of a so-called pseudomedia and pseudocubitus. These are highly complex veins, the first being formed by the fusion of M_{1+2}, M_{3+4} and portions of the four proximal branches of Rs. The pseudocubitus is formed by Cu, by the distal portion of M_{1+2} and M_{3+4} and by part of the three proximal branches of Rs.

The eggs of the Chrysopidae are commonly laid in batches, and a small amount of secretory fluid accompanies each act of oviposition. A spot of this substance is applied to a leaf or other object and the abdomen is then uplifted, with the result that a viscous thread of the secretion is drawn out perpendicularly to the substratum. The thread rapidly hardens and is surmounted by an egg, the latter being thus supported upon a delicate pedicel. In *Chrysopa flava*, and certain other species, the pedicels of an egg-group are joined into a common bundle. Chrysopid larvae (Fig. 382) resemble those of the Hemerobiidae in their general characters but differ according to Withycombe in the following points. They are shorter and broader with the jaws more slender and curved. The body is provided with setae arising from dorsolateral tubercles. The larvae are often concealed by the remains of their victims, which are retained in position by means of hooked hairs situated on the dorsal aspect of the abdomen. A trumpet-shaped empodium is present between the tarsal claws in all instars. *Chrysopa flava* differs from most other members of the family in its larva having no tubercles and in being more elongate. In coloration the larvae are exceedingly variable: the ground colour is generally white, yellowish or green, usually with darker markings of red, chocolate or black. They are familiar objects on aphid-infested vegetation and are commonly obscured by their coating of debris. Economically, they are of importance on account of the large numbers of soft-bodied insects which they consume: their prey consists principally of aphides, but Jassids, Psyllids, coccids, together with thrips and acari, are also attacked. According to Wildermuth (1916) *Chrysopa californica* will destroy 300–400 aphides during its larval existence. Fourteen species of the family are British but about 800 are known.

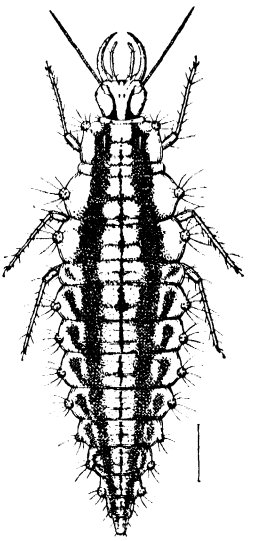


FIG. 382.—*Chrysopa carnea*, larva in 3rd instar

After Withycombe, *Trans. Entom. Soc.*, 1922.

4. Superfamily **Myrmeleontoidea**

Antennae stoutly cylindrical, or apex thickened or even clubbed. Larva broad, body with at least a few dolichasters (see p. 502), mandibles usually stout and curved, usually (except some Nemopterid larvae with a very long prothorax) with one or more internal teeth.

The **Myiodactylidae** resemble the Osmylidae in the adult stage but the larva is of an exaggerated Ascalaphid type. The **Nymphidae** is a small family of Australian insects, perhaps remnants of a group which gave rise to the Myrmeleontidae from which they differ in having cross-veins between Sc and R_1.

FAM. NEMOPTERIDAE.—A highly specialized family with enormously elongate, ribbon-like hind wings and with the head usually prolonged into a kind of rostrum. They are striking and beautiful insects flying with a curious up-and-down motion after the manner of Ephemerids, with the long hind wings streaming in the air. The form of the latter is somewhat variable: in *Croce* they are filiform, and taper to a point, while in other cases they are sometimes expanded before their extremities (Fig. 383). The mid-rib, which lends support to these greatly attenuated organs, is formed, according to Comstock, by the closely approximated stems of R and M. The life-history of the Indian *Croce filipennis* (Fig. 384) occupies about a year (Imms, 1911). The imagines are crepuscular and frequent buildings. The eggs are laid among dust and refuse on floors, and the fully-grown larva has a large quadrate head and long, curved, finely dentated mandibles. The head is connected with the hind-body by a conspicuous 2-segmented 'neck'; the meso- and metathorax are imperfectly differentiated and merged into the abdomen. The larvae cover themselves with dust particles and are hard to detect: they prey upon Psocids and other small insects. The pupa is notable on account of its method of accommodating the long hind wings. These are many times coiled after the manner of watch-springs: they cross each other near their bases, so that the right wing lies on the left side and *vice versa*. The pupa

is enclosed in a cocoon composed of sand and debris bound together by silk. In *Nina joppana* and *Pterocroce storeyi* the neck of the larva is so greatly attenuated that it

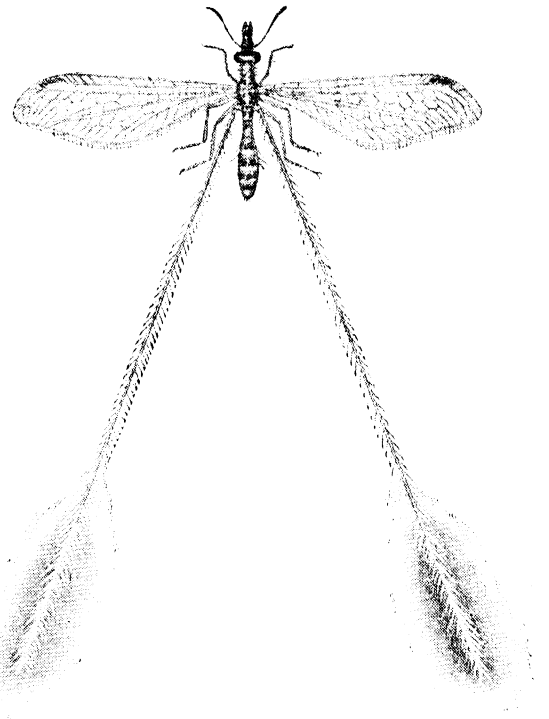


FIG. 383.—*Croce filipennis* × 2·5. India

equals in length the whole of the rest of the body (Fig. 385): these remarkable larvae have been found in caves in Egypt and Palestine (Withycombe, 1923). The family is widely distributed and several species occur in S. Europe.

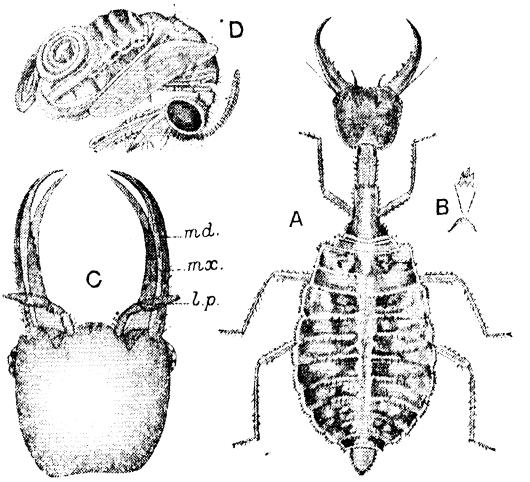


FIG. 384.—*Croce filipennis*

A, larva in last instar. B, a dolichaster × 230. C, ventral aspect of head of larva × 50; *md*, mandible; *mx*, maxilla; *lp*, labial palp. D, pupa. *After* Imms, *Trans. Linn. Soc.*, 1911.

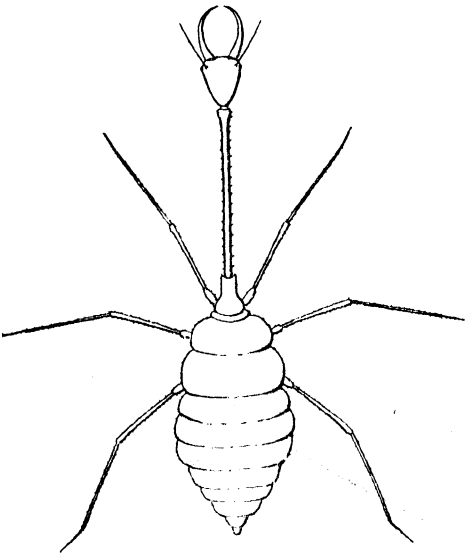


FIG. 385.—*Pterocroce storeyi*, larva in last instar × circa 8
After Withycombe.

FAM. ASCALAPHIDAE.—This family is closely related to the Myrmeleontidae and has a very similar distribution. Some of the species are active fliers, and are on the wing during daytime, hawking their prey after the manner of dragonflies: others, however, are nocturnal and very seldom seen. The eggs are deposited in rows upon grass stems, twigs, etc., and the batches are often fenced in below by circles of rod-like bodies or repagula which possibly guard them from the attacks of predacious enemies. The larvae closely resemble those of the next family and have similar dentate mandibles: they are often provided with lateral segmental processes fringed with modified setae (dolichasters). These processes are particularly well developed in *Pseudoptynx* and *Ulula*, while they are usually quite rudimentary in the Myrmeleontidae. The larvae do not construct pitfalls but live concealed on the ground among stones, leaves, etc., or more rarely on the bark of trees. The family has been monographed by Van der Weele (1908), who figures larvae of several genera: the life-history of *Ulula* is described by McClendon (1902). Several species are common in southern Europe and *Ascalaphus longicornis* occurs as far north as Paris.

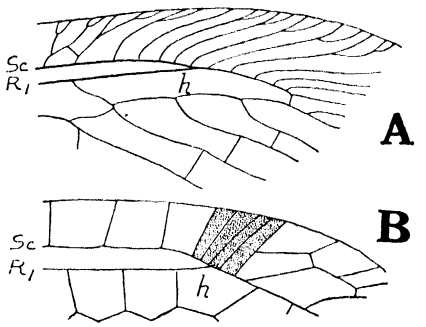


FIG. 386.—Portion of fore wing of A, a Myrmeleontid; B, an Ascalaphid, showing hypostigmal cell *h*
Based on figures by Comstock.

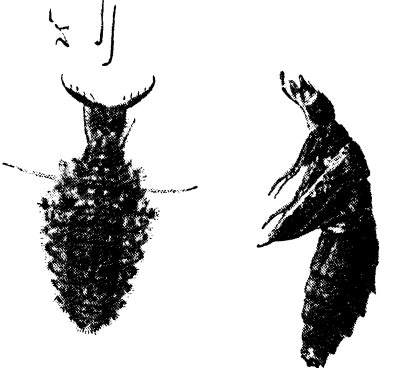


FIG. 387.—*Myrmeleon*, larva and pupa × 3. Switzerland
From enlarged photos by H. Main.

FAM. MYRMELEONTIDAE (Ant Lion Flies).—In their general appearance these insects resemble dragonflies of the narrow-bodied type and in their larval stages they are known as 'ant lions' (fourmilions). They comprise a considerable number

of often large, handsome species which, however, are seldom seen. During the day they hide among trees and bushes, only appearing on the wing towards dark. Myrmeleontidae are easily distinguished from other Neuroptera by their short knobbed antennae: their wings are long and narrow, usually marked with brown or black, and furnished with many accessory veins and cross-veins. They are closely related to the Ascalaphidae, but the latter insects have longer antennae and lack the elongate hypostigmal cell (Fig. 386). Although most abundant in tropical countries, species of *Myrmeleon* occur in Europe, one representative being found as far north as Finland, but the family is not found in the British Isles: the European species are enumerated by Navás (1916). The biology of *M. formicarius* was accurately observed by the early naturalist Réaumur. The ova are deposited in sand and the newly emerged larvae excavate pits in the ground for the purpose of securing their prey. The Myrmeleontid larva buries itself at the bottom of the pit, leaving only its large jaws protruding. An ant or other insect wandering over the edge of the pit usually dislodges the sand of the sloping sides and soon finds itself in difficulties. The ant lion jerks some of the sand by means of its head towards its victim and continues to do so until the latter is brought to the pit. Here it is seized and not released until its juices are extracted. The larvae of this family (vide Meinert, 1889; Redtenbacher, 1884; Gravely & Maulik, 1911) are flattened and ovoid with large heads, and long, protruding mandibles, armed with exceedingly sharp spiniform teeth (Fig. 387). The pit-forming habit is characteristic of *Myrmeleon* and several other genera, but the larva of *M. contractus* lives on the mud-covered trunks of trees in Bengal, and doubtless preys upon the ants which are constantly streaming up and down. Other larvae of this family hide away under stones and debris, or cover themselves with a coating of foreign substances, and thereby secure concealment. Some account of the anatomy of the imago is given by Dufour (1841) and Wheeler (1930) has published a striking review of the family.

Literature on Neuroptera

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Order 22. **MECOPTERA** (Scorpion Flies)

Slender, moderate or small-sized, usually carnivorous insects with elongate, filiform antennae, head usually produced into a vertically deflected rostrum, with biting mouthparts: ligula wanting. Legs long and slender. Wings similar and membranous, carried longitudinally and horizontally in repose: venation primitive, Rs dichotomously branched, Cu_1 simple. Abdomen elongate with short cerci, male genitalia prominent. Larvae eruciform with biting mouthparts and three pairs of thoracic legs: abdominal feet present or absent. Pupae exarate: wings with reduced tracheation.

This small order comprises about 300 species, the greater number of which belong to the genera *Panorpa* and *Bittacus*. The majority of the members of the group are easily recognized by the beak-like prolongation of the front of the head, and their often maculated wings. The 'scorpion flies' (*sen. str.*) belong to the Panorpidae, which include many species widely spread over the northern hemisphere (Fig. 388). Their vernacular name is due to the fact that the males carry the terminal segment of the abdomen upwardly curved, somewhat after the manner of Scorpions. The Bittacidae are very slender Tipula-like insects with prehensile tarsi: they are found in most parts of the world excepting the northern portion of the holarctic region. The Boreidae are characterized by their vestigial wings and occur in Europe and N. America. The order is represented in the British Isles by three species of *Panorpa* and a single species of *Boreus* (Hobby & Killington, 1934).

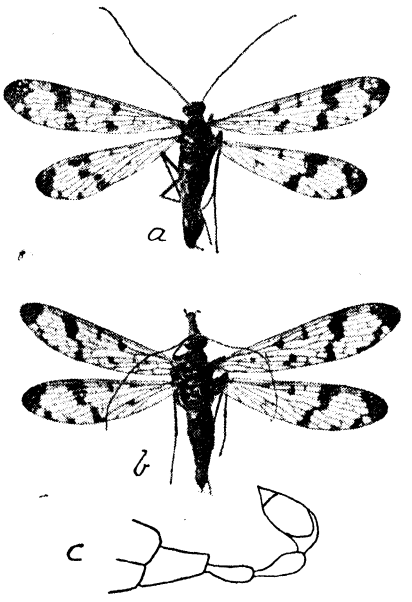


FIG. 388.—*Panorpa communis*. A, male; B, female (from Photos by W. J. Lucas); C, apex of abdomen of male *After* MacLachlan.

The Mecoptera are essentially terrestrial insects undergoing their transformations in the soil: a possible exception is found in *Nannochorista*, which is believed by Tillyard to be aquatic. Both their larvae and imagines are carnivorous, but the extent to which the Panorpidae prey upon living uninjured insects or other animals is doubtful. Brauer and Felt have reared larvae of *Panorpa* upon fragments of meat, but Miyake found wounded or dead insects more acceptable. The adults are mostly found in shaded situations where there is a growth of rank herbage. *Bittacus* rests suspended

from grasses or twigs by its fore legs, and preys upon small Diptera, seizing them by means of its raptorial tarsi. *Boreus* lives among moss or beneath stones in autumn and early winter, appearing occasionally on the surface of snow; it is exceptional in feeding upon vegetable matter.

External Anatomy (Fig. 389).—The anterior region of the head (Heddergott, 1938) is usually prolonged into a rostrum which is formed by the elongation of parts of the head-capsule together with the clypeus, labrum and maxillae. The compound eyes are well developed and there are usually three ocelli. The antennae are more or less filiform and many-jointed, there being about 40–50 segments in *Panorpa*, and about 16–20 in *Bittacus*. The mandibles are slender and elongate: they are only dentate at their apices, each bearing from 1 to 3 sharp teeth. The maxillae are complete: their palpi are 5-segmented, and the galeae and laciniae are hairy lobes of somewhat complex structure (Miyake, 1913). The labium consists of an elongate submentum, not always clearly differentiated from the short mentum: the prementum exhibits traces of a bilobed structure, but the ligula has disappeared. The labial palpi are 1- to 3-segmented; in some cases they are in the form of fleshy lobes in which, according to Crampton, traces of pseudotracheae may be present, resembling those found in the labium of Diptera. The mouthparts of *Nannochorista* are considerably specialized (Tillyard, 1917; Imms, 1944). The labrum forms a sharply projecting process, the mandibles are vestigial, and the labial palpi (paraglossae of Tillyard) are partially fused at their bases. This genus, which is accorded separate family rank by Tillyard, exhibits a tendency towards the development of suctorial mouthparts and foreshadows the condition found in the lower Diptera.

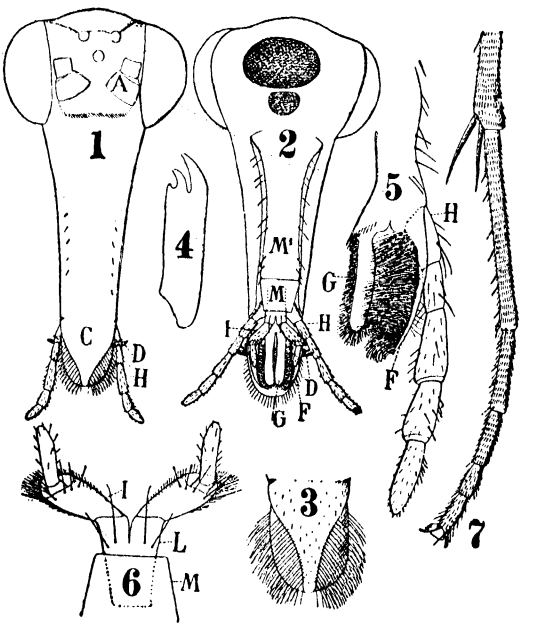


FIG. 389.—*Panorpa communis*. 1, frontal view of head; 2, ventral view; 3, labrum; 4, mandible; 5, maxilla; 6, labium; 7, apex of tibia and tarsus

A, antenna; *C*, labrum; *D*, mandible; *F*, galea; *G*, lacinia; *M*, mentum; *M'*, submentum. *After* Silvestri, with legend modified.

The prothorax is very small, its largest region being the notum, which is divided by transverse lines into four areas. Both the meso- and metathorax are well developed. The legs are generally adapted for walking, the claws are usually paired and in *Panorpa* they are strongly pectinated. In *Bittacus* the claws are single, and the 4th and 5th tarsal segments are provided with fine teeth along their inner margins: the 5th segment is capable of closing on to the 4th after the manner of the blade of a pocket-knife. The two pairs of wings are similar in form and nearly equal in size: in many species they are conspicuously spotted or banded. These organs are totally absent in the

Californian *Apterobittacus*: in the males of the Boreidae (Fig. 390) they are represented by two pairs of slender bristle-like vestiges, and in the females there is a single pair of scale-like lobes on the mesothorax. In the Nannochoristinae and Choristinae there is a definite wing-coupling apparatus with a well-developed frenulum (vide p. 41). Microtrichia are generally present, and macrotrichia occur on the veins and their branches, but not on the cross-veins; the latter type of setae is also often present on the wing-membrane. The venation is extremely archaic, the principal veins and their primary branches (excepting those of Cu_1) frequently being present (Fig. 391). The wing tracheae, on the other hand, are highly specialized by reduction. The primary dichotomies of the veins usually occur fairly close to the bases of the wings, and cross-veins are numerous, but without definite arrangement. In their venational features the two pairs of wings are also very alike, the principal difference being the basal fusion of Cu_2 and 1A in the hind wing. A marked deviation

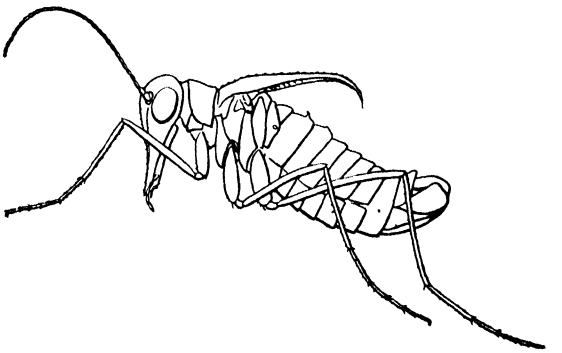


FIG. 390.—*Boreus hyemalis*, male × 15
After Withycombe.

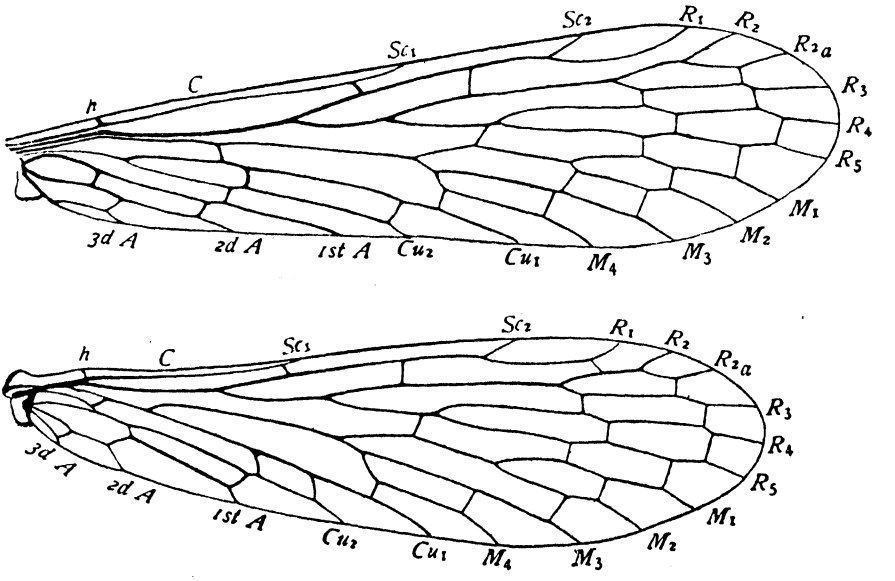


FIG. 391.—Wings of *Panorpa*
After Comstock, *Wings of Insects*.

from the primitive type is exhibited in *Nannochorista* in which R_{2+3} is unforked and $M + Cu_1$ are fused for about half their length.

The abdomen has 10 distinct segments but there appears to be an 11th segment in the female at least of *Panorpa* (Ferris & Rees, 1939). In the male of that genus (Grell, 1942) the hind margin of the 9th sternum is prolonged

into a deeply cleft process, the two arms of which are styliform. The 9th tergum is prolonged into a subquadrate plate. Between the dorsal and ventral processes thus formed there is a pair of laterally inserted 2-segmented claspers. The 10th segment is very inconspicuous, and bears a pair of short 1-segmented cerci. Between the base of the claspers is the longitudinally cleft aedeagus. In the female the 7th to 10th segments are cylindrical, and each is telescoped into the preceding segment: at the apex of the abdomen is a pair of 2-segmented cerci.

Internal Anatomy.—The internal anatomy (Miyake, 1913; Grell, 1938; Potter, 1938a) has been investigated in several genera. In *Panorpa* the *alimentary canal* is a tolerably straight tube, the only convolution present occurring in the hind intestine. The oesophagus is curiously dilated at two points along its course to form what appears to be a kind of muscular pumping-apparatus. A short distance further backward there is an elliptical chamber which is regarded as the proventriculus: the latter is provided with longitudinal and circular muscles, and its inner lining is beset with numerous long setae. The mid intestine is an elongate tube of large calibre, and the commencement of the hind intestine is marked by the insertions of 6 Malpighian tubes. A pair of tubular salivary glands is also present. The *nervous system* consists of the usual cephalic centres (Bierbrodt, 1942), 3 thoracic and 6–8 (♂) or 5–7 (♀) abdominal ganglia: the first of the latter is located in the metathorax. The *respiratory system* is well developed: there are two pairs of thoracic and six to eight pairs of abdominal spiracles. The *reproductive system* in the male consists of a pair of testes, each composed of 3–4 follicles arranged side by side around a longitudinal axis: the vasa efferentia are densely convoluted (except *Boreus*), forming a kind of epididymis at the posterior end of the testis. The two vasa deferentia open separately into a large median vesicula seminalis which also receives a pair of accessory glands. Each ovary consists of 7–19 polytrophic ovarioles, the number varying according to the species. The two oviducts unite to form a common canal which opens into a kind of genital pouch: the latter also receives the opening of the duct leading from small pyriform spermatheca and that of the duct of a pair of colleterial glands. The genital pouch communicates with the exterior on the 9th abdominal segment but in *Boreus* there is a true vagina.

Life-History and Metamorphosis.—The eggs of several species have been obtained by confining the adults in vessels containing damp soil. In the European and American species of *Panorpa* they are laid in small batches in crevices in the soil: in the Japanese *P. klugi* Miyake mentions nearly 100 eggs being deposited in a group. In form they are ovoid in *Panorpa* and more or less cuboidal in *Bittacus*. The life-history of *Panorpa* was first observed by Brauer (1863); Felt (1895) describes the larva of *P. rufescens*, but the most complete account is that of Miyake (1912) which refers to *P. klugi* (Fig. 392). The first stage larva is yellowish-grey with the head testaceous. It is eruciform and bears a close resemblance to a caterpillar. The head is rather large with prominent 3-segmented antennae and it bears a group of about 20–28 simple eyes on either side. The mandibles are sharply toothed, and the maxillae are divided in lobes apparently corresponding with a galea and lacinia: the maxillary palpi are 4-segmented. The labium is small and its palpi 3-segmented. The thorax bears 3 pairs of legs, each composed of 4 segments: the abdomen is 10-segmented and the first 8 somites each carry a pair of abdominal feet. A median dorsal sclerotized shield is present on all the body segments. The first 9 abdominal shields each carry a pair of annulated pro-

cesses, the last two pairs being considerably the larger: the 10th segment bears a single median process of a similar character together with a curious retractile lobed vesicle on its ventral side. Nine pairs of spiracles are present: they are located on the prothorax and first 8 abdominal segments. After the first ecdysis the annulated processes practically disappear except those of the last three segments. The number of ecdyses that occur has not been observed. Felt, from head-measurements, recognized seven stages in *Panorpa rufescens*. Pupation takes place in an earthen cavity below ground: the pupa is of the

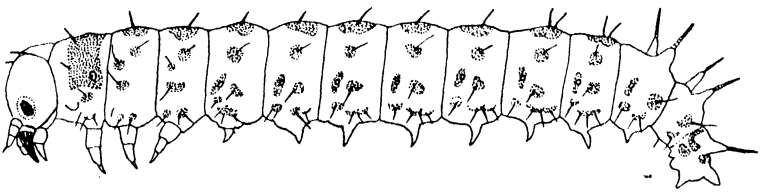


FIG. 392.—*Panorpa*, larva in last instar × 5
Adapted from Miyake.

usual exarate type and is capable of movement when disturbed: according to Miyake it works its way to the surface prior to the emergence of the imago. The European species probably pass through a single generation in the year. The larva of *Boreus* is strongly curved: the thoracic legs are well developed but there are no abdominal feet. It lives among moss and, when about to pupate, constructs a vertical tube leading near to the surface. The internal anatomy of the larvae of *Panorpa* and *Boreus* is described by Potter (1938), Grell (1938) and Bierbrodt (1942).

Classification.—The scheme adopted is mainly that of Tillyard. The family Boreidae is more distinct than the arrangement indicates.

1. Body depressed. Wings short and broader, costal field of fore wing with at least 2 rows of polygonal cells, Rs arising near wing-base with more than four branches, M forking well before middle of wing, with more than four branches. Male genitalia not swollen (Suborder **Protomecoptera**) 2
–. Body almost cylindrical. Wings elongate, narrower, costal field of fore wing with simple veins, Rs not arising before proximal third of wing, M forking at about the middle, and at least one of these veins with 4 branches or less (or wings very reduced). Male genitalia usually swollen (Suborder **Eumecoptera**) . 3
2. Ocelli present . . . . . NOTIOTHAUMIDAE (1 sp. Chile)
–. Ocelli absent . . MEROPIDAE (2 gen., 1 sp. N. America, 1 sp. W. Australia).
3. Legs very long and thin with only one claw, last tarsal segment opposable. Ocelli present. Male abdomen not scorpion-like . . BITTACIDAE (Cosmopolitan)
–. Legs normal, with 2 claws, and last tarsal segment not opposable against penultimate. Male genitalia scorpion-like 4
4. Wings rudimentary without venation. Labial palpi short. Ocelli absent. Female abdomen terminally with an ovipositor-like structure BOREIDAE (Holarctic)
–. Wings normal. Labial palpi long. Ocelli present. Female abdomen with no conspicuous ovipositor-like structure . . . . PANORPIDAE (Cosmopolitan)

Two groups, here included in the Panorpidae, are usually treated as the families **CHORISTIDAE** and **NANNOCHORISTIDAE.** They are much less distinct from the Panorpidae than are the other families.

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Order 23. **LEPIDOPTERA** (Butterflies and Moths)

Insects with 2 pairs of membranous wings; cross-veins few in number. The body, wings and appendages clothed with broad scales. Mandibles almost always vestigial or absent, and the principal mouthparts generally represented by a suctorial proboscis formed by the maxillae. Larvae eruciform, peripneustic, frequently with 8 pairs of limbs. Pupae usually more or less obtect, and generally enclosed in a cocoon or an earthen cell: wing tracheation complete.

Lepidoptera are the most familiar and easily recognizable of all insects, and it is in this order that coloration has reached the highest degree of specialization. These insects have always been popular objects for study, and probably not far below 100,000 species have been described. Staudinger & Rebel (1901) enumerated over 9,500 Palaearctic species which are represented by more than 2,000 in the British Isles.

On the whole the imagines exhibit a remarkable constancy as regards their fundamental structure, and this uniformity has led to great difficulties in evolving a division of the order into major groups for classificatory purposes. On the other hand, the more superficial or adaptive characters exhibit almost endless variation in the larvae. As might be anticipated from this structural similarity, the habits of these insects are remarkably uniform. The imagines live entirely upon the juices of flowers, over-ripe fruit, honey-dew and other liquid substances: in a considerable number of species the mouthparts have atrophied. The larvae possess masticatory mouthparts and differ from those of other orders in feeding, with but few exceptions, entirely upon phanerogamic plants.

Economically Lepidoptera are of a great importance in the larval stage. The majority of injurious species devour the foliage and shoots of trees and crops; a smaller number bore into the stems or attack underground parts, and several species are injurious to timber; others attack manufactured goods such as carpets, clothing and their like, while a few are extremely destructive to stored products, including grain, flour, etc. Several predacious species are enemies of *Laccifer lacca*, and are thereby injurious to lac cultivation, and one or two species live in beehives, destroying and fouling the combs. The Saturniidae and *Bombyx mori*, on the other hand, confer a direct benefit upon man from the fact that they yield silk of commercial value.

Among the more recent general works on the order are those of Seitz (1906 *et seq.*) on the larger Lepidoptera of the world, and Hering (1933) on the European forms. The world's species are listed in the catalogue edited by Wagner (1911, etc.) and those of the Palaearctic region by Staudinger & Rebel (1901). The leading treatises on the British species are those of Meyrick (1928), Barrett (1893–1907) and Tutt (1899–1909). The work of the last-mentioned author contains a great deal of biological information but was not completed. Works on the butterflies (that is superfamilies Hesperioidea

and Papilionoidea) are particularly numerous: the Swedish and Italian species have been dealt with by Nordström, Wahlgren, and Tullgren (1935–41) and by Verity (1940–50), respectively; those of North America by Edwards (1868–97) and Clark (1932), both works also containing much general information. Among numerous other works, the volumes by Godman & Salvin (1879–1901) on Central America, by Corbet & Pendlebury (1934), Talbot (1939, 1947), and by Woodhouse & Henry (1942) on the Oriental region, and by Waterhouse (1932) on the butterflies of Australia, are important.

THE IMAGO

External Anatomy

The Head (Fig. 393).—The greater part of the head is formed by the clypeus and the large globular *compound eyes*. The *ocelli* are two in number and lie close behind the latter: they are seldom conspicuous, and generally much concealed by scales or often absent. In some families they are replaced

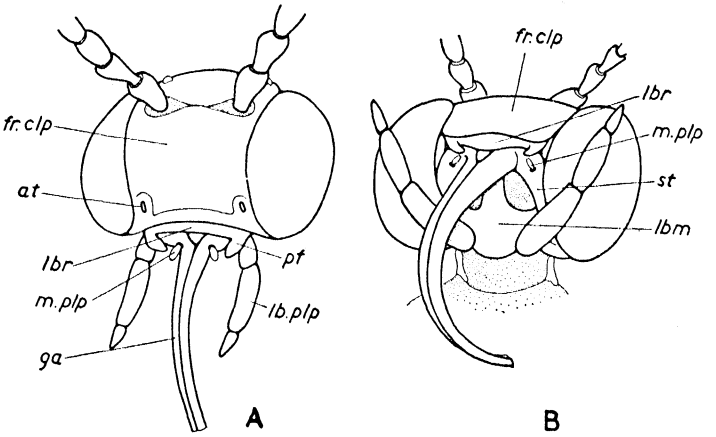


FIG. 393.—Head and mouthparts of Lepidoptera. A. Frontal view (*after* Snodgrass, 1935). B. Ventral view (based on Weber, 1933)

a.t, anterior tentorial pit; *fr. clp*, fronto-clypeus; *ga*, galea; *lbm*, labium; *lbr*, labrum, *lb.plp*, labial palp; *m.plp*, maxillary palp; *pf*, pilifer; *st*, stipes.

by a pair of sensory organs known as the *chaetosema* (Jordan, 1923; Eltringham, 1925b). The anterior region of the head (Short, 1951) is occupied by the large *clypeus*, which is frequently demarcated from the *frons* by an epistomal suture. The *labrum* is narrow and pointed in *Micropteryx* and its allies but forms a short transverse plate in other Lepidoptera. It is provided with a small pointed median projection which is usually regarded as an extension of the *epipharynx* and often also with lateral ones known as *pilifers*. Between the fronto-clypeus and the eyes are the narrow *genae* and, when mandibular rudiments are present, they either articulate or fuse with the latter sclerites. The *antennae* (Jordan, 1898) are composed of an indefinite number of segments and vary greatly in length and structure. In the male they frequently show an increased development as compared with the female which is particularly well exhibited in the Saturniidae. They are generally scaled dorsally and very often ventrally also: in some cases scales are absent as in the Saturniidae and many butterflies.

Mouthparts.—In the majority of Lepidoptera, mandibles are totally wanting and the maxillae are highly modified to form a suctorial proboscis. The latter is composed of the two greatly elongated galeae, each being channelled along its inner face, and the two are held together by means of hooks and interlocking spines. In this manner the combined grooves form a tube through which liquid food is imbibed. The laciniae are either entirely atrophied or, according to Berlese, rudiments thereof may be embodied in the base of the proboscis. When fully developed, the maxillary palpi are 5- or 6-segmented and usually more or less folded, as in the Tinaeidae; in the great majority of Lepidoptera they are either much reduced or wanting, their functions presumably being assumed by the labial palpi. Among Noctuidae they are 2- to 3-segmented; in the Sphingidae, Papilionoidea and most Geometridae they are single-segmented (Walter, 1884). The labium is reduced to a small plate on the ventral aspect of the mouth: its palpi are normally 3-segmented and vary greatly in size, shape and scaling. A hypopharynx is present on the floor of the mouth and in *Danais* it is provided with gustatory papillae.

When not in use the proboscis is spirally coiled and stowed away beneath the thorax: it presents an extraordinary variation in length, attaining its maximum in the Sphingidae. In *Danais*, according to Burgess (1880), each half of the proboscis is seen to be composed of an immense number of sclerotized rings, which are incomplete since they are absent from its inner or grooved aspect. These rings are separated by intervening bands of membrane which admit of the spiral coiling of the organ. Each ring is made up of a row of quadrangular plates which are provided with spine-like processes directed towards the proboscis channel, hence the plates are somewhat nail-like in form. Scattered over the surface of the proboscis, and more especially at the apex, are small circular plates each bearing a minute central papilla, which are perhaps tactile in function (Börner, 1939). According to Breitenbach they are often developed into denticulate spines which enable the proboscis to lacerate the tissues of fruit and imbibe their juices: this condition is particularly well exhibited in *Aletia xylina*. The interior of each half of the proboscis is hollow and occupied throughout its length by a nerve and a trachea, but the bulk of its cavity accommodates two sets of muscles which diagonally cross it. From their attachment the action of these muscles would result in shortening of the posterior wall of the maxilla and produce the spiral coiling of the organ.

According to Schmitt (1938), the proboscis is extended by means of blood-pressure created in the stipes of each maxilla. There are three muscles which by their contraction press the stipes against the cranial wall while a valve closes the passage from the stipital cavity into the head (cf. also Pradhan & Aren, 1941).

In some Lepidoptera (*Orgyia*, *Zeuzera*, etc.) the proboscis is reduced and non-functional, the two galeae remaining separate; in many others the galeae are represented by two minute papillae (*Hepialus*) or entirely atrophied. In the reduced or atrophied condition it is evident that no food can be imbibed and the mouth may be wanting also, as in the Saturniidae (cf. Naumann, 1937, and Gohrbrandt, 1940).

The mouthparts are exhibited in their most primitive form in *Sabatinca* (Tillyard, 1923a) where they are clearly of the mandibulate type. The mandibles are functional dentate organs, with evident ginglymus and condyle, and movable by means of well-developed abductor and adductor muscles. In the maxillae cardo and stipes are evident, the galea is short and 2-segmented, the lacinia blade-like, and the palpi are long and 5-segmented. In the labium, however, there is no ligula and lobes formerly regarded as paraglossae are in reality processes of the palpi (Tillyard): the basal sclerites are represented by a single mental plate. The hypopharynx in *Micropteryx ammanella* is laterally provided with small accessory pieces which are regarded by

Busck and Böving as the superlinguae. In *Eriocrania* the mandibles are non-dentate and in *Mnemonica* they are unsclerotized with the ginglymus and condyle rudimentary: proof that these are true mandibles is afforded by the fact that they lie within those of the pupa. In both the above genera the laciniae are lost, and the 2-segmented galeae are greatly elongated. The terminal segment of the galea of either side is opposed to that of its fellow, thus exhibiting the first step in the formation of the Lepidopterous proboscis. Vestigial mandibles are also present in *Hepialus*, in various Tinaeoids including *Argyresthia*, *Tinaea*, *Tineola* and *Hyponomeuta*, and in Sphingidae (Walter, 1885; Packard, 1895; Petersen, 1900; Short, 1951). Some authors have mistaken the pilifers for the mandibles, but Kellogg shows that both occur together in *Protoparce*.

The maxillae of *Tegeticula* are exceptional in exhibiting sexual dimorphism: in the male they are normal but the galeae are quite separate, and in the female there is an elongate inner lobe often known as the maxillary tentacle. The two latter organs are adapted for holding a large mass of pollen beneath the head: their morphology is doubtful and it has been suggested that they are the greatly produced palpifers.

In the **Thorax** (Fig. 394) the prothorax is evident in the lower forms but compressed and reduced in all the higher families where it assumes the form of a collar. It frequently carries a pair of small lateral processes or *patagia* which are peculiar to the higher Lepidoptera and appear as thin, lobe-like, erectile expansions, well developed in many Noctuidae (e.g. *Agrotis*). The mesothorax is the largest and most prominent segment of the three; its tergum consists of a narrow band-like prescutum, a very large, longitudinally divided scutum and a well-developed more or less rhomboidal scutellum. *Tegulae* are particularly well developed and very characteristic of the order; each is carried on a special tegular plate of the notum supported by means of a tegular arm arising from the base of the pleural wing process (Snodgrass). The metathorax is relatively small as compared with the previous segment; Snodgrass finds that in *Phassus* (Hepialidae), however, it is larger and more like the mesothorax than is usual among the higher insects. In most other Lepidoptera it is very much shortened antero-posteriorly and greatly reduced. A postnotum is present in both the meso- and metathorax but largely concealed.

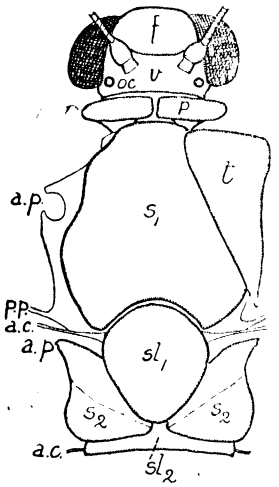


FIG. 394.—Dorsal view of head and thorax of *Agrotis promuba* (left tegula removed)

a.c, axillary cord; *a.p*, anterior wing process; *oc*, ocellus; *p*, patagium; *pp*, posterior wing process; s_1, mesoscutum; sl_1, mesoscutellum; s_2, metascutum; sl_2, postnotum; *t*, tegula.

With regard to the **Legs** a meron is present in relation with the meso- and metathoracic coxae and, as a rule, the coxae have but little mobility upon the pleuron, the principal movement of the base of the leg being in the articulation between the coxa and trochanter (Snodgrass). The anterior legs exhibit special features in certain families of butterflies and are reduced and modified so as to become useless for walking, either in the male only (Riodinidae) or in both sexes (Nymphalidae). The anterior tibiae are comparatively short in most Lepidoptera and in certain families they are provided on the inner surface with a peculiar lamellate spur ('epiphysis') which is regarded by Haase as the vestige of an organ formerly developed for cleaning the antennae. Frequently in the male the posterior tibiae (more rarely the middle pair) are provided with an expansible tuft of hair which is located in a groove and functions as a scent-producing organ. The tarsi are normally 5-segmented, the first segment being much the longest and in the males of

certain Lycaenidae it is conspicuously swollen. In the Pieridae the claws are exceptional in being cleft or bifid, and among Lycaenidae either one or both claws are wanting in the male. In the degenerate females of the Psychidae the legs have atrophied.

Wings.—The most characteristic feature is the covering of overlapping scales which are, morphologically, flattened and highly modified macrotrichia. Transitional stages between the latter and short broad scales are readily observable and the identity of the two types of structures is clearly established. Thus, in *Prototheora* Tillyard mentions that macrotrichia remain in an unmodified condition on the veins. The scales on the wing-membrane lying closest to the veins are linear and narrow, becoming shorter and broader the further they are away from a vein. Microtrichia or *aculei* are present on the wing-membrane except in the Ditrysia.

The innervation of the wings has been studied by Vogel (1911) who finds that each wing is supplied by three nerve branches whose fibres are ultimately distributed to the various sensory organs present. Vogel (1912)

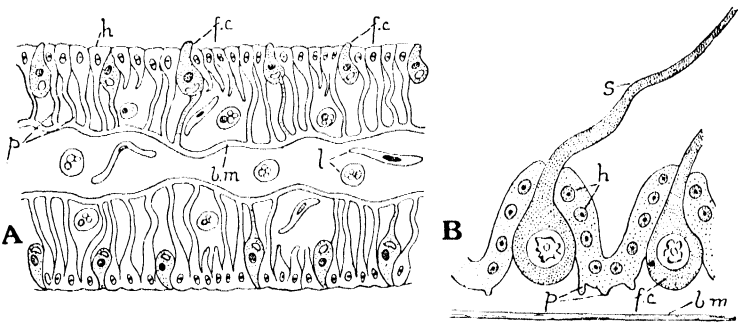


FIG. 395.—A, portion of a young pupal wing of *Nymphalis antiopa* in longitudinal section. B, the same of *Danais plexippus*, about 8 or 9 days before emergence

h, hypodermis; *f.c*, formative cell of scale; *l*, leucocytes; *bm*, basement membrane; *p*, processes of hypoderm cells; *s*, developing scale. *After* Mayer, *Bull. Mus. Harvard*, 1896.

recognizes four types of the latter, each organ having a sensory cell at its base. Possibly tactile are sensory scales and setae, while certain papillae suggest on account of their structure an orientating function. At the bases of the wings are chordotonal organs and, in some cases, a well-developed 'tympanal organ' is associated with them (see p. 519). The scales of Lepidoptera are secreted by evaginated and greatly enlarged hypodermal cells—the formative cells of Semper (Fig. 395). Their structure and development have been studied in considerable detail, more especially by Mayer (1896) and Reichelt (1925). Each scale is provided with a short pedicel which fits into a minute socket in the wing-membrane. In the more primitive forms they are irregularly scattered but in the butterflies, for example, a regular arrangement is very noticeable. On its exposed or outer surface, each scale is ornamented with longitudinal ridges or striae, often with transverse trabeculae between them. These ridges are in the form of longitudinal thickenings of the outer scale-wall, and their presence imparts rigidity very much after the manner of the corrugations of a sheet of roofing iron. In many cases these striae are extremely fine, and Kellogg (1894) found that in a species of *Morpho* they are placed from 0·0007 to 0·00072 mm. apart, or at the rate of 35,000 to the inch, and are responsible for producing beautiful iridescent colours (vide

p. 14). Seen in microtome sections scales are greatly flattened hollow sacs (Fig. 397) strengthened by minute transverse bars. Although they may only contain air, in the majority of cases a layer of pigment is enclosed between the two walls. In surface view they exhibit a wide range of variation of both form and sculpturing. In the males of various Lepidoptera groups of more specialized scales or *androconia* (plumules) occur on the upper surface of the wings and likewise assume very varied shapes (Fig. 396). They are found either scattered over portions of the wings, or in limited areas such as the 'brand' or discal patch of *Thymelicus*, the discal patch of certain Lycaenids, as well as on folds of the wings and other situations. Physiologically they are scent scales which serve as the outlets of odoriferous glands (Thomas, 1893); they are often fringed distally, with each tip of the fringe finely divided, thus probably ensuring the ready diffusion of the odour so characteristic of many Lepidoptera. Among the Danaine butterflies (Nymphalidae) a glandular scent patch is present on each hind wing and the odoriferous secretion is exuded at the surface of the wing by means of cuticular 'cups'. These latter are provided with a covering membrane pierced in the centre by a minute pore. Each cup is protected by a small scale differing from normal wing-scales in size and shape (Eltringham, 1915). In *Amauris niavius* the insect has been observed to brush the odoriferous area with the anal tuft of hairs which thus acquires some of the characteristic odour. Included in the anal tuft are numerous delicate filaments having the property of breaking up transversely into minute particles thus forming a kind of dust which assists in the diffusion of the scent. It is noteworthy that Dixey has shown that in certain Pieridae an alcoholic extract may be made from the wings and it possesses the same odour as the species concerned.

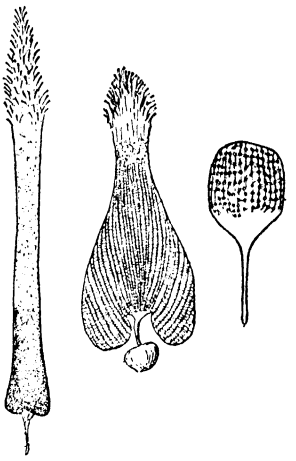


FIG. 396. — Androconia of male butterflies
From Comstock *after* Kellogg.

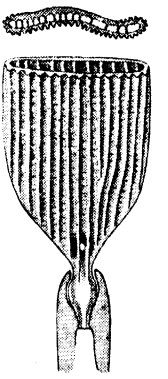


FIG. 397. — Upper (i.e. exposed) portion of a scale of *Danais plexippus* with the distal portion cut away to show the cross bars: above is seen a scale in transverse section
After Mayer, *loc. cit.*, 1896.

With regard to the VENATION (Figs. 399, 400) wherever specialization is evident it has been the result of the atrophy or coalescence of veins and not by addition. Throughout the order the principal cross-veins are few in number and vein M_4 is distally fused with Cu_{1a}. The researches of Tillyard (1919) provide strong evidence indicating that 1A of Comstock is in reality Cu_2, a conclusion which has been adopted in the present work. One of the most characteristic features of the Lepidopterous wing is the *trigamma* or 3-pronged fork, whose prongs are represented by M_3, Cu_{1a} and Cu_{1b} and whose base completes the closure of cell M or its regional equivalent. Among the Cossidae the stem R_{4+5} (chorda of Turner, 1918) divides the cell R into the basal cell 1st R, and an apical cell 2nd R (areole of Turner). In the vast majority of Lepidoptera, however, the stem R_{4+5} has atrophied and also the main stem M. This condition has resulted in the

formation of a single enormous discal cell on account of cells R + M + 1st M_2 thus becoming confluent.

The most primitive type of venation is found in the family Micropterygidae where that of both pairs of wings is closely alike. Most of the archaic features are exhibited in *Mnemonica* (Fig. 399) in which Sc and R_1 are separate in both pairs of wings, and bifurcated in the fore wings; Rs is 3-branched in the hind wings and the three branches of Cu are complete. In the family Hepialidae both Sc and R_1, although almost always distinct, are typically unbranched, and there is a considerable reduction or partial atrophy of Cu_2 in one or both pairs of wings.

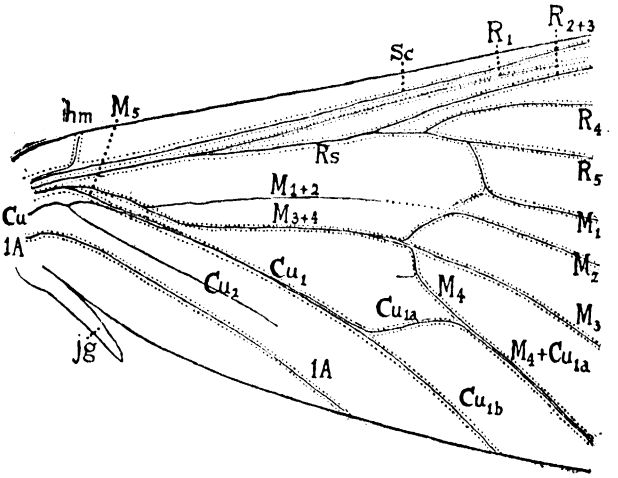


FIG. 398.—Basal part of fore wing of *Charagia* (Hepialidae) showing venation (double dotted lines) and tracheation × 4

After Tillyard, *Proc. Linn. Soc. N.S.W.*, 44, pt. 3.

Among the Ditrysia there is a marked divergence in the venation of the two pairs of wings (Fig. 400) but no annectent type has yet been discovered unless in the Gracillariidae (Busck, 1914). The most ancient type of venation is found among the Cossidae (Turner) which, however, exhibits the characteristic specializations of the hind wing, viz.—the fusion of Sc and R_1, the reduction of Rs, and the coalescence of 1A and 2A. As we ascend the Lepidopterous series the vein Cu_2 disappears from both pairs of wings.

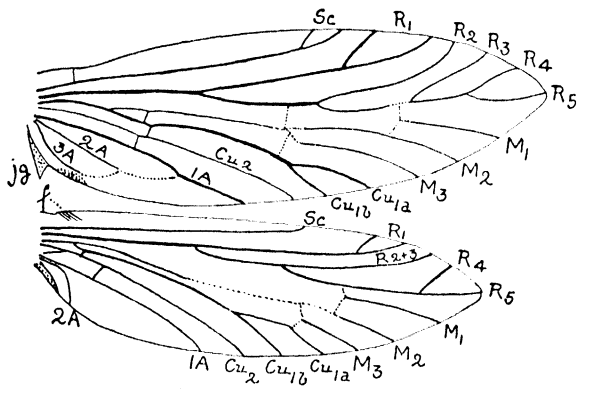


FIG. 399.—Venation of Eriocraniidae (*Mnemonica subpurpurella*)

jg, fibula; *f*, costal spines. Adapted from Tillyard, *Proc. Linn. Soc. N.S.W.*, 44, pt. 1.

The *wing-coupling apparatus* attains a high degree of specialization among various Lepidoptera (Griffith, 1898; Tillyard, 1918; Braun, 1917; 1919; 1924; Philpott, 1924; 1925). In the Micropterygidae, Eriocraniidae and females of some other Monotrysia, the base of the fore wing is produced into a small lobe or *fibula*. This rests on the *upper* surface of the hind wing and partially engages with the small *costal spines*. In the Hepialidae, the jugum replaces and is only an enlargement of the fibula. It also rests on the upper surface of the hind wing but

there are no costal spines. In the males of the Stigmelloidea and Incurvarioidea, the fibula and costal spines are reduced or absent but there is a true *frenulum* or spine composed of a fused group of bristles arising from a humeral sclerite proximal to the origin of the spines. Among the Ditrysia there are two main types of wing-coupling apparatus, viz. the *frenate* and the *amplexiform*. In the *frenate type* a sexual difference is very noticeable; thus in the male the frenulum consists of a single stout bristle which, however, can be clearly seen to be composed of several setae fused together; in the female the bristles remain separate and vary from 2 to 9 in number. In strongly flying males the frenulum is often large and powerful, while among species in which the females are weak fliers or fly but little the frenulum is correspondingly reduced. In both sexes it arises from a small swelling at the humeral angle of the hind wing, and passes beneath the fore wing where its apex is retained in position by a locking mechanism or *retinaculum*, and in this manner the wings are held together. The retinaculum (Braun, 1919; 1924) varies somewhat in structure, especially amongst the Tinaeoidea. Typically, in the female, it is little more than a group of somewhat stiffened hairs or scales arising near Cu_1. In the male, there is usually a strong hook from the underside of Sc but the cubital retinaculum is often present as well (e.g. *Synemon*, Castniidae). In many Sesiidae, in which both sexes are swift fliers, the females exhibit the male type of frenulum and possess the hook-like retinaculum. In the *amplexiform type* the frenulum is lost, and the two wings of a side are maintained together owing to their overlapping to a very considerable degree. This condition is met with for example in the Saturniidae, Lasiocampidae, and in all the families of the butterflies. The humeral lobe of the hind wing is enlarged and often strengthened by the development of one or more short humeral veins, and projects far beneath the fore wing. In the Castniidae both the frenulum and humeral lobe are well developed, and from such a condition as this it is evident that the amplexiform type may have been derived through the loss of the frenulum. The course which necessitated the change is obscure but may perhaps be correlated with a change in the manner of flight. Intermediates between the above two types of wing-coupling apparatus are to be met with; thus in *Bombyx mori*, the frenulum is vestigial and the humeral lobe well developed;

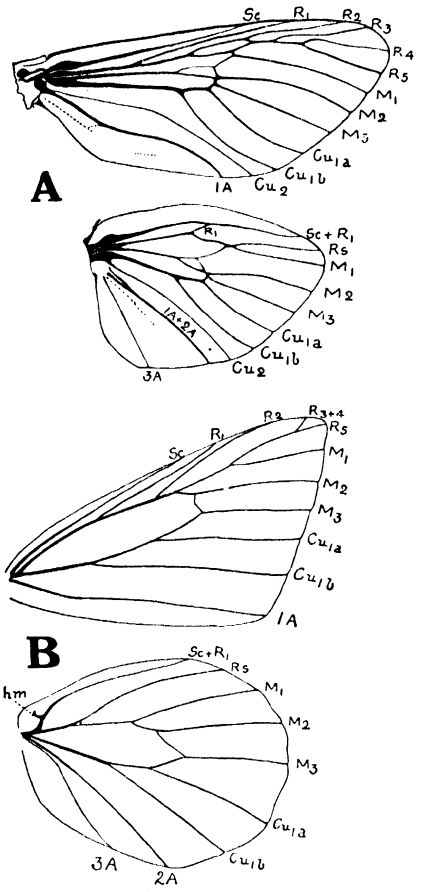


FIG. 400.—Venation of Ditrysia. A, *Prionoxystus robiniae* (Cossidae). *After* Comstock, lettering modified. B, *Pieris brassicae* (Pieridae). Original

this same condition is found among other frenulum-losers such as the Lacosomidae.

In the females of certain Geometridae and Psychidae, also of *Orgyia*, etc., wings are either totally wanting, or reduced to small non-functional vestiges. This flightless condition evidently confines the females to a great extent to their larval food-plants and it is noteworthy that the latter are almost always very common and generally distributed species. The fact that the flightless females of the Geometridae, etc., belong to forms which occur during the colder months of the year has often been commented upon. This peculiarity has been explained as being an adaptation to prevent their leaving food-plant and perishing owing to inclement weather. Some other explanation, however, needs to be formulated to account for the flightless condition of such eminently summer insects as *Orgyia* and the Psychidae.

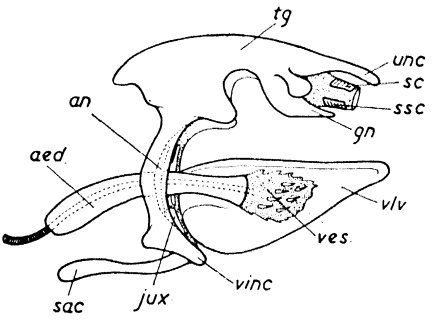


FIG. 401.—Diagrammatic lateral view of male genitalia of Lepidoptera, left valve removed (based on Viette, 1948)

aed, aedeagus; *an*, anellus; *gn*, gnathos; *jux*, juxta; *sac*, saccus; *sc*, scaphium; *ssc*, subscaphium; *tg*, tegumen; *unc*, uncus; *ves*, vesica; *vinc*, vinculum; *vlv*, valve.

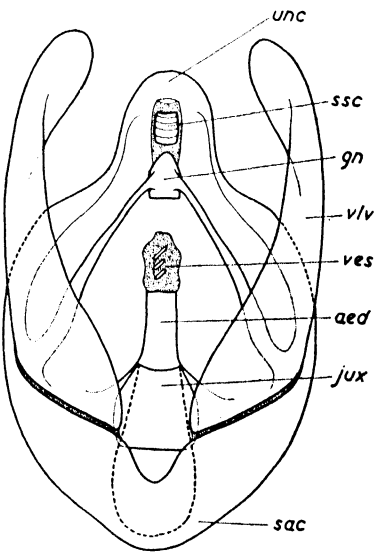


FIG. 402.—Diagrammatic ventral view of male genitalia of Lepidoptera

Lettering as in Fig. 401.

The **Abdomen** consists of ten segments; the 1st segment is reduced and its sternum wanting or wholly membranous, the 7th and 8th are sometimes slightly modified in relation to the genitalia and the 9th and 10th segments are greatly modified in the latter respect. On either side of the metathorax or the base of the abdomen in many Lepidoptera there is a complex organ, the *tympanum*. This structure is well seen in the Geometridae and appears as a bladder-like vesicle closely associated with the 1st abdominal spiracle of its side and certain of the neighbouring tracheal air-sacs. It is innervated from the last thoracic ganglion and, from its general structure (Eggers, 1919; 1928; Richards, 1933), and from the responses made to sounds produced by a Galton whistle, it is probably an auditory organ (see also p. 93).

The nomenclature of the male genitalia has become much involved, but a summary has recently been published by Viette (1948). The 9th segment or *tegumen* (Figs. 401, 402) is a narrow ring encircling the apex of the body and its sternal region or *vinculum* is usually invaginated to form a median *saccus* which extends into the preceding segment. A pair of *claspers* or valves (harpes of Pierce, harpagones of White) are hinged to the *vinculum* and form the most prominent organs of the external genitalia. The *harpes* are spine-like

structures often present in the inner aspect of the claspers. Attached to the hind margin of the 9th tergum is a median process or *uncus* which is usually hook-like or bifid, and in many Lepidoptera there is a median ventral sclerite or *gnathos* lying a short distance below it. The uncus and the gnathos are usually regarded as the tergum and sternum of the 10th segment, but according to Zander (1903) they are secondary processes, the segment itself remaining membranous. The anus opens just beneath the uncus and between that sclerite and the gnathos. The *aedeagus* is situated below the gnathos and is enclosed in a sheath and at the point where the latter joins the body there is a sclerotized support or *juxta* (penis-funnel or ringwall). For further information on the male genitalia reference should be made to the writings of Zander (1903), Pierce (1909–43) and Mehta (1933). In the female the terminal segments of the abdomen are sometimes attenuated and telescoped, thus functioning as a retractile ovipositor. An exserted sclerotized ovipositor is present in most Monotrysia and in some Ditrysia.

Internal Anatomy

The Digestive System.—The cavity of the proboscis communicates with the pharynx and we owe to Schmitt (1938) an account of the structure of the latter organ. It is an ovoid chamber provided with powerful muscular walls and issuing from between the fibres of the latter are five muscles, which pass outwards to be attached to the head-capsule. When the latter muscles contract the pharyngeal cavity enlarges and a partial vacuum is created; this becomes filled by an ascent of fluid through the proboscis. The walls of the pharynx then contract, thereby forcing the food backwards into the oesophagus, and the closure of a pharyngeal valve precludes the return flow down the proboscis. The oesophagus is a long tube of very narrow calibre and, in the more primitive forms, expands distally into a well-developed crop (Monotrysia, Cossidae, Psychidae, many Tinaeoids, *Attacus*, *Apocheima*). In other species the crop takes the form of a lateral dilatation connected with the oesophagus by means of a wide-mouthed channel (*Adela*, some Tinaeoids, Zygaenidae, certain Saturniidae, *Ematurga*, etc.). In the majority of Lepidoptera the crop forms a large food reservoir connected with the fore intestine by a short narrow duct. The stomach is a straight tube of relatively small capacity, and the hind intestine consists of a narrow coiled ileum, a distended chamber or colon, and a short muscular rectum. Salivary glands take the form of a long coiled filamentous tube on either side, the silk glands of the larva degenerating in the pupa and being no longer evident. The Malpighian tubes are six in number, three of a side opening by a common duct into the commencement of the ileum. Exceptions are found in certain Tinaeina (*Tinaea pellionella*, *Tineola biselliella* and *Monopis rusticella*) which possess only a single pair, and in *Galleria mellonella* there are similarly two vessels but each is irregularly ramified (Cholodkovsky, 1887; Bordas, 1920; Dauberschmidt, 1934).

The Nervous System (vide Newport, 1834; Brandt, 1879; Petersen, 1900; Buxton, 1917; Bretschneider, 1921; 1924) exhibits a certain amount of concentration with regard to the ganglia of the ventral nerve-cord. The most primitive condition is found in *Hepialus* in which there are three thoracic and five abdominal ganglia. In the Micropterygidae and also *Tinaea pellionella*, *Cossus*, *Sesia*, *Zygaena*, *Phalera* and *Ematurga* the 4th and 5th abdominal

ganglia are fused into a large common centre. The majority of Lepidoptera, however, are characterized by two thoracic and four abdominal ganglia; those of the meso- and metathorax are fused and the abdominal ganglia lie in the 2nd to 6th segments. The Psychidae are primitive but variable: thus Petersen records three thoracic and six abdominal ganglia in the female *Psyche unicolor*, while in *Fumea intermedia* and other species there are four abdominal ganglia in both sexes.

The Dorsal Vessel has been very little investigated: Newport states that in most Lepidoptera there are eight pairs of lateral ostia, and in *Danais* Burgess states that slight constrictions divide the heart into a number of segments corresponding to those of the abdomen. In *Protoparce*, as Brocher has pointed out, the aorta makes a sharp loop in the thorax and at the apex of the bend it is connected with a pulsatile organ. This condition is probably general but it needs further research.

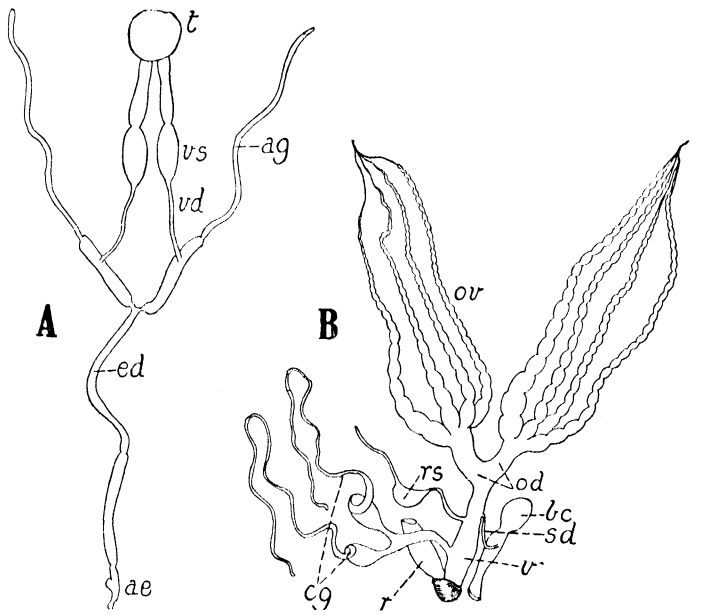


FIG. 403.—Reproductive organs of *Smerinthus populi*

A, Male: *ae*, aedeagus; *ag*, accessory gland; *ed*, ejaculatory duct; *t*, testis; *vd*, vas deferens; *vs*, vesicula seminalis. B, Female: *bc*, bursa copulatrix; *cg*, colleterial gland; *od*, oviduct; *ov*, ovary; *r*, rectum; *rs*, receptaculum seminis; *sd*, seminal duct; *v*, vagina.

The Male Reproductive Organs (Fig. 403, A) have been studied by Cholodkovsky (1884) in many species, and also by Stitz (1900), Petersen (1900) and Ruckes (1919). Typically each testis consists of four follicles exhibiting varying degrees of coalescence while among the higher Lepidoptera the two organs are intimately fused into a single median gonad. *Nemotois* is exceptional in that each gonad consists of twenty follicles. Two principal types of reproductive system are distinguishable. (1) The testes are paired and each is enclosed in a separate scrotum. In *Hepialus* the follicles are separate and the gonad presents a digitate appearance: this condition is evidently the most primitive found in the order. In other cases the follicles are compressed together and surrounded by a common scrotum. This type is met with in the Micropterygidae, certain Saturniidae, *Bombyx mori*, *Maculinea arion*,

Parnassius and a few others. (2) The testes are fused and enclosed in a common scrotum: in some cases the paired nature of the gonad is still evident while in others the fusion is complete. This type (no. 2) is the prevalent one, and usually the follicles are spirally wound around the longitudinal axis of the gonad. The organs in *Platysamia cecropia* have been studied by Ruckes and in *Bombyx mori* by Verson. The testes lie in a dorso-lateral position, close to the alimentary canal and just beneath the 5th and 6th abdominal terga. The vasa deferentia are narrow tubes which enlarge proximally to form the vesiculae seminales. Each receives a long filamentous accessory gland but, according to Ruckes, the structure of the latter is not markedly glandular, its walls being provided with longitudinal muscle fibres and it appears probable that the gland serves, along with the vesiculae seminales, as a receptacle for storing the spermatozoa. The vesiculae seminales unite to form a common ductus ejaculatorius which terminates in a bulbus ejaculatorius at the base of the aedeagus.

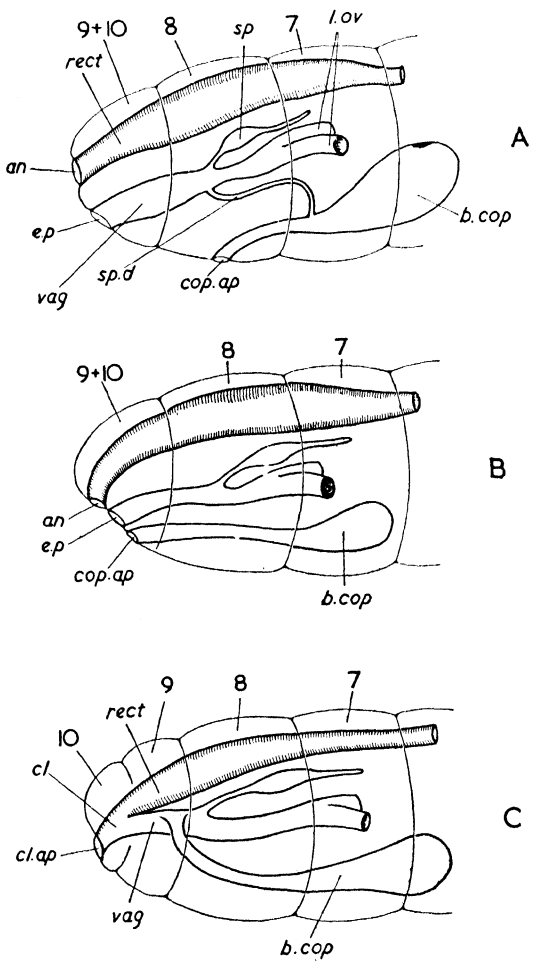


FIG. 404.—Relationships of female reproductive ducts and rectum in Lepidoptera. A. Ditrysian type. B. Hepialid type. C. Micropterygid type

an, anus; *b.cop*, bursa copulatrix; *cl*, cloaca; *cl.ap*, cloacal aperture; *cop.ap*, copulatory aperture; *e.p*, egg pore; *l.ov*, lateral oviduct; *rect*, rectum; *sp*, receptaculum seminis; *sp.d*, sperm duct; *vag*, vagina; 7–10, 7th–10th abdominal segments.

The Female Reproductive Organs (Fig. 403, B). Each ovary consists typically of four polytrophic ovarioles but a certain number of exceptions to this rule are known among the lower members of the order. Thus, there are six ovarioles to each ovary in *Cochliotheca helix*, 10 to 12 in *Adela*, 14 in *Aegeria scoliaeformis*, and 12 to 20 in *Nemotois*. The structure of the female genital apparatus is of fundamental importance in the classification of the order (Petersen, 1900, 1904; Busck, 1932; Williams, 1941, 1947; Oiticica, 1948; Bourgogne, 1949). In the Zeugloptera and in the Monotrysia (except the Hepialoidea) there is a single cloacal opening on sternite IX. In the Zeugloptera and some Monotrysia, the rectum and the common oviduct join near the aperture, so that the *cloacal duct* is short; in other Monotrysia there is a long cloacal duct. In either case the *bursa copulatrix* and the *recepta-*

culum seminis join the common oviduct before it meets the rectum. In the Hepialidae, there are three openings on the membranous area behind sternite VIII, viz. the opening of the ductus bursae, that of the common oviduct (egg-pore), and the anus. In some genera there is a duct connecting the ductus bursae to the common oviduct; in others the connexion is a mere groove on the surface of the sternite. Finally in the Ditrysia, the ductus bursae opens on sternite VIII and the egg-pore and the anus on sternite IX. The bursa copulatrix is connected to the common oviduct by a *ductus seminalis*. In the more primitive condition, as in some Psychidae, this duct is very short and broad; in higher forms it is often very long and narrow. It seems that no living form retains a primitive arrangement, which was probably a single genital aperture on sternite VIII. The backward extension of the common oviduct beyond this may have first occurred as a groove, as is suggested by the ontogeny of these structures (Hatchett-Jackson, 1890; Dodson, 1937). The condition in *Hepialus* is difficult to interpret but appears to be specialized, at least as regards the position of the two apertures.

A pair of ramified or filiform colleterial glands open into bladder-like ducts which communicate with the common oviduct just behind the aperture of the receptaculum seminis. In many species (*B. mori*, etc.) an accessory gland is also present in relation with the latter structure, and the whole organ then resembles a colleterial gland in general appearance and has often been referred to as such. During copulation, a spermatophore is deposited in the bursa copulatrix (Norris, 1932). Owing to the absence of muscles in the walls of that chamber, the spermatozoa migrate by their own motility into the ductus seminalis. They subsequently enter the oviduct and then pass up the duct leading into the receptaculum seminis, and are stored in the latter organ until the eggs enter the oviduct for fertilization. For detailed information on the female genital system reference should be made to the works of Eidmann (1929), Petersen (1900; 1904) and Stitz (1901).

The Tracheal System communicates with the exterior by means of usually nine pairs of spiracles, two being thoracic and the remainder abdominal in position: the pair on the 8th segment of the abdomen, although present in the larva, is aborted.

The general **Literature** dealing with the morphology of adult Lepidoptera is relatively small. The principal anatomical treatise is that of Petersen (1900) and a good deal of information on the external structure will be found in Rothschild & Jordan's monograph (1903). The most completely investigated species is *Bombyx mori* whose anatomy has been studied by many workers including Blanc, Verson, Tichomirov and others: for the general structure of *Danais*, vide Burgess (1880), while Brandt has dealt with that of *Hepialus* (1880) and the Sesiidae (1890), and Nigmann (1908) with *Acentropus*, Della Beffa (1938) with Gracillariidae, Madden (1944) with a Sphingid, Freeman (1947) with a Tortricid and Matthes (1948) with the Psychidae.

The Egg

The eggs of Lepidoptera (vide Tutt, 1899) are roughly divisible into two forms: (1) ovoid or flattened, with the long axis horizontal: in this type the shell is usually only ornamented with rough pittings and rarely with longitudinal ribs; (2) upright and either fusiform, spherical or hemispherical, with the axes either equal, or the vertical axis the longest. The ornamentation is usually more complex and often exhibits a cell-like structure divided by longitudinal ribs.

The *micropyle* is usually placed in a slight depression at one extremity of the horizontal axis of an ovoid type of egg, and at the summit in the upright form. It consists of a number of minute radiating microscopic canals by means of which the spermatozoa gain access into the interior of the egg.

The average number of eggs laid by many species is high, sometimes exceeding 1,000 (*Lampra fimbriata*, *Zeuzera pyrina*), and they are deposited in a great variety of ways and positions. Certain Hepialids, and also *Charaeas graminis*, drop their eggs at random among the herbage on which the larvae feed. Others, such as *Malacosoma neustria* and *Alsophila aescularia*, deposit them in orderly necklace-like rings around the twigs of their respective food-plants. Certain Geometridae lay them in imbricate groups, while the Incurvariids are provided with a complex cutting apparatus with which they excise pockets in a leaf. The duration of the egg stage is subject to great variation: in *Sterrha virgularia* it may be as short as two days, but for species which hatch out during the year of deposition 10–30 days may be taken as the usual developmental period. A number of species hibernate in this stage, which is then often of longer duration than the combined larval, pupal and imaginal periods.

The Larva

Lepidopterous larvae have a well-developed head, 3 thoracic and 10 evident abdominal segments. Nine pairs of spiracles, borne respectively on the prothoracic and first 8 abdominal segments, are present. In the *head* (Figs. 405, 406) the median epicranial suture is well developed and the frons is usually represented by a pair of narrow oblique plates termed the *adfrontals* (Short, 1951; but cf. Hinton, 1947). Both clypeus and labrum are evident and the typical number of ocelli is 6 which are situated just behind, and a little above the bases of the short 3-segmented antennae (Dethier, 1941). The mandibles are powerful and adapted for mastication; in sap-feeding larvae, however, they are concerned with the laceration of tissues and may even be wanting (*Phyllocnistis*). The maxilla consists of a cardo and stipes; there is usually a single maxillary lobe and the palpi are 2- or 3-segmented organs. The ventral region of the head, between the proximal portions of the maxillae, is occupied by the labium. The mentum is relatively very large and lightly sclerotized; the submentum is usually divided into a pair of triangular sclerites. Distally, the prementum carries a median process or *spinneret*. The labial palpi usually each consist of a principal cylindrical, and a minute apical segment. On the oral surface of the labium is a median pad or hypopharynx. Paired lobes, which have been interpreted as superlinguae, overlie the sides of the hypopharynx and have been recognized in *Mnemonica* by Busck & Böving (1914), and by De Gryse (1915) and Heinrich (1918) in other Lepidopterous larvae. In some leaf-mining larvae, the mouthparts are much modified (Jayewickreme, 1940).

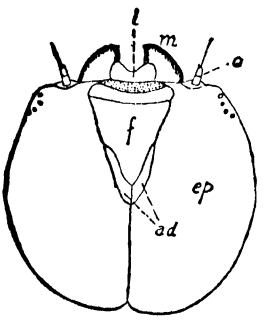


FIG. 405.—*Macrothylacia rubi*, frontal view of head of fully-grown larva

a, antenna; *ad*, adfrontal sclerites or frons; *f*, clypeus; *ep*, epicranial plate; *l*, labrum; *m*, mandible.

The *thorax* carries a pair of legs on each segment; these are 5-segmented and the terminal segment or tarsus is provided with a single curved claw. The *abdomen* commonly bears five pairs of so-called 'prolegs' which are

present on segments 3 to 6 and on 10: the first 4 pairs may be termed the abdominal feet and remaining pair the claspers. A typical abdominal leg is a fleshy, more or less conical, retractile projection whose apex or *planta* is rounded or flat. The latter is provided with a series of hooks or crochets

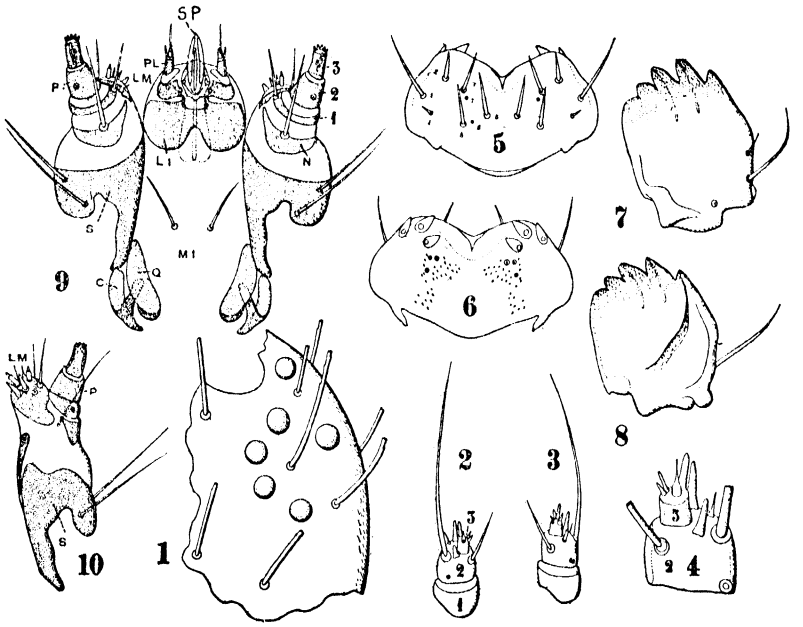


FIG. 406.—*Bombyx mori*; structural details of larva in 1st instar (bivoltine Japanese race). 1, portion of epicranium with ocelli. 2, 3, different aspects of antenna. 4, distal portion of antenna more highly magnified. 5, labrum (dorsal). 6, labrum (ventral). 7, mandible (dorsal). 8, mandible (ventral). 9, maxillae and labium (ventral). 10, maxilla (dorsal)

C, cardo; *LI*, prementum; *LM*, maxillary lobe; *MI*, mentum; *N*, palpiger; *P*, maxillary palp; *PL*, labial palp; *Q*, submental sclerites; *S*, stipes; *SP*, spinneret. *After* Grandi, *Boll. Lab. zool. Portici*, 1922.

which aid the larvae in locomotion, and to the centre of the planta is attached a muscle by means of which it can be completely inverted. The arrangement of the crochets is diverse, and the variations present afford important classificatory characters (Fig. 407).

In the detailed studies of Fracker (1915) the following terminology is adopted with reference to the arrangement of the crochets. In the most generalized forms the planta bears a complete circle of well-developed hooks, surrounded by several circles of smaller ones. This arrangement is a *multiserial circle* and is found in the Hepialidae, *Yponomeuta*, etc. When the crochets are absent from the mesial and lateral parts of the circle, as in *Adela*, two transverse *multiserial bands* are formed. When the outer circles of smaller crochets disappear we get a *uniserial circle*. The latter occasionally has crochets of uniform length (*uniordinal*), but more usually they are of two lengths alternating (*biordinal*). When a portion of a uniserial circle is wanting, and the remainder is more than a semicircle in extent, we get a *penellipse* as in the Psychidae; the gap, moreover, is variable in position. Frequently more than half the circle may be absent, and a *mesoseries* results, as in nearly all the higher Lepidoptera excepting the Hesperiidae.

Departures from the usual number of abdominal limbs are the rule in certain families. Thus in the Geometridae they are generally present only on the 6th and 10th segments. In the early instars of many Noctuidae the abdominal feet on the 3rd and 4th segments are rudimentary, and the method

of progression resembles that of Geometrid larvae; the limbs of those segments generally attain their full development in a later instar. In the Plusiinae and several other subfamilies, however, they are permanently absent and the looping habit is maintained throughout life. Larvae of the Micropterygidae are exceptional in possessing eight pairs of abdominal limbs. At the opposite extreme are certain leaf-mining larvae, including those of *Phyllocnistis* and *Eriocrania*, which are totally apodous.

The armature of the body consists of simple hairs or setae, tubercles of various types, and *verrucae*: the latter are somewhat elevated portions of the cuticle bearing tufts of setae. More rarely the body-wall is produced into spinous processes or *scoli* as in the Saturniidae, or into a median dorsal horn as in the Sphingidae: other modifications are dealt with under the respective families. The setae are arranged in a definite manner, and have been extensively studied by Dyar (1895), Fracker (1915), Gerasimov (1935), and Hinton (1946). According to Hinton, the setae are of two types, viz. microscopic, probably *proprioceptor* setae and long *tactile* setae which are more numerous The setae, especially ir the first instar, can b homologized in the various families, but the detailed arrangement provides important taxonomic characters.

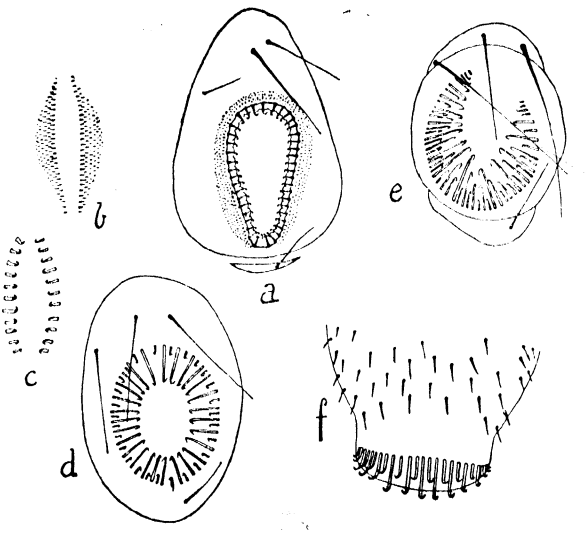


FIG. 407.—Arrangement of crochets

a, multiserial circle; *b*, transverse multiserial bands; *c*, transverse uniserial bands; *d*, biordinal uniserial circle; *e*, penellipse; *f*, biordinal mesoseries. Adapted from Fracker, 1915.

Repugnatorial glands are a common feature and there is an extensive literature on the subject. In the Papilionidae there occur very characteristic organs known as *osmeteria*. An osmeterium consists of a bifurcate protrusible sac which is thrust out through a slit in the 1st thoracic segment. It exhales a distinct odour varying according to the species and in some cases is extremely disagreeable. In many larvae, including those of the Nymphalidae, certain Noctuidae and Notodontidae a ventral defensive gland is present in the form of an internal sac opening on to the prothoracic sternum, and is capable of discharging a jet of spray. In the Lymantriidae a pair of eversible glands is present on the dorsum of the 6th and 7th abdominal segments. In many Lycaenidae also there is a dorsal gland on the 7th abdominal segment, its presence being indicated by a transverse slit through which a minute globular vesicle may be protruded. In the Megalopygidae there are lateral abdominal glands permanently everted, and metamerically arranged (Packard). Many larvae obtain protection through the possession of *urticating hairs* which bristle with minute lateral points. Whether their irritating properties are due to mechanical action alone, or to the presence of a poisonous secretion, has not been satisfactorily ascertained. These urticating hairs

are known to most entomologists who have handled larvae pertaining to the Lymantriidae, Lasiocampidae or Arctiidae. Such structures evidently produce marked irritation if they come into contact with the epithelial lining of the digestive tracts of an insectivorous bird or mammal. *Glandular hairs* are present in some larvae and take the form of hollow, smooth setae. Being filled with a poisonous secretion and extremely liable to fracture, they are capable of causing great irritation and smarting when a larva bearing such setae is handled. In certain Megalopygidae these setae are developed into spines and, according to Packard, the secretion is formed in specialized hypodermal cells situated at their bases.

A very large number of larvae obtain protection by other means which may be grouped under three chief headings: (1) Concealment. This is evident in case-bearers such as *Coleophora*, the Psychidae, etc., while in *Stigmella*, *Lithocolletis*, and other Tinaeoids, the larvae are leaf-miners, and in numerous Tortricidae they are leaf-rollers. Others construct silken galleries or spin together adjacent leaves as in *Gelechia*, *Pyrameis* and *Drepana*; in certain Lymantriidae, and species of *Yponomeuta*, the larvae live gregariously in dense silken webs. (2) Protective resemblance. This extensive subject has received a good deal of attention from Poulton and other observers. Protection is attained owing to the remarkable resemblance which many larvae exhibit to portions of their food-plant, or other objects in their immediate environment. Perhaps the most striking instances are afforded by Geometrid larvae which bear such a close resemblance to twigs as to render detection often a matter of very great difficulty. The fully-grown larva of *Stauropus fagi* resembles a withered and irregularly curled-up leaf of its food-plant (*Fagus*). Tutt (1899) states that the larva of *Smerinthus ocellatus* bears a remarkable resemblance to a curled apple leaf, its lateral stripes giving an idea of light and shadow on the supposed leaf. The larva of *Anarta myrtilli* with its intricate green pattern is hardly discernible while resting on a twig of heather. A very long list of such instances of protective resemblance might be drawn up, and the phenomenon has probably been induced in the first instance by the presence of chlorophyll in the food-plants, derivatives of which are utilized in the larval coloration. In certain cases experiments of Poulton tend to show that larval coloration may be due to 'phytoscopic', rather than phytophagic influences. In other words, it is the superficial colour of a leaf, for example, rather than its pigmentary substance, that functions as a stimulus in producing differences of coloration under varying environmental conditions. Larvae of *Catocala*, when subjected to green surroundings, become bluish-green, and in a darkly-coloured environment become bluish-grey. Similarly it has been found that those of *Opisthograptis luteolata* and other Geometridae tend to exhibit responses of a like nature. We are unacquainted with the mechanism that produces this result, but it is suggested by Poulton that the reflection of light, from the immediate environment of a susceptible larva, produces a nervous response resulting in a physiological change in the accumulation of pigment within the hypodermis. In addition to the writings of this authority an admirable discussion of the subject is given by Tutt (1899). (3) Warning coloration. This is evident in striking colours or patterns which readily catch the eye and their possessors usually feed openly and are distasteful to insectivorous vertebrates.

It has already been mentioned that Lepidopterous larvae feed almost entirely upon Phanerogamic plants. There is probably not a single family of the latter that is not resorted to by one or more species of these insects.

In N. America Scudder states that 52 families are represented in the food-plants of butterflies alone. Exceptions to the habit of feeding upon Phanerogamic plants do occur, but they are not numerous; references thereto will be found in the sections devoted to the Noctuidae and Tinaeoidea.

The number of ecdyses passed through varies greatly in different species and, in some instances, even within the limits of a single species. Edwards (1880) finds that four moults is the usual number in N. American butterflies, with an additional moult in hibernating larvae. Buckler records nine moults in *Nola centonalis*, while in *Acronycta* five is the usual number; Gosse (1879) finds the same in *Attacus atlas*, and Soule records a similar number in other Lepidoptera. Species of *Smerinthus* undergo three or four moults, *Sphinx lingustri* six, and three occur in *Callosamia promethea*. *Arctia caia*, on the other hand, may moult seven times—four before hibernation and three after; the number, however, varies between five and eight (Tutt). In a few cases a sexual difference has been noted, the female larva undergoing one more moult than the male, as in *Orgyia*. Chapman observes (1887) that, in *O. antiqua*, larvae which moult three times produce males, those which moult five times produce females, and those which moult four times give rise to imagines of both sexes.

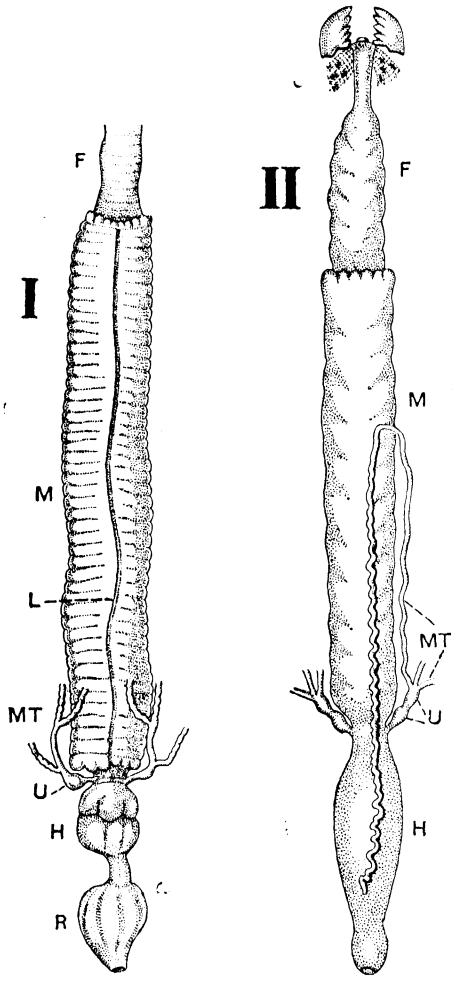


FIG. 408.—Alimentary canal of larva of I, *Acherontia atropos*; II, *Phragmatobia fuliginosa*

F, fore intestine; *H*, hind intestine; *L*, dorsal longitudinal muscle band; *M*, mid intestine; *MT*, Malpighian tubes; *R*, rectum; *U*, excretory chamber. *After* Bordas, 1911.

The **Internal Anatomy** of Lepidopterous larvae is relatively simple. The *digestive canal* is a straight or almost straight tube, from the mouth to the anus (Fig. 408). The oesophagus is short and frequently enlarged posteriorly (in the mesothorax). The stomach is a tube of wide calibre, extending to the hind margin of the 6th abdominal segment or to the middle of the 7th segment, and is lined by a peritrophic membrane. It is provided with conspicuous muscle bands and, in *Protoparce* for example, its walls are transversely constricted by means of the circular fibres and further divided by six bands of longitudinal muscles. Enteric caeca are rare, but in some species small diverticula are present near the anterior end of the stomach. The hind intestine is always extremely short and devoid of convolutions: in some cases it is divisible

into three more or less globular chambers separated by constrictions and probably corresponding to the ileum, colon and rectum. In other larvae two dilatations (colon and rectum) only are present, while in further examples the hind gut consists of a single large chamber (Bordas, 1911). With very few exceptions, six Malpighian tubes are present (Poll, 1939), and they open, on either side, by means of a common duct into a small excretory chamber communicating with the hind intestine. The common duct bifurcates and one branch subdivides, thus giving rise to three tubes to a side. The *silk glands* are the most conspicuous appendages of the digestive system (Fig. 409). Morphologically they are labial glands homologous with the true salivary glands of other insects. Each gland is in the form of an elongate cylindrical tube of exceedingly variable length, and it lies partly at the side of and partly beneath the digestive canal. These glands are longest in the Saturniidae and Bombycidae: thus in *Telea polyphemus* they measure about seven times the length of the body and are complexly folded, while in *Bombyx mori* they are four times the body length, and folded so as to envelop the hinder region of the gut. Anteriorly, each gland is prolonged to form a duct, and the two latter converge and unite to open at the apex of a median cylindrical organ known as the spinneret. The morphology of this structure has not been satisfactorily ascertained, but it appears to be the highly modified ligula. It will be recalled that the labial glands of insects normally open on the hypopharynx, but in Lepidopterous larvae their aperture has been carried beyond that organ on to the anterior margin of the labium. Histologically, silk glands consist of a single layer of extraordinarily large secretory cells disposed around a central cavity. The cells have large characteristically branched nuclei, and are limited exteriorly by a peritoneal membrane: internally the gland cavity is lined by cuticle, spirally thickened as in tracheae.

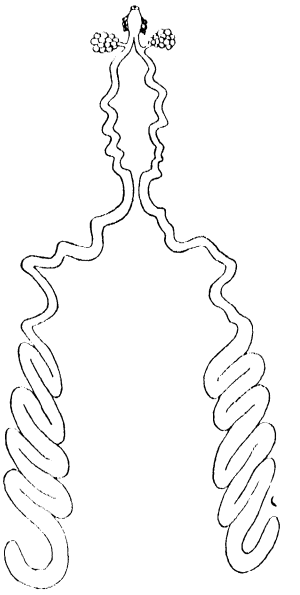


FIG. 409.—Spinning glands with small acinose accessory glands of the larva of *Saturnia pyri*

After Bordas, 1910.

The silk ducts possess the same essential histology as the glands, but the epithelial cells are more flattened, and the cuticular lining is closely striated radially (Fig. 144). The spinning apparatus is divisible into two portions, a hinder part, or *thread-press*, and an anterior division known as the *directing tube*. The fluid silk passes into the press which is provided with three pairs of muscles. Action of the latter forces the silk through the directing tube, very much as wire is made by molten iron being driven through an iron plate, perforated by two fine holes (Packard). The entire spinning apparatus lies within the spinneret, and the thread as it issues from the aperture of the latter is in the form of a double ribbon-like band. Associated with the silk glands in most species is a pair of *accessory glands*, often termed Filippi's glands, though they were recognized by Lyonnet so long ago as 1762 (Bordas). They are paired organs, often voluminous, and each opens by a separate duct into the silk duct of its side. In *Arctia caia* and *Enarmonia pomonella* they are rudimentary, and reduced to a group of follicles surrounding the

silk duct. Among the Sphingidae they are also rudimentary or entirely absent. The function of these glands is to secrete a substance of a liquid or viscid nature which enables the two threads to adhere within the spinneret and, at the same time, facilitates the process of hardening. *Mandibular glands* (Fig. 142) are present in almost all Lepidopterous larvae, and are situated in the thorax one on either side of the fore intestine. They communicate with the buccal cavity by means of a pore placed on the inner side of the base of each mandible. As a rule they are tubular and often of considerable length, but in *Papilio alexenor* and *Stauropus fagi* they are short and sac-like. Histologically they consist of the same layers as the silk glands and their nuclei are lobed or irregular in form. Functionally they are salivary glands and, in some cases, according to Bordas, they may exercise a defensive rôle also.

The *nervous system* is subject to but little variation. In addition to the usual cephalic ganglia the central nervous system consists of three thoracic and seven or eight abdominal ganglia. The connectives between the meso- and metathoracic ganglia are, typically, double and widely separated, but those uniting the remaining ventral ganglia appear as single cords. As a rule, the 7th and 8th abdominal ganglia are intimately united owing to the elimination of the connective between them. In *Sphida* the number of paired nerves arising from the terminal ganglion suggests that three or more nerve-centres have undergone coalescence (Du Porte): in *Cossus* the 7th and 8th abdominal ganglia are separate and united by a short connective (Brandt). The *dorsal vessel* extends from the 8th abdominal segment into the 1st segment, or the commencement of the metathorax, and from there it is continued as the *aorta* into the head. According to Newport there are nine chambers separated by eight pairs of lateral ostia. The *reproductive organs* take the form of a pair of small ovoid bodies situated in the 5th abdominal segment and in close relation with the dorsal vessel on either side. They are present in the newly hatched larvae and undergo a certain amount of differentiation during later instars. The ovaries are slightly larger than the testes and may also be recognized histologically by the rudiments of ovarioles.

The **Literature** on Lepidopterous larvae is very extensive: larvae of the British species are illustrated by Buckler (1887–99), while for the European species reference should be made to the work of Hofmann (1893). For a general account of the external structure of the larvae of the order the works of Tutt (1899) and Forbes (1910) are useful: for the butterflies see Scudder (1889). For the larval characteristics of the different families and diagnostic keys, vide Dyar (1894), Forbes (1910) and Fracker (1915). The internal anatomy has been mainly studied in isolated species, notably in *Cossus* by Lyonnet (1762), *Bombyx mori* by Blanc (1889) and others, and *Protoparce* by Peterson (1912). The digestive system and Malpighian tubes have been extensively studied by Bordas (1911); and many investigators, more especially Helm (1876), Gilson (1890), Bordas (1910) and Lesperon (1937), have pevoted attention to the silk and other glands. The nervous system has been studied by Newport (1832), Brandt (1879), Cattie (1881) and DuPorte (1915).

The Pupa

The change from the larva to the pupa usually first becomes evident by cessation of feeding. In many cases the larvae desert the food-plant and wander in search of a suitable site in which to undergo the transformation.

The contents of the digestive canal are voided and the larval skin loses much of its characteristic colour, becoming darker and wrinkled. The body becomes contracted and distended, the hypodermis secretes a fresh layer beneath the old cuticle, and ecdysis is greatly aided by the secretion of the exuvial glands which gradually loosens the two layers. When the latter process is complete, dehiscence of the larval skin takes place along the middle of dorsal aspect of the thorax, and the exuvia is gradually slipped off from behind, thus liberating the pupa. In the majority of species pupation takes place in a cocoon of some description, which is constructed by the larva. It may be composed of silk as in Bombycidae, Saturniidae, Lasiocampidae, etc.; or of leaves drawn together by a silken meshwork, or of a mixture of silk and various foreign particles. In other cases, as in *Dicranura* and *Cerura*, the cocoon is formed of gnawed fragments of wood agglutinated together by means of a fluid secretion which quickly hardens. Also, in the construction of the earthen cells of many Noctuidae the soil particles are cemented together by a fluid secretion, and no silk appears to be utilized. Among the butterflies the pupa is very frequently naked and protectively coloured, and suspended by the caudal extremity which is hooked on to a small pad of silk: the latter, and the silken girdle which is often present, may possibly represent the last vestige of a cocoon. The usual division of the body into head, thorax and abdomen is easily recognized in the pupa and the general external structure has been studied by Poulton (1890–91), Packard (1895), Chapman (1893–96), Mosher (1916) and others (vide Figs. 196 and 410).

The Head.—The *vertex* forms the dorsal area of the head behind the epicranial suture while the region anterior to the latter is the *fronto-clypeus.* In a few generalized forms, however, the frons and clypeus are separately demarcated. Invaginations of the anterior arms of the *tentorium* are evident as small pores or slit-like openings associated with the lateral margins of the clypeus. The *labrum* is usually very distinct but a clypeo-labral suture appears seldom to be developed: in many families the labrum bears lateral projections or *pilifers* and according to Mosher they are notably conspicuous in the Pyralididae and Papilionoidea. Definite *genae* are rarely evident except among a few of the lower forms. The *eyes* are always prominent and are divided into smooth and sculptured portions, the former being regarded as the true pupal eye. The *antennae* exhibit less marked sexual differences than in the imago and, in *Saturnia pavonia* for example, the pupal differences are extremely small in the two sexes, notwithstanding their divergence in the imago. *Mandibles* are only functional in the Zeugloptera and the Eriocranioidea: in *Eriocrania* they are very large and are used by the pupa to cut its way through the cocoon. In other families they are only represented by small elevated areas. The *maxillae* are exceedingly variable, and attain their greatest development in certain Sphingidae where their great length is accommodated by their becoming looped to form the familiar 'jug-handle' appendage. *Maxillary palpi* are wanting in certain groups, notably in the Cossidae, Hepialidae and in butterflies. *Labial palpi* are visible in many pupae but, in others, they are almost entirely concealed by the maxillae.

The Thorax.—The three segments are distinct on the dorsum but ventrally they are concealed by the appendages. The anterior pair of wings almost entirely conceals the posterior pair, except for a narrow strip along the dorsal margin of the latter. Among the apterous or subapterous females of certain genera the pupal wings are likewise less developed than in the male. In *Erannis defoliaria* and *Nyssia zonaria* the sexual divergence is but little marked

in the pupa, although the female imagines are almost apterous. In such forms as *Orgyia*, and the Psychidae, the degeneration appears to be sufficiently ancient to have caused a corresponding reduction of the wings of the female pupae. The thoracic *spiracles* consist of a single pair placed between the pro- and mesothorax, towards the dorsal aspect.

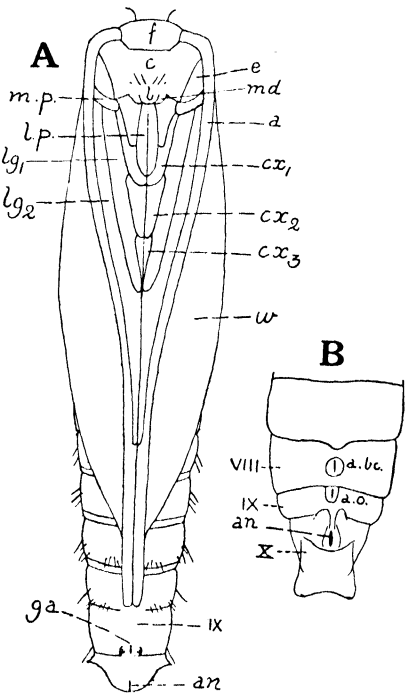


FIG. 410.—A, *Tinaea pellionella*, male pupa, ventral aspect (adapted from Mosher, 1916). B, *Pieris brassicae*, terminal segments of female pupa, ventral aspect

a, antenna; *a.bc*, aperture of bursa copulatrix; *an*, anus; *a.o*, aperture of oviduct; *c*, clypeus; cx_1–cx_3, coxae; *e*, eye; *f*, frons; *ga*, male genital aperture; *l*, labrum; *l.p*, labial palp; lg_1lg_2, legs; *md*, mandible; *m.p*, maxillary palp; *w*, wing; VIII–X, 8th to 10th abdominal segments.

The Abdomen.—Ten abdominal segments are present and a certain number are always fixed and immovable. The greatest number of free segments is found in the more generalized forms, thus in *Mnemonica* all the segments are movable excepting the last three (Mosher). In the Hepialidae and Psychidae the 1st segment is fixed and segments 2 to 7 are free in the male and 2 to 6 in the female; in the Cossidae the first two abdominal segments are fixed and consequently the movable segments are 3 to 7 in the male and 3 to 6 in the female; in the Noctuidae, Geometridae, Sphingidae, etc., the only free segments are the 4th, 5th and 6th in both sexes, while among certain of the butterflies all the segments are immovable. *Spiracles* are present on the first eight segments: the first pair is usually covered by the wings and the last pair is vestigial. In male pupae the genital aperture is situated on the 9th sternum and in the female there is either a single common aperture on the 8th sternum (10th sternum in *Micropteryx* according to Chapman) or, more usually, two apertures which are associated with the 8th and 9th sterna. These openings in some cases become confluent and represent those of the bursa copulatrix and oviduct respectively. The anus is carried on the caudal margin of the 10th segment, and this somite is produced to form the *cremaster*, which is the homologue of the suranal plate of the larva. It is an organ of attachment and exhibits many modifications: it may take the form of a pointed spine or of hooklets, and the latter may be grouped together, or scattered irregularly over the surface of the anal segment. In many of the more generalized families the cremaster is absent, while among the butterflies, with their suspended pupae, it is particularly well developed.

Internal Structure.—The internal anatomy differs in important features both from that of the larva and imago but more closely approaches the latter. The digestive system has undergone extensive modifications as compared with that of the larva; the oesophagus is long and narrow and the stomach greatly reduced in size. The food-reservoir is undeveloped and the hind intestine less convoluted than in the imago. The larval silk glands have atrophied, and the salivary glands of the imago replace them. The changes

undergone by the nervous system have been studied in great detail by Newport, and briefly it may be said that it undergoes a gradual process of concentration during about the first 60 hours of pupal life. By that time its whole arrangement is very nearly as it exists in the imago.

Types of Pupae and Method of Emergence from the Cocoon.—Chapman (1893) divides Lepidopterous pupae into two main groups, the Incompletae and Obtectae. The *pupae incompletae* have the appendages often partially free and more than three of the abdominal segments are mobile. As pointed out by Hinton (1946), a more fundamental contrast is between *decticous* (p. 231) *exarate* pupa of the Zeugloptera and Eriocranioidea and the *adecticous obtect* or *incomplete* pupa of the remaining Lepidoptera. Dehiscence is accompanied by the freeing of segments and appendages previously fixed, and the pupae exhibit considerable power of motion, usually emerging from the cocoon to allow of the escape of the imago. They are provided with a varied armature of hooks, processes and spines to facilitate the process. Many species also work their way to the surface of the ground, or to the entrance of the larval gallery in the case of those whose larvae are internal feeders. Most pupae incompletae possess some kind of hard process adapted for tearing open the cocoon. This *cocoon cutter*, as it may be termed, is well seen in *Lithocolletis hamadryadella* and according to Packard there are rough knobs or slight projections answering the same purpose in the Hepialidae, *Megalopyge*, *Zeuzera* and in *Datana*. The *pupae obtectae* represent a more highly specialized type: they are smooth and rounded and the only free segments in both sexes are the 4th, 5th and 6th. Dehiscence takes place by an irregular fracture, the pupa rarely emerges from the cocoon, and a cremaster is generally present. This pupa is prevalent in all the higher Lepidoptera, and exhibits a hard exterior, the appendages being all soldered down to form a smooth surface. The areas which are hidden are covered by a delicate pellicle and there is no separation of the appendages during emergence. Certain species (*Saturnia pavonia*, *Deilephila elpenor*) have retained the habit of pupal emergence, but in other forms the presence of the cremaster and the reduced mobility of the abdominal segments usually preclude it. Many different methods have been adopted to allow of the freeing of the imago. These may consist of weak places in the cocoon, a particular arrangement of the silk to allow of easy egress (*Saturnia pavonia*), a softening fluid applied by the emerging insect (certain Saturniids, *Dicranura*), provisional imaginal spines (Attacine moths), etc.

CLASSIFICATION

The familiar division of the Lepidoptera into Rhopalocera (butterflies) and Heterocera (moths) has little to recommend it other than convenience founded upon usage. Again, the old divisions of Macro- and Microlepidoptera were founded mainly upon the size criterion. The adoption of these two groups led to the inclusion of certain families among the Macrolepidoptera, whereas their true affinities lay with the division which comprised the 'micros' in a literal sense. As generally understood, the 'Microlepidoptera' are the Zeugloptera, Monotrysia and the sections Tortricoidea, Pyralidoidea and Tinaeoidea of the Ditrysia in the present work. Comstock's classification was founded upon the venation and wing-coupling apparatus. He recognized two suborders, the Jugatae and Frenatae—the former possessing a jugum

and the latter a frenulum. The presence of a frenulum, however, is too variable even within the limits of a single family to have very much classificatory value. In 1895 Packard laid stress upon Walter's researches on the mouthparts and separated the order into the Lepidoptera Laciniata (or Protolepidoptera) and the Lepidoptera Haustellata, the main feature being the presence of biting mouthparts in the former suborder (which includes *Micropteryx*) and their absence in all other Lepidoptera. The Haustellata he further divided into the Palaeolepidoptera (which includes the Eriocraniidae) and the Neolepidoptera. The latter he divided into two sections corresponding in the main to the Pupae Incompletae and Pupae Obtectae of Chapman. In the same year Meyrick brought out a classification based upon the venation in conjunction with other features and in 1895 Hampson published a revision of his earlier scheme (1892) also founded upon the venation. In addition to the above-mentioned systems, the eggs have been examined by Chapman (1896) and Tutt (1899), while classifications based upon larval characters have been advanced by Dyar (1894), Forbes (1910), Fracker (1915) and others: Mosher (1916) has re-examined the pupa from the same standpoint. The recent tendency (Busck, 1932; Börner, 1939; Hinton, 1946; Bourgogne, 1951) to base the primary divisions on the female genital system seems to be well-founded. Three suborders, the Zeugloptera, the Monotrysia and the Ditrysia have been adopted. The separation of the numerous families of the Ditrysia into major groups is extremely difficult as is witnessed by the lack of general agreement in the recent systems put forward in the works of Meyrick, Schröder, Forbes and Tillyard. The classification given in the pages which follow attempts to take into account the importance of the tympanal organs combined with venational and other features while the family keys are mainly after Hampson. The larval and pupal characters are chiefly based upon those given by Fracker (1915) and Mosher (1916) respectively.

Key to the major groups of Lepidoptera.

1. Adult with functional mandibles, maxilla with lacinia developed, galea not haustellate. Larva with a small transverse post-clypeus and with 8 pairs of abdominal legs, each terminating in a single hook.
   Female bursa copulatrix opening into common oviduct which joins the rectum to form a short cloaca with its aperture behind sternite IX; sternites VIII and IX without apodemes. Male sternite IX fused with tergite, in ventral view square, without anterolateral apodemes. Wings with aculei, venation of fore and hind pair very alike, Rs 4-branched, in hind wing R_1 not running into Sc. Fore wing with fibula, hind wing with some costal spines but no frenulum. Pupa exarate, with functional mandibles. (Suborder **ZEUGLOPTERA**) . MICROPTERYGIDAE (p. 537)

–. Adult without functional though sometimes with vestigial mandibles, maxilla without lacinia, galea more or less haustellate unless the mouthparts are very reduced. Larva with a triangular post-clypeus and not more than 7 pairs of abdominal legs. 2

2. Female with 1 or 2 genital openings behind sternite IX. Wings more or less distinctly aculeate (except Heliozelidae). Male sternite IX without a saccus. (Suborder **MONOTRYSIA**) 3

–. Female with the opening of the bursa copulatrix on sternite VIII and that of the egg-pore on sternite IX. Wings not aculeate, venation of fore and hind wings different, in latter R_1 running into Sc and Rs a single vein (except in a few Gracillariidae). Fore wing without jugum or fibula, hind wing with frenulum or else the coupling is amplexiform. Male sternite IX usually U- or V-shaped, often produced into a large saccus. Larva with not more than 5 pairs of crotchet-bearing abdominal legs. Pupa obtect, without functional mandibles. (Suborder **DITRYSIA**) 14

3. Venation of fore and hind wings much alike, hind wing with Rs 3- or 4-branched, R_1 separate from Sc, frenulum not developed 4
–. Venation reduced, different in fore and hind wings, hind pair with Rs unbranched and R_1 coincident with Sc. Male with rudimentary fibula on fore wing and strong frenulum on hind; female with stronger fibula but hind wing with no frenulum but with a more distal group of costal spines. Pupa obtect, mandibles rudimentary. Female with bursa copulatrix opening into the common oviduct which joins the rectum to open behind sternite IX 10

4. Female with bursa copulatrix opening into the common oviduct which joins the rectum to form a long cloacal duct with a single aperture behind sternite IX; sternites VIII and IX with long apodemes. Male sternite IX nearly square with 2 short anterolateral apodemes. Fore wing with fibula, hind wing with some costal spines. Larva apodous. Pupa exarate, with hypertrophied mandibles **(Eriocranioidea)** 5
Female bursa copulatrix, common oviduct and rectum all opening separately behind sternite IX; sternites VIII and IX without apodemes. Male sternite IX a small widely U-shaped sclerite. Fore wing with a strong humeral veinlet and a long jugum, hind wing without costal spines, aculei not numerous. Larva subterranean, with 5 pairs of crotchet-bearing abdominal legs. Pupa obtect, with rudimentary mandibles **(Hepialoidea)**. 7

5. Fibula reduced. Both mid and hind tibia with spurs. NEOPSEUSTIDAE (p. 538)
–. Fibula well developed 6

6. Maxillary palpi with 5 segments. R_1 in fore wing forked. Mid tibia with 1, hind tibia with 4 spurs . . . . . ERIOCRANIIDAE (p. 538)
–. Maxillary palpi with 3 small segments. R_1 in fore wing simple. Mid tibia with 2, hind tibia without spurs . . . . . MNESARCHAEIDAE (p. 538)

7. Both main branches of M running through the cell. 8
–. Only the main stem of M_{3+4} running through the cell 9

8. M_4 oblique, forming a Y-vein with Cu_{1a}, R_{2+3} with a long fork, Sc in fore wing rarely forked, hind wing with 2 anal veins. Tibiae without spurs. Maxilla with galea and palpi rudimentary . . . . . HEPIALIDAE (p. 538)
–. M_4 transverse, R_{2+3} with a short fork, Sc forked in fore wing, hind wing with 1 short anal vein. Tibial spurs present. Maxilla with small galea and rudimentary palpi . . . . . PROTOTHEORIDAE (p. 538)

9. Tibial spurs present. Maxilla small . . . . ANOMOSETIDAE (p. 538)
–. Tibial spurs and maxilla absent . . . . . PALAEOSETIDAE (p. 538)

10. 1st antennal segment enlarged or thickened with scales to form an eye-cap. Female cloacal duct short and sternites VIII and IX without or with short apodemes. Male sternite IX a small U-shaped or even transverse sclerite. Larva with 5–6 pairs of abdominal legs, with or without crotchets, or apodous **(Stigmelloidea)** 11
—. 1st antennal segment not forming an 'eye-cap'. Female with cloacal duct long and sternites VIII and IX with long apodemes. Male sternite IX a very long U-shaped sclerite with a membranous disk. Larva with 5 pairs of crotchet-bearing abdominal legs, or apodous **(Incurvarioidea)** 13

11. Fore wing with 10 separate veins reaching the margin. Hind tibia with a large mass of hairs . . . . . TISCHERIIDAE (p. 539)
—. Fore wing with at most 8 separate veins reaching the margin 12

12. Fore wing with branched veins and usually a small cell STIGMELLIDAE (p. 539)
—. Fore wing with 3 or 4 simple veins and no cell . OPOSTEGIDAE (p. 539)

13. Wings not aculeate. Head with appressed scales . HELIOZELIDAE (p. 539)
—. Wings aculeate. Head with outstanding scales . . INCURVARIIDAE (p. 539)

14. Hind wing with Cu_2 present. 15
—. Hind wing with Cu_2 absent. If present in some Castniidae the antennae are clubbed, the chaetosema is absent, and the frenulum is present 27

15. Antennae clavate. Frenulum absent except in the male of *Euschemon*. Chaetosema present (Butterflies) 16
—. Antennae acuminate or, if clavate, a frenulum is present 17

16. Fore wing with all veins arising separately from cell (R_1, 4 branches of Rs, 3 branches M, Cu_{1a}, Cu_{1b}). Antennae wide apart at bases **Hesperioidea** (p. 560)
—. Fore wing with at least R_3 and R_4 stalked, and sometimes 1 or 2 branches missing. Antennae close together at their bases. . . **Papilionoidea** (p. 554)

17. Wings very narrow, venation degenerate. Chaetosema absent . . . **Tinaeoidea** (part) (p. 539)
—. Venation well developed 18

18. Wings cleft into plumes. Chaetosema absent 19
—. Wings entire 20

19. Plumes at most 4 to each wing . . . **Pyralidoidea** (part) (p. 548)
—. Plumes more than 4 to each wing . . . **Tinaeoidea** (part) (p. 539

20. Tympanal organs present, rarely atrophied in brachypterous species . . 21
—. Tympanal organs absent 22

21. Tympanal organs in metathorax. Chaetosema absent. Fore wing with M_2 and M_3 usually basally approximated . . . . . **Noctuoidea** (p. 564)
—. Tympanal organs in abdomen. Chaetosema sometimes present. Fore wing with M_2 and M_3 rarely approximated basally . . **Geometroidea** (p. 560)

22. Antennae dilated towards tip. Chaetosema present SEMATURIDAE (? Geometroidea) (p. 561)
—. Antennae not dilated or chaetosema absent 23

23. Antennae gradually clavate, apex pointed and usually hooked. Frenulum almost always present. . . . . **Sphingoidea** (p. 562)
—. Antennae pectinate or simple 24

24. Frenulum nearly always lost. Chaetosema absent. Large, stout species. . **Bombycoidea** (p. 551)
—. Frenulum present, even if reduced. Species of moderate or small size. . 25

25. Chaetosema absent. Wing-margins often scalloped. Hind wing with Rs approximated closely to Sc + R_1 beyond cell THYRIDIDAE (Pyralidoidea) (p. 549)
—. Chaetosema present. Wing-margins straight or rounded 26

26. Small species. Hind wing with Sc + R_1 not closely approximated to cell or to Rs **Tortricoidea** (part) (p. 547)
—. Moderate sized species. Hind wing with Sc + R_1 closely approximated to cell or to Rs. . . . . **Calliduloidea** (p. 554)

27. Antennae clavate. Stem of M strongly developed in fore wing but M_{1+2} often reduced. Frenulum present. Chaetosema absent . . **Castnioidea** (p. 547)
—. Antennae pectinate or simple 28

28. Stem of M more or less and Cu_2* developed in fore wing. Proboscis usually atrophied 29
—. Stem of M and Cu_2 absent or very reduced in fore wing. Proboscis usually present. Frenulum present 30

29. Both branches of M present in cell of fore wing. Frenulum present . . **Cossoidea** (p. 543)
—. M rarely forked in cell of fore wing. Frenulum sometimes absent. Females sometimes apterous . . . . . **Psychoidea** (p. 544)

30. Tympanal organs present. Hind wing with Sc + R_1 approximated to, or fused with, Rs beyond the cell, then diverging . **Pyralidoidea** (part) (p. 548)
—. Tympanal organs absent. Hind wing with Sc + R_1 remote from Rs beyond the cell 31

31. Chaetosema present. 3rd segment of labial palpi short, usually obtuse. M_1 and Rs usually approximated or stalked in hind wing **Tortricoidea** (part) (p. 547)
—. Chaetosema absent. 3rd segment of labial palpi slender and pointed. M_1 and Rs separate in hind wing, less often approximated or stalked **Tinaeoidea** (part) (p. 539)

* Absent in Metarbelidae.

Suborder **ZEUGLOPTERA**

Adult with functional mandibles, lacinia developed, galea not haustellate.

FAM. MICROPTERYGIDAE. *Mouthparts well developed, tibial spurs present, wing-coupling apparatus fibulate, without a frenulum.* This family is of great importance from the standpoint of phylogeny as it includes the most primitive of all Lepidoptera. They are small diurnal moths with a wing-expanse sometimes less than 7 mm., and rarely exceeding 15 mm. The fore wings are ovate-lanceolate with metallic colouring. Like many ancient groups, they enjoy an extremely wide distribution, but the family has probably yet to be identified in many parts of the world. The well-known British genus is *Micropteryx* (*Eriocephala*), and *M. calthella* is a common insect during late spring in many parts of the British Isles. The New Zealand genus *Sabatinca* exhibits the most primitive venation, which is almost identical with that of the Trichopteron *Rhyacophila*. Functional mandibles and laciniae are present and the galeae are free (Fig. 411), there being no proboscis. As in all members of the family the ligula is atrophied and the labial palpi are 3-segmented organs. These insects are pollen feeders and use their maxillae for the purpose. The larva of *Micropteryx* feeds on moss and is characterized by the presence of eight pairs of abdominal limbs (vide Chapman, 1894). These appendages closely resemble the thoracic legs in being jointed and each is terminated by a claw. The mouthparts exhibit both lacinia and galea and the five ocelli are grouped into a sort of compound eye. The body bears eight rows of metamerically arranged globose processes. The larva of *Sabatinca* (Tillyard, 1923) lives among liverworts and has a similar number of reduced abdominal limbs: the pupa is characterized by the possession of functional mandibles.

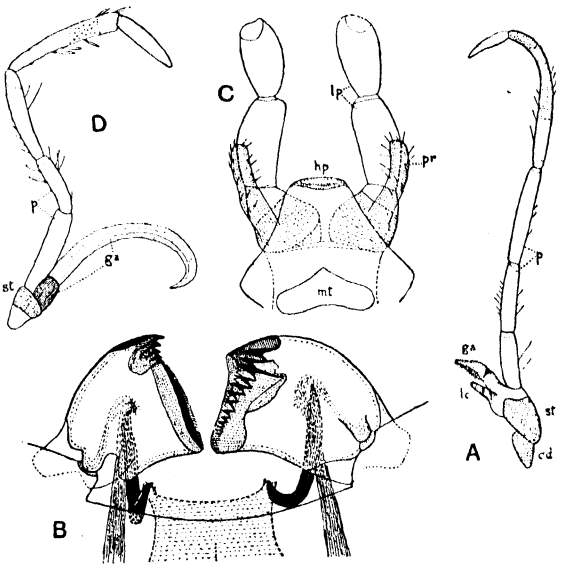


FIG. 411.—Mouthparts of Micropterygidae and Eriocraniidae. A, *Micropteryx*, 1st maxilla. B, *Sabatinca*, mandibles. C, *Sabatinca*, labium, oral aspect; D, *Eriocrania*, 1st maxilla

cd, cardo; *ga*, galea; *hp*, hypopharynx; *lc*, lacinia; *lp*, labial palp; *mt*, mentum; *p*, maxillary palp; *pr*, process of labial palp; *st*, stipes. *After* figures by Tillyard, *Trans. ent. Soc.*, 1923.

Much difference of opinion has been expressed with regard to the systematic position of the Micropterygidae, and their affinities are fully discussed by Tillyard (1919). Both the latter observer and Meyrick regard these insects as being true Lepidoptera, Comstock considers that they are terrestrial Trichoptera while Chapman (1917), followed by Hinton (1946), takes the extreme step of separating the genus *Micropteryx* into an independent order—the Zeugloptera. Tillyard enumerates four salient differences between this family and the Trichoptera, viz. M_4 is not present as a separate vein in the fore wing whereas it exists in archaic Trichoptera; the pupal wing-tracheation is complete whereas in Trichoptera it is reduced to two tracheae only; the characteristic Trichopterous wing-spot is absent: and broad scales with numerous striae are present, whereas scales only appear in a few isolated and highly specialized Trichoptera, and then only of narrow primitive form with few striae. Most authors, however, have laid insufficient stress on the primitive mouthparts of both adult and larva and on the peculiar, probably specialized, female genitalia.

Suborder **MONOTRYSIA**

Female with one, rarely with two, genital apertures on sternite IX. Wings nearly always aculeate.

Superfamily **Eriocranioidea**

Venation of fore and hind wing similar. Female cloacal duct long. Pupal mandibles hypertrophied.

FAM. ERIOCRANIIDAE.—The adult moths have lost the laciniae and the galeae are adapted to form a short proboscis. Mandibles are frequently erroneously stated to be absent: they are reduced though distinct, and are non-denticulate (Walter, 1885). They are visible within the bases of the pupal mandibles and possess strongly developed abductor and adductor muscles identical with those of the pupa (Busck & Böving). The larvae of *Eriocrania* are apodous leaf-miners in birch, hazel, oak and chestnut: the head is very small and partly hidden by the large prothorax and the usual number of spiracles are present. Pupation takes place in a tough cocoon of silk and earthen particles and the pupa closely resembles that of a Trichopteran. It is of the typical exarate type, with the appendages free and the abdominal segments movable. The most conspicuous organs are the long curved serrated mandibles which are used to rupture the cocoon and aid the pupa in making its way to the surface of the soil. For the metamorphosis and detailed structure of all stages of *Mnemonica*, vide Busck and Böving (1914); and for the pupa of *Eriocrania*, vide Chapman (1893a).

The **Mnesarchaeidae** are much more specialized and are represented by the New Zealand genus *Mnesarchaea*. Mandibles are wanting, the maxillary palpi are 3-segmented only, laciniae are absent and the galeae form a rudimentary proboscis used as a sucking-organ. Their metamorphoses are unknown. The **Neopseustidae,** with three species in India and Formosa, are very little known.

Superfamily **Hepialoidea**

Venation of fore and hind wings similar. Female with two genital openings on segment IX.

FAM. HEPIALIDAE (Swift Moths).—*Antennae very short, mouthparts vestigial. Wing-coupling apparatus of jugate type, the jugal lobe elongate and resting upon the hind wing. Tibial spurs absent.* A family comprising about 300 species which are widely distributed but best represented in Australia (Tindale, 1932–42). It is a peculiarly isolated group and although primitive in many features of the external and internal anatomy it is specialized in certain others. The significance of the peculiar female genitalia (p. 523) is uncertain. The species are extremely rapid fliers and vary greatly in size: some are relatively gigantic, attaining a wing-expanse of about 180 mm. Although the five British representatives are sombre-coloured insects certain of the great Australian and S. African forms (*Charagia*, *Leto*) are magnificently decorated with green and rose or adorned with metallic markings. The European species are crepuscular, or fly before dusk, and in two cases at least the mating habits are exceptional in that the female seeks the male. In *Hepialus humuli* the male is commonly white and is readily sought out by the female: in *H. hectus* the female discovers the male by means of an odour diffused by the latter. The larvae are subterranean, feeding upon roots, or are internal wood feeders. Those of several European species are described by Fracker (1915), and Quail (1900) and Evans (1941) have contributed observations on the metamorphoses of certain Australian forms. They are elongate, devoid of colour pattern and both tufted and secondary setae are wanting. The crochets are disposed in a complete multiserial circle. The pupae are unusually elongate and active and are armed with spines, toothed ridges, and cutting plates on the abdominal segments, which are special adaptations for making their way to the surface. The 2nd to 6th abdominal segments are free in the female, and the 7th also in the male (vide Packard, 1895).

The **Prototheoridae,** with seven S. African and Australian species, is related to the Hepialidae but has somewhat more primitive venation. The Australian **Palaeosetidae** and **Anomosetidae,** with four species, are also related to the Hepialidae.

Superfamily **Stigmelloidea**

Wing-venation reduced, especially in hind wing. Male with frenulum. Female with short cloacal duct and fleshy ovipositor.

FAM. STIGMELLIDAE (Nepticulidae).—*Stigmella* and its allies include the smallest of the Lepidoptera, *S. microtheriella* having a wing-expanse of only 3 to 4 mm. The wings are clothed with aculei and are narrowly lanceolate, with a peculiar venation unlike that of all other Lepidoptera (Fig. 412). A jugum is present on the fore wing in the female together with a row of hooked spines on the hind wing: in the male a true frenulum is present (Braun). The larvae are mostly leaf-miners and are devoid of jointed legs or crochets: two pairs of leg-like swellings are present on the thorax and similar structures on the 2nd to 7th abdominal segments. *Stigmella* includes 67 British species, and is nearly world-wide in range.

The family **Opostegidae** has the wing-venation (Fig. 432, B) extremely reduced with no cell and the larva is an apodous miner in stems or bark. The group is widespread and there are four British species. The **Tischeriidae** have somewhat more complete venation and the larva, which is also a miner, sometimes has five pairs of abdominal legs. The species are widespread and moderately numerous.

Superfamily **Incurvarioidea**

Wing-venation reduced in hind wing. Male with frenulum. Female with long cloacal duct and sclerotized ovipositor.

FAM. HELIOZELIDAE.—These are the only Monotrysia in which the scales of the head are depressed, as in many of the higher Tinaeoids. There are about 100 widely distributed (not in N. Zealand) species. The larvae are apodous leaf-miners.

FAM. INCURVARIIDAE.—In *Adela* and *Nemotois* the moths are often metallic and fly in sunshine. In the males, the antennae are longer than in the females and often many times longer than the insect: the eyes in the males are often greatly enlarged and approximated dorsally. The larva in later instars lives in a case and feeds on vegetable refuse. *Incurvaria* and its allies do not have long male antennae and the haustellum is reduced. The larva is a leaf-miner or lives in a case on vegetable refuse (Saalas, 1935–36). In the North American subfamily Prodoxinae there is an intimate relationship between the moths and species of Yucca. The female *Tegeticula yuccasella* is associated with *Y. filamentosa* and by the aid of her specially modified mouthparts collects the pollen and applies it to the pistil in which she has deposited an egg. In this way development of the fruit, upon which the larva feeds, is ensured. In *Prodoxus* the above relationship does not exist and the insect is dependent upon the *Tegeticula* for the pollination of the Yucca flowers, within which the larval growth similarly takes place.

Suborder **DITRYSIA**

Female with a copulatory pore on sternite VIII and an egg-pore on sternite IX. Fore wing without jugum or fibula; hind wing often with frenulum, its venation reduced.

Superfamily **Tinaeoidea** (Figs. 412, 413)

Maxillary palpi often fully developed: labial palpi with 3rd segment usually slender and pointed. Cu_2 generally present in both wings but often reduced in fore wing. Hind wing with Sc + R_1 free, less often joined to cell by a bar. M_1 and Rs separate, sometimes approximated or stalked: or, venation degenerate in many small species: or, wings divided into plumes.

Table of groups:

1 (4).	Wings entire	
2 (3).	Sc + R_1 evident in hind wing	**Tinaeina** (p. 540)
3 (2).	Sc + R_1 apparently absent in hind wing . . .	SESIIDAE (p. 540)
4 (1).	Wings divided into plumes	ORNEODIDAE (p. 543)

FAM. SESIIDAE (Aegeriidae: Clearwings).—This family is distinguishable by Sc + R_1 in the hind wings being concealed by a fold of the costa. Their most striking character, however, is the absence of scales from the greater part of both pairs of wings: the antennae are often dilated or knobbed and the abdomen is terminated by a conspicuous fan-like tuft of scales. The fore wings are extremely narrow owing to the great reduction of the anal area and in most species the bristles of the frenulum in the female are consolidated as in the male. The family is characteristic of the northern hemisphere, and the species are diurnal, flying rapidly during warm sunshine. Many resemble wasps, bees, ichneumons, etc., in appearance, which is largely due to their clear wings, slender bodies and often bright colours. They are in many ways an aberrant group, especially as regards the internal anatomy (vide Brandt, 1890). The larvae feed in the wood of trees and bushes or in the root-stocks of plants. They are colourless with greatly reduced setae; the abdominal feet bear two transverse bands of uniordinal crochets, and a single row on the anal claspers. Among other

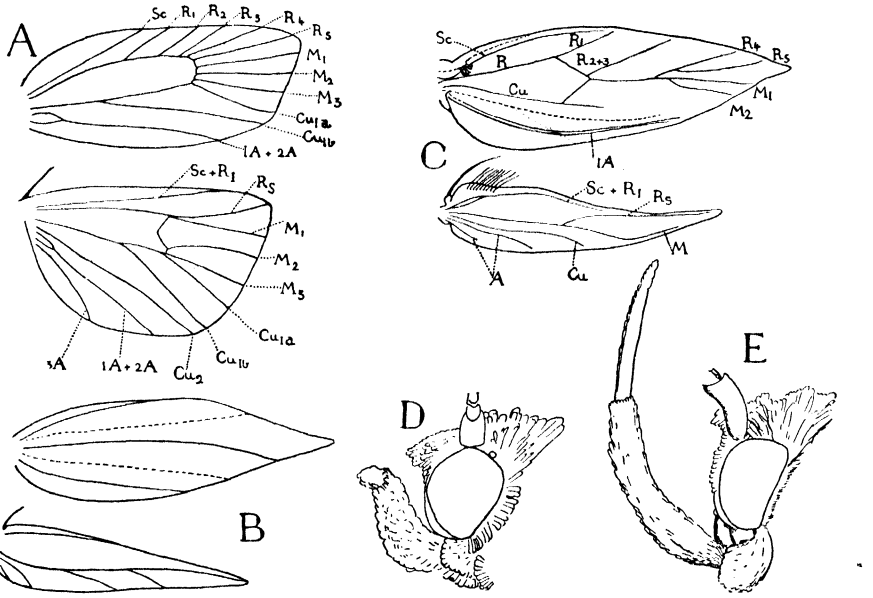


FIG. 412.—Wings of A, *Peronea* (Tortricidae), B, *Opostega* (Opostegidae) and C, *Obrussa* (Stigmellidae). D, side view of head showing labial palp of *Enarmonia pomonella* (Eucosmidae): E, the same of *Cryptolechia tentoriferella* (Oecophoridae). Adapted from Meyrick (A, B), Braun (C) and Forbes (D, E)

characters Fracker states the spiracles of the 8th segment are much larger and higher up than on other abdominal segments. Pupation takes place in the larval gallery and the pupae are provided with various forms of cutting plates for working their way to the surface: these are mostly situated on the head which is heavily sclerotized. There are two rows of spines on most of the abdominal segments which extend around to the ventral surface, and a definite cremaster is wanting. Owing to their internal feeding habit several species have attracted the notice of economic entomologists, particularly the European and American Currant Borer (*Sesia tipuliformis*) and the Peach Tree Borer (*Sanninoidea exitiosa*) of the latter continent (Gossard & King, 1918). Over 100 species of the family are Palaearctic and no less than 90 belong to the genus *Sesia*: 15 species have been found in the British Isles but several are rare and local. The N. American species have been revised by Engelhardt (1946).

Tinaeina. The majority of the Tinaeoidea belong to this series, which includes about one-third of the Lepidoptera and over 750 British species. Most of them are easily recognizable as narrow-winged insects bordered with long hair fringes: the larger and broader winged forms have shorter fringes and can usually be identified by the venational characters previously enumerated. The classification of the group presents great difficulties owing to the fact that notwithstanding the marked differences

of the structure found in the extreme forms, the latter are closely inter-connected by numerous gradational genera. The leading authorities are at variance as to the number of families that exist, and recent research has tended towards the recognition of an increasing number. Among this vast assemblage greater variation of larval habits and structure is found than in any other group of Lepidoptera.

FAM. GELECHIIDAE.—*Antennae rarely with basal pecten. Fore wings trapezoidal. Hind wings with Rs and M_1 stalked or approximated at base, posterior margin usually sinuate.* This family includes nearly 400 genera and about 4,000 species of small moths represented nearly all over the world. A few forms have the hind wings elongate-ovate and resemble Oecophoridae, but may be separated from them by Rs and M_1 being basally approximated or stalked. The larvae usually feed among spun leaves or shoots, sometimes in seedheads or roots, but are seldom leaf-miners or case-bearers (Meyrick). One of the best known species is the nearly cosmopolitan Angoumois Grain Moth (*Sitotroga cerealella*), whose larvae are destructive to wheat, maize, etc. The Pink Boll-worm (*Platyedra gossypiella*) is the widest spread and one of the most destructive of all cotton pests, few cotton regions being free from it. The Potato Tuber Moth (*Phthorimaea operculella*) is a widespread pest of stored potatoes, more rarely affecting the field crop, and *Holcocera pulverea* is an important enemy of lac in India, its larvae being predacious on the latter insect. Over 130 species of the family are British.

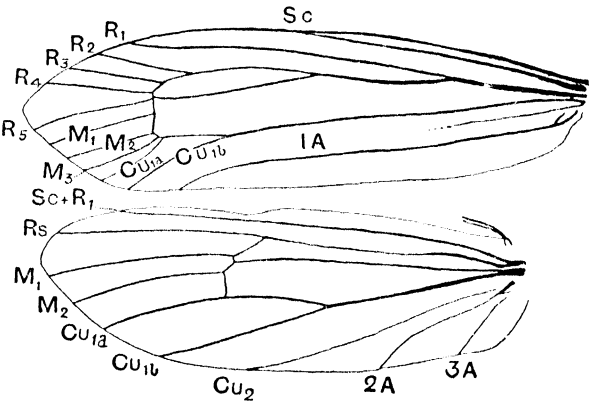


FIG. 413.—*Yponomeuta euonymella*, left wings. × 15

FAM. COSMOPTERYGIDAE.—*Antennae with a slight basal pecten. Fore wings lanceolate or linear: hind wings as in Gelechiidae.* A neglected but widely distributed group of about 1,200 species of small narrow-winged moths, of which 27 are British. The larvae have varied habits, usually fixed for a genus: many are leaf-miners, some feed in shoots or seeds, others among dry refuse or attack scale-insects. The species of *Cosmopteryx* are elegantly marked with black, orange and gold and the larvae usually form blotch mines in leaves.

FAM. OECOPHORIDAE.—*Antennae usually with a basal pecten. Hind wings with Rs and M separate and parallel.* A family comprising at least 3,000 species, many of which are Australian: 19 genera and 75 species are British and there are 117 N. American species (Clarke, 1941). The larvae feed among spun leaves or seeds, in decaying wood, etc. In the large genus *Depressaria* the larvae affect more especially Compositae and Umbelliferae: the common *D. heracliana* spins together the flower heads and seeds of the parsnip and other plants in Europe and N. America. *Blastobasis* and its allies are often regarded as a separate family: their larvae feed on dry refuse, seeds, etc., or live as parasites of scale-insects.

FAM. XYLORYCTIDAE.—*Antennal pecten absent. Hind wings with Rs and M_1 basally approximated or stalked.* This family includes some of the largest Tinaeoidea, and is especially well represented in Australia with a smaller number of species in S. America, India, etc. Some of the finest species belong to the genera *Cryptophasa, Maroga, Uzucha* and *Xylorycta*: they are often conspicuously coloured and attain a wing-expanse up to about 3 inches. The larvae are concealed in shelters or coverings, or tunnel in wood, carrying in leaves for food.

FAM. YPONOMEUTIDAE.—A family of about 800 species whose tropical representatives are often brightly coloured and of relatively large size. The small ermine moths (*Yponomeuta*, Fig. 413) are very widely distributed and their larvae live gregariously on shrubs and fruit trees. The large genus *Argyresthia* is well represented in Europe and N. America, the larvae living in shoots, leaf-buds, fruit, etc. The species of *Ethmia* are sometimes regarded as a separate family: the larvae are partial to Boraginaceae living in a slight web on the leaves.

FAM. ELACHISTIDAE (Cycnodidae).—A restricted family whose most important genus is *Elachista*, with over 200 species. The larvae mostly mine leaves, especially of grasses or allied orders of plants (vide Braun, 1948). Mention needs also to be made of the small families **Douglasiidae,** and **Scythridae,** which appear to belong here and are sometimes included as subfamilies.

FAM. COLEOPHORIDAE (Eupistidae).—In this small family the only extensive genus is *Coleophora*, which is represented by over 400 holarctic species: about 90 species occur in N. America and 79 species in Britain. They are narrow-winged insects, usually recognizable by the antennae being held in a porrect position in repose. With regard to the larval habits, Meyrick remarks that they are leaf-mining when very young, afterwards inhabiting a portable case. The latter is attached to a leaf or seed-vessel and the larva bores into the interior. In the case of leaves a pale blotch is usually produced, with a distinctive round hole in one membrane (vide Barasch, 1934).

FAM. GRACILLARIIDAE.—A cosmopolitan family of about 1,000 small species with narrow, long-fringed wings. They are often recognizable by their habit of resting with the fore part of the body upraised by the rather widely separated two anterior pairs of legs. According to Busck (1914), some species retain more branches of Rs in the hind wing than do any other members of the suborder. The larvae are leaf-miners: when young are very much flattened with blade-like mandibles and vestigial maxillae and labium. At this stage they lacerate the cells and suck the exuding sap: later they usually undergo hypermetamorphosis, acquiring normal mouthparts and devour the parenchyma. The mines in *Lithocolletis* are small blotches, of which one surface is silk-lined and caused to contract, thus producing a hollow chamber: the contracting surface may be either on the upper or lower leaf surface, but is constant for a species (Meyrick). The two larger genera, *Lithocolletis* and *Gracillaria*, together include over 450 species: *Phyllocnistis*, with over 50 species, includes some of the smallest and most delicate of all moths, and is remarkable in that the larvae are apodous.

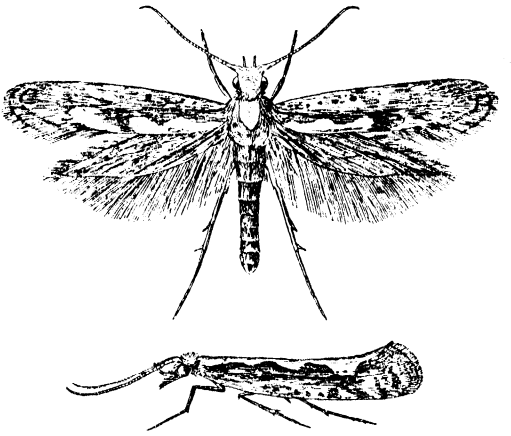


FIG. 414.—*Plutella maculipennis*, enlarged
Reproduced by permission of the Ministry of Agriculture.

FAM. PLUTELLIDAE.—A family of about 200 species, occurring in most regions. They resemble the Yponomeutidae, but may be distinguished by the short porrect maxillary palpi. The larvae feed in a slight web in leaves or occasionally mine leaves or stems: those of the cosmopolitan genus *Plutella* feed on the leaves of Cruciferae. The Diamond-back Moth (*Plutella maculipennis*: Fig. 414) is very destructive to vegetables and, owing to its ability to flourish in about all climates, it has become one of the most universally distributed of Lepidoptera and appears to be still extending its range through the agency of commerce. The small family **Epermeniidae** is closely related to the Plutellidae.

FAM. HELIODINIDAE.—A moderate-sized cosmopolitan family, whose members when at rest have the trait of displaying the hind legs either upraised or applied to the back or sides of the body: the posterior legs have the tibiae and tarsi furnished with whorls of bristles. An important genus is *Stathmopoda*, whose larvae in some species prey upon Coccids, in others they bore into fruits, leaves, etc. Out of about 400 known species six are British.

FAM. GLYPHIPTERYGIDAE.—A large family (about 900 spp., 12 British), especially abundant in the southern hemisphere. *Glyphipteryx* includes metallic-winged moths which fly in sunshine and whose larvae feed chiefly on grasses and sedges. In *Choreutis* the moths resemble Tortrices in form and their larvae often form webs among leaves or seeds.

FAM. TINAEIDAE.—A world-wide family of over 2,400 species characterized by

the head being usually rough-haired, the proboscis short or absent and the maxillary palpi often long. The labial palpi are usually porrected and the posterior tibiae hairy. The wings have all the usual veins present and separate, the hind pair being narrow. *Tinaea* is universally distributed; its larvae show diverse habits and sometimes live in portable cases. Those of most European species feed upon various dry animal or plant material. Thus, the larva of *T. vastella* feeds upon dried fruit, horns of antelopes, and other dried matter: those of *T. pellionella*, *Tineola biselliella* and *Trichophaga tapetzella* are 'clothes moths'—household pests attacking clothing, carpets, furs, feathers, etc. In *Melasina energa* (Ceylon) Fryer states that the larva inhabits a tubular tunnel of earth and vegetable particles, which partly projects above the surface of the ground.

Mention needs also to be made of four small families which are either largely or entirely Australasian. The **Epipyropidae** have larvae which are parasites upon Jassids and Fulgoroids (Kato, 1940). The **Cyclotornidae** also include parasites; the 1st instar larvae of the Australasian *Cyclotorna* parasitize Homoptera, while in their 2nd instar, they live in ants' nests (Dodd, 1912). The **Amphitheridae** and **Copromorphidae** each include a small number of species.

FAM. ORNEODIDAE (**Alucitidae:** Many-plume Moths).—A small isolated family characterized by both pairs of wings being cleft into six or more narrow plume-like divisions, densely fringed with hairs along both margins (Fig. 415). They are related to the Pyralidids and Tinaeids, but exhibit no close affinity with the Pterophoridae. With the exception of *Orneodes hexadactyla*, which is European, the various species have a restricted range: the former insect is common in Britain, where it is the sole representative of the family. The larvae burrow into shoots, flower-stalks and buds giving rise to galls, and the known food-plants include *Lonicera*, *Scabiosa* and *Stachys*. They are hirsute, cylindrical and rather stout; the crochets are uniordinal, arranged in a complete circle. The pupae are very different from those of the Pterophoridae and have affinities with Tinaeids and Pyralids. A cocoon is formed on the surface of the ground and consists of loose silk or of fine earthen particles. Most of what is known concerning the family will be found in papers by Chapman (1896), Hofmann (1898), Fletcher (1910) and by Meyrick (1910).

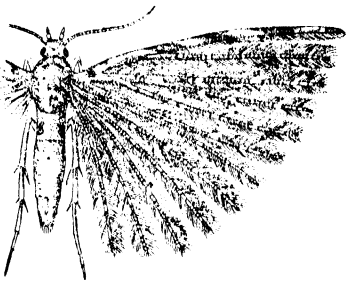


FIG. 415.—*Orneodes pygmaea*, enlarged, Ceylon
After Fletcher.

Superfamily **Cossoidea** (Figs. 400, 416)

Both pairs of wings with Cu_2 present and M furcate within the cell. Areole present in fore wing. Haustellum absent.

FAM. COSSIDAE (Goat Moths, Carpenter Moths).—Insects of moderately large or exceedingly large size, the females of *Duomitus leuconotus* attaining a wing-expanse of 180 mm. The family is generally distributed and, according to Turner (1918), it retains the most ancient form of venation among Ditrysia. The antennae are frequently bipectinate in both sexes, rarely simple: in other cases they are bipectinate in the male for a portion of their length and filiform distally. The frenulum is sometimes short and apparently non-functional, more often it is well developed: in the female it may consist of as many as nine bristles (Hampson). These moths are nocturnal fliers and lay their eggs on the bark of trees, or in the tunnels from which they have emerged. The larvae are internal feeders boring large galleries in the wood of forest, shade and fruit trees or in the pith of reeds, etc., often causing serious injury. The head is closely united to the enlarged prothorax, and the mandibles are very large. Only primary setae are present and the full number of limbs is retained, the crochets being usually either bi- or tri-ordinal, arranged in a complete circle. In certain species the larvae attain a very large size and in *Cossus cossus* (*ligniperda*) and *Prionoxystus robiniae* they live for at least two years. The pupae lack maxillary palpi: the 3rd to 6th abdominal segments are movable in the female and the 7th also in the male. The dorsum of the segments is armed with a toothed ridge along each margin and a cocoon of silk and gnawed wood is usually constructed. *Cossus* is one of the most primitive genera and is universally distributed. *Xyleutes* includes numerous species

found in all warmer regions, particularly Australia. *Zeuzera* includes the Leopard Moth (*Z. pyrina*) whose larva is destructive to the wood of fruit trees (Fig. 431): that of *Z. coffeae* is known as the 'White Borer' of coffee.

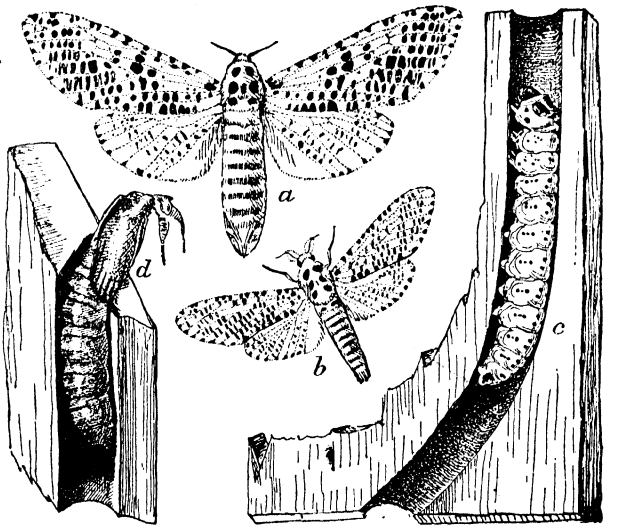


FIG. 416.—*Zeuzera pyrina*

a, female; *b*, male; *c*, larva; *d*, pupal case. Actual size. *After* Howard & Chittenden. *U.S. Dept. Agric. Circ.* 109 (reduced).

Superfamily **Psychoidea**

Maxillary palpi absent or vestigial. Proboscis usually atrophied. Tympanal organs wanting. Posterior tibial spurs very short with middle spurs often absent. Both wings with Cu_2 present (rarely wanting in fore or hind wing only) and M almost always present within the cell. Hind wing with Sc + R_1 remote from Rs beyond the cell.

1. Hind wing with Sc + R_1 coincident with the cell to middle or near extremity. Palpi absent . . . . . MEGALOPYGIDAE (p. 545)
–. Not as above 2

2. Hind wing with Sc + R_1 anastomosing with cell. Palpi present . . . 3
–. Hind wing with Sc + R_1 free or connected with the cell by a bar . . 4

3. Frenulum absent . . . . . CHRYSOPOLOMIDAE (p. 545)
–. Frenulum present. . . . . COCHLIDIIDAE (p. 546)

4. Proboscis, frenulum and chaetosema present. Female always winged . . ZYGAENIDAE (p. 546)
–. Proboscis and chaetosema absent. Female apterous or frenulum absent. . 5

5. Female winged. Tibial spurs short or wanting 6
–. Female apterous. Tibial spurs present. Cu_2 present in fore wing . . . 7

6. Cu_2 present in fore wing . . . . . RATARDIDAE (p. 547)
–. Cu_2 absent in fore wing. . . . . METARBELIDAE (p. 545)

7. Females and larvae case-dwellers . . . . . PSYCHIDAE (p. 544)
–. Females and larvae not case-dwellers . . . HETEROGYNIDAE (p. 545)

FAM. PSYCHIDAE (Bag-worm Moths).—A family with 800 species and an extremely wide distribution: about 150 species occur in the Palaearctic region but very few are British. The family has evolved along totally different lines in the two sexes, the males being highly specialized and swift fliers, while the females include

the most degenerate of all Lepidoptera (Fig. 417). In the former sex the wings are thinly clothed with hairs and imperfect scales, and are almost devoid of markings. The labial palpi are very short, the antennae are strongly bipectinated, and the frenulum exceptionally large. The females are always apterous, but exhibit various degrees of degeneration: in extreme forms the antennae, mouthparts and legs are totally wanting. The larvae inhabit cases which exhibit great variety of shape and of materials used in their construction: they carry their cases with them as they move about their food-plants. These habitations are formed of silk covered with fragments of leaves, twigs, grass and other objects. In *Cochliotheca* they are wholly constructed of silk and are extremely close copies of Helix-like shells. Pupation takes place within the larval case, and the pupae are provided with a row of sharp spinules on the abdominal segments. There is much diversity of structure in the female pupae: thus according to Heylaerts wings are present in *Fumea*, while in *Thyridopteryx* and *Oiketicus* there are no traces either of these organs or of antennae, maxillae, or eyes and only slight vestiges of legs are present (Mosher). The imago of this sex is little more than an egg-sac and spends her whole life within the larval habitation. Copulation takes place by the male alighting on the case and inserting his protrusible abdomen between the wall of the former and the ventral surface of the female. *Fumea* is exceptional in that the female emerges from the case prior to copulation. Parthenogenesis is known to occur in *Cochliotheca crenulella* var. *helix* and in *Solenobia* and *Luffia* (Seiler, 1923, etc.). Heylaerts (1881) has monographed the European species and gives much general information on the family: for the habits and structure of *Acanthopsyche opacella*, vide Chapman (1900); and Matthes (1948) for *Amicta*. The affinities of the Psychidae appear to lie with the Heterogynidae, and Heylaerts regards them as being intermediate between this family and the Lymantriidae; other naturalists claim that they are also connected through the Heterogynidae with the Zygaenidae or with the Tinaeids. The larvae of a few species are pests of fruit or other trees in N. America, S. Africa, etc.

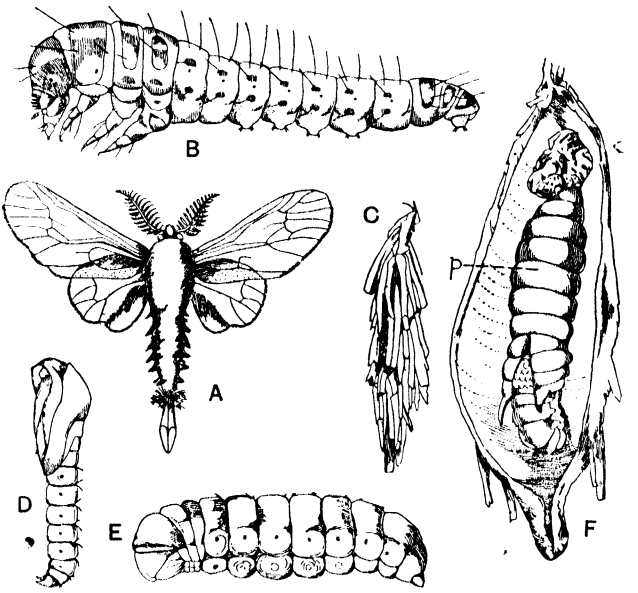


FIG. 417.—*Thyridopteryx ephemeraeformis*

A, male imago; B, larva; C, larval 'bag'; D, male pupa; E, female pupa; F, female imago within 'bag'; *p*, pupa case. All enlarged. Adapted from Howard & Chittenden, *U.S. Bur. Entom., Circ.* 97.

The **Heterogynidae** are an extremely small family represented by the southern European genus *Heterogynis*. The larvae are not case-bearers, and the females resemble those of the Psychidae in being vermiform and degenerate. They are stated to remain in the cocoons and lay their eggs there.

The **Chrysopolomidae** are similarly a very small family comprising only two genera and about 24 species which inhabit parts of Africa.

FAM. METARBELIDAE (Teragriidae).—A small tropical family of Ethiopian and Oriental range whose larvae, so far as is known, are wood-borers. The moths are nocturnal and closely resemble the Cossidae, but have a more reduced type of venation.

FAM. MEGALOPYGIDAE (Lagoidae). An essentially American family with only few Palaearctic species which occur in Africa. Their affinities apparently lie nearest to the Cochlidiidae, particularly with regard to larval characters. According to

Dyar their larvae possess two series of abdominal feet. The normal ones occur on segments 3 to 6 and on 10, and are provided with crochets; the secondary feet lie on segments 2 to 7 and are of the nature of sucker-discs. Mosher states that in *Lagoa* the pupa has the head and thoracic segments free, and abdominal segments 1 to 6 are free in the female, with segment 7 also in the male. The whole pupal covering is thin and membranous with the appendages entirely free from each other and from the body-wall. The cocoon is furnished with a circular operculum to allow of the emergence of the imago. An account of the metamorphoses and anatomy of *Lagoa crispata* is given by Packard (1894).

FAM. COCHLIDIIDAE (Limacodidae, Heterogeneidae or **Eucleidae).**—A small family allied to the Zygaenidae and Megalopygidae and including less than 40 Palaearctic species: *Heterogenea* and *Cochlidion* are British. Their larvae are commonly known as 'slug caterpillars', which have thick, short flesh bodies, a small retractile head and minute thoracic legs. Segmentation is indistinct and there are no abdominal feet, but according to Chapman (1894) secondary sucker-discs are present on the first eight abdominal segments. A valuable series of papers on the structure of these anomalous larvae has been contributed by Dyar (1895–99). Those of different genera have very little in common beyond the features enumerated: many are smooth and glabrous while others are provided with a conspicuous armature of spine-bearing scoli which, in the case of *Empretia stimulea*, are said to be poisonous. The pupae strongly resemble those of the preceding family and are enclosed in a hardened oval or round cocoon. The latter is provided with an operculum which is constructed by the larva and allows of the free escape of the imago (Fig. 418).

FAM. ZYGAENIDAE.—The members of this family closely resemble the Amatidae but are readily separable therefrom by the presence of Cu_2 in the hind

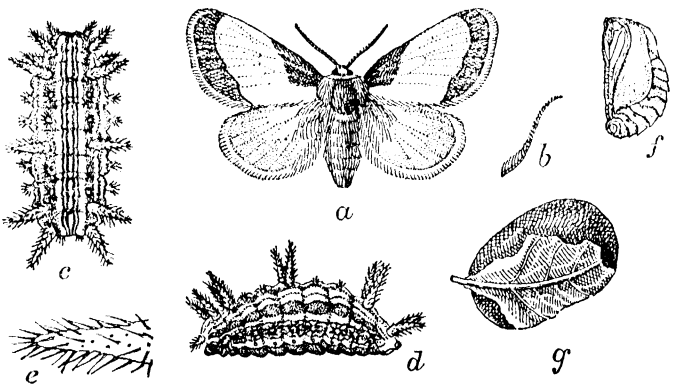


FIG. 418.—*Euclea indetermina*, N. America

a, female imago; *b*, antenna of male; *c*, *d*, larva; *e*, scolus, much enlarged; *f*, pupa; *g*, cocoon. *After* Chittenden, *U.S. Dept. Agric. Ent. Bull.* 124.

wings (Fig. 419). Many are very brilliantly coloured and there is considerable diversity of structure. They are diurnal in habit, with a slow heavy flight, and are inclined to be very locally distributed. The larvae (Fig. 420) possess the full number of limbs, and, so far as known, they are short and cylindrical with numerous verrucae from which arise short hairs; they live exposed on herbaceous plants. The pupae are enclosed in tough elongate membranous cocoons above ground; owing to their great capacity for movement, they are enabled to work their way out prior to the emergence of the imagines.

The subfamily Zygaeninae is characteristic of the Palaearctic region where it is represented by 12 genera and over 100 species; 2 genera and 10 species inhabit the British Isles. *Zygaena* includes the 'Burnets' which have the antennae distally enlarged and *Ino* includes the brilliant metallic green 'Foresters'. The Chalcosiinae are far the largest group and are essentially tropical, only two species entering the Palaearctic region. Many species are butterfly-like with slender bodies and broad large wings; in *Elcysma* and *Histia* the hind wings are tailed. The Phaudinae are a small and very aberrant subfamily in which the mouthparts are wanting. In *Himantopterus* the hind wings are filiform as in the Nemopteridae (p. 500) and there is no frenulum: the

genus is placed by some authorities in a family of its own—the **Himantopteridae** (Thymaridae).

FAM. RATARDIDAE.—A small group found in the Oriental region.

Superfamily **Castnioidea**

Maxillary palpi present. Proboscis present or absent. Chaetosema absent. Antennae clavate. Tympanal organs wanting. Tibial spurs present. Fore wing with Cu_2 present and M developed within the cell. Hind wing with Cu_2 present or absent, Sc + R_1 remote from Rs beyond the cell.

FAM. CASTNIIDAE.—Included in this family are about 160 brightly coloured day-flying moths often bearing a resemblance either to Nymphaline butterflies or 'Skippers'; they are confined to tropical America and the Indo-Malayan and Australian regions. Their metamorphoses have been very little studied. The eggs are

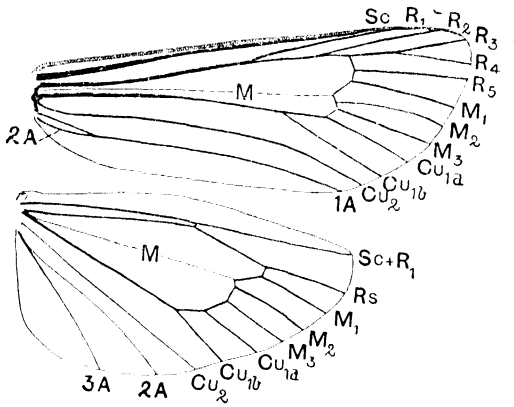


FIG. 419.—*Zygaena filipendulae*, venation



FIG. 420.—*Zygaena filipendulae*, larva, nat. size
After Hampston, (F.B.I.).

upright and the larvae feed within the stems of plants; for remarks on the pupa, vide Chapman (1895). *Castnia licus* is destructive to sugar cane in tropical America and its metamorphoses are figured by Marlatt. *Tascinia*, with the proboscis absent, has sometimes been put in a separate family. By some authorities the family is regarded as being closely related to the butterflies, but, with the removal of both *Megathymus* and *Euschemon* to the Hesperiidae, the affinities appear to be less evident.

Superfamily **Tortricoidea** (Tortrices: Fig. 412 A, D)

Maxillary palpi vestigial or absent: labial palpi with 2nd segment more or less rough-scaled, 3rd segment short and usually obtuse. Cu_2 generally present in both wings though often vestigial, especially in fore wing. Hind wing with Sc + R_1 approximated, or less often joined, to cell then diverging; M_1 and Rs usually approximated or stalked.

Table of families:

1.	Fore wing with Cu_{1b} arising from or near lower angle of cell	2
–.	Fore wing with Cu_{1b} arising from near middle of cell	3
2.	Hind wing with 1 or 2 branches to M	CARPOSINIDAE
–.	Hind wing with 3 branches to M	PHALONIIDAE
3.	Hind wing with cubital pecten on margin of cell	EUCOSMIDAE
–.	Hind wing usually without cubital pecten	4
4.	Fore wing with R_3 and R_4 stalked or coincident: end of palpus pointed	CHILIDANOTIDAE
–.	Fore wing with R_3 and R_4 separate, if not end of palpus obtuse	TORTRICIDAE

The Tortrices are moths of small size with wide wings, and the hair-fringes of the latter are always shorter than the width of the wing. The family is

more characteristic of temperate regions than tropical, and the imagines are mainly crepuscular in habit. In the males of many species there is a basal costal fold to the fore wings, often including expansible hairs, probably functioning as a scent organ. The eggs are flattened and oval, usually smooth, occasionally reticulated. The larvae live concealed, usually in rolled or joined leaves, or in shoots spun together. Others live in stems, roots, flower-heads or seed-pods. They are rather elongate, slightly hairy and have the full number of abdominal limbs. The crochets on the abdominal feet are usually bi- or tri-ordinal, and arranged in a complete circle. The pupae have two rows of spines on most of the abdominal segments; the 4th to 6th segments are movable in the female and the 7th also in the male. The pupa is protruded from the cocoon prior to the emergence of the imago and is usually found in the situation where the larvae feed.

FAM. EUCOSMIDAE (Olethreutidae).—A family of over 2,000 species and including nearly two-thirds of the British Tortrices. *Enarmonia*, with over 300 species, is widely distributed and its larvae usually feed in fruits or stems. *E. molesta* is the Oriental Peach Moth which has become an established pest in N. America and S. Europe, probably from Japan. *Evetria* includes the destructive Pine-Shoot Moths and *Enarmonia* (*Carpocapsa*) *pomonella* is the Codling Moth, whose larva burrows in the fruit of the apple and is a world-wide enemy of the cultivator.

FAM. TORTRICIDAE.—A family of about 1,500 species of world-wide range. In the large genus *Tortrix*, with some 300 species, *T. viridana* of Europe is a well-known defoliator of the oak: its economy and parasites have been studied by Silvestri (1923). *Sparganothis* is exceptional in retaining the cubital pecten and *S. pilleriana* is a European pest of the grape. The larvae of species of *Cacoecia* live on a variety of trees and shrubs.

FAM. PHALONIIDAE (Conchylidae).—A family of mainly Holarctic range, and whose larvae are internal feeders, usually in flowers, seed-heads or stems. In *Phalonia* (over 220 species) the larvae especially affect Compositae. The **Carposinidae** are a small family mainly found in Hawaii and Australasia and have Tineoid affinities, while the **Chlidanotidae** are an Indo-Australian group.

Superfamily **Pyralidoidea** (Fig. 421)

Maxillary palpi usually present. Legs almost always long and slender. Abdominal tympanal organs present in most species. Cu_2 vestigial or absent in fore wing, almost always present in hind wing. In hind wing Sc + R_1, with few exceptions, partly fused with Rs beyond the cell and M_1 stalked with or approximated to Rs. Or, each wing divided into not more than four plumes, and hind wing with double row of spine-like scales at edge of cell on ventral surface.

Table of families:

1. Tympanal organs absent. Sc + R_1 not fused with Rs in hind wing . . 2
–. Tympanal organs present. Hind wing with Sc + R_1 partly fused with Rs and Cu_2 present (**Pyralidina**) 3

2. Wings almost always divided into plumes: with spine-like scales on ventral surface of hind wing . . . . . PTEROPHORIDAE (p. 551)
–. Wings not as above: Cu_2 absent in hind wing . . . THYRIDIDAE (p. 549)

3. Hind wing with cubital pecten on upper side 4
–. Hind wing without cubital pecten 6

4. Fore wing with R_5 present 5
–. Fore wing with R_5 absent . . . . . PHYCITIDAE (p. 549)

5. Maxillary palpi strongly triangularly dilated with scales . CRAMBIDAE (p. 549)
–. Maxillary palpi filiform . . . . . GALLERIIDAE (p. 549)

6. Fore wing with R_5 stalked with R_3 and R_4 . . . PYRALIDIDAE (p. 550)
–. Fore wing with R_5 free . . . . . PYRAUSTIDAE (p. 550)

The Pyralidoidea form an enormous assemblage of small to medium-sized moths of fragile slender build and with relatively long legs. The approximation, or partial fusion, of Sc + R_1 with Rs in the hind wings (Fig. 421) readily separates them from any other major division of Lepidoptera. Their larvae have very varied habits, and many live in concealment. They are markedly active, and often exhibit a forward and backward wriggling motion when disturbed. They are usually slender and nearly bare, with little or no colour pattern. The abdominal feet are short, and provided with either a pair of transverse bands, or a more or less complete circle of biordinal crochets. The pupae are not protruded from the cocoon in emergence, and abdominal segments 5 to 7 are free. Maxillary palpi are always present, and the surface of the body is seldom roughened with spines or setae except in the Pterophoridae.

FAM. THYRIDIDAE.—A small tropicopolitan family of particular interest on account of the relationships which it exhibits with other of the larger groups of the Lepidoptera. Both Hampson and Meyrick claim that they are the ancestral group from which the butterflies have been derived. They are mostly small moths resembling Pyralidids or Geometrids in general appearance, and can usually be recognized by the presence of white or yellowish translucent areas on the wings. They are widely distributed in the tropics but only three genera, embracing four species, are listed by Staudinger & Rebel as entering the Palaearctic region, *Thyris* alone being European. *Rhodoneura* includes over 100 species distributed from the W. Indies and S. America, through S. Africa and the whole Oriental region, to Australia. The larvae, so far as known, exhibit Pyralidid characters. For a revision of the family vide Hampson (1897).

Related to the Thyrididae are the small Indo-Australian families **Tineodidae** and **Oxychirotidae.** In the latter family *Cenoloba* has each wing divided into two plumes.

Pyralidina

FAM. GALLERIIDAE.—The Galleriidae are a small but widely distributed family whose larvae feed on a variety of dried substances, including the combs of beehives and of wasps' nests, dried fruits, and in a few cases in roots, beneath bark, etc. Pupation takes place in a peculiarly tough cocoon. The best known species is the Wax Moth, *Galleria mellonella*, which has become artificially spread among hives in many parts of the world, including Australia. The biology and method of nutrition of this species have been studied by Metalnikov (1908).

FAM. CRAMBIDAE.—This family includes the Grass Moths, of which the genus *Crambus* comprises about 400 species (29 British). They are small insects with narrow elongated fore wings and porrected labial palpi. They are extremely abundant in grass land and rest by day in an upright position with the wings folded on the stems. Their larvae usually feed in silken galleries on grasses, reeds and allied plants, or on moss. Among other forms *Diatraea saccharalis* is the American Sugar-cane Borer and species of *Chilo* are similar pests in India.

FAM. PHYCITIDAE.—The Phycitidae are a very large group with elongate fore wings which lack vein R_5: the hind wings have, on the dorsal side, a well-defined pecten of hairs on the lower margin of the cell near the base. These insects are exceptional in that the frenulum is simple in both sexes. Secondary sexual characters are well seen in the swollen basal antennal segment of the males, and the same sex is often provided with a conspicuous row, or tuft, of hairs or scales on the fore wings. The larvae vary greatly in habits and usually live in silken tubes by day, coming out to feed at night. Nearly 50 species of the family are British, and over 800 are found in the Palaearctic region. *Ephestia* includes the Mediterranean Flour Moth (*E. kühniella*) whose larvae are great pests in flour mills; those of other species attack dried fruits, biscuits, and other commodities, *E. cautella* being the nearly cosmopolitan Fig Moth. The Indian-meal Moth (*Plodia interpunctella*) is even more widely distributed and attacks maize, figs and seeds of various kinds. *Laetilia coccidivora* is remarkable on account of its predacious larva which lives upon various Coccidae in N. America. A detailed study of the metamorphosis and larval and pupal structure of a Phycitid

is given in Beeson's paper (1910) on the Oriental Toon Moth (*Hypsipyla robusta*), which is a shoot-borer. Larvae of various other genera live in rolled or spun leaves, others affect flower-heads, and many live on the bark of trees. The Anerastiinae, which have a vestigial proboscis, are often regarded as a separate family.

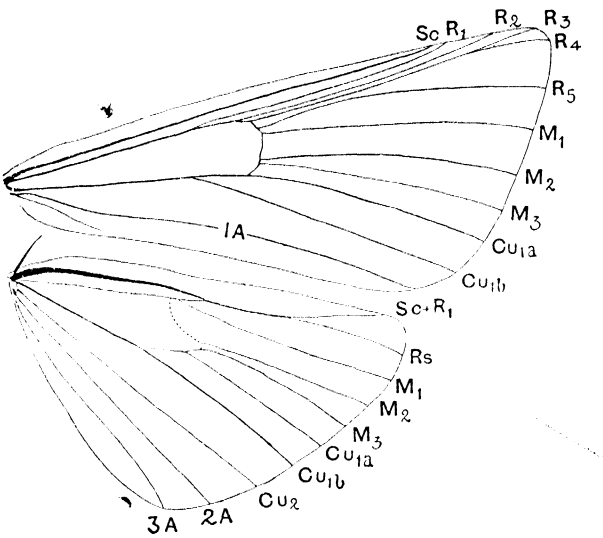


FIG. 421.—*Notarcha ruralis* (Pyraustidae) venation

FAM. PYRALIDIDAE.—This family is fairly numerous in the tropics, but scarce elsewhere, and absent from New Zealand. The larvae feed, as a rule, upon dry or decaying vegetable substances. Those of the cosmopolitan *Pyralis farinalis* form silken galleries among corn and flour debris; species of *Aglossa* mainly live among hay and chaff refuse, while *Synaphe angustalis* frequents damp moss. The subfamilies Chrysauginae, Endotrichinae and Epipaschiinae are often regarded as separate families.

FAM. PYRAUSTIDAE (Fig. 421).—These form an immense family, which includes most of the larger Pyralidina. They are all characterized by R_5, in the fore wing, arising separately from the cell, but are frequently divided into a number of families based upon relatively trivial characters. The Schoenobiinae have the proboscis vestigial and their larvae live among aquatic plants. The anomalous genus *Acentropus* is the most truly aquatic of all Lepidoptera, and its structure and biology has been studied in detail by Berg (1941). The young larva tunnels in the petioles of *Potamogeton* and other water plants; it subsequently constructs a tube of portions of leaves spun together, but open at the two extremities. A cocoon is spun in a rather similar leaf-shelter, the pupa being almost completely submerged. Respiration in the larva appears to be cutaneous at first and it is only in the later stages that the tracheae become filled with air. The females are dimorphic: the long-winged forms are aerial while those with reduced wings live entirely in the water, using their wings for swimming. The Nymphulinae are of special interest for the reason that some species are also aquatic. In the genus *Nymphula*, the larvae are usually leaf-miners at first and live throughout life below the surface of the water. Their biology has been frequently studied, notably by Miall, Müller (1892) and Welch (1916). Two definite larval types occur; those without gills when mature (*N. nympheata*), and those in which such organs are present (*N. stratiotata*, etc.). The life-history of *N. maculalis* has been studied by Welch, who states that tracheal gills are wanting in the first instar but increase numerically after each moult. The pupa is enclosed in a silken cocoon on the submerged surface of a leaf, and the imago is not affected by contact with water during emergence. The method of respiration in this genus requires further study: during early life it is cutaneous and spiracles, if present, are closed. In *N. nympheata* and also in *Cataclysta lemnata* respiration subsequently takes place by open spiracles. In other species it is performed by means of tracheal gills: non-functional spiracles co-exist with the latter in *N. stratiotata*, but apparently not in *N. maculalis*.

The Scopariinae are a small group characterized by a raised tuft of scales in the cell of the fore wing. The large genus *Scoparia* mostly inhabits temperate regions and is extensively developed in New Zealand. The larvae feed on moss and lichen, among which they form silken galleries. The Pyraustinae are the largest group with 68 British species, and differ from the Scopariinae in the absence of raised scales from the fore wings. They are common in nearly all parts of the world and are exceedingly abundant in the tropics. Their larvae usually feed in a slight web amongst spun-up leaves, or in stems, fruits or roots. The most notorious species is the European Corn

Borer (*Pyrausta nubilalis*), which is an introduced pest of corn (maize) in Ontario and the eastern U.S.: although abundant on the continent of Europe, it is rare in Britain.

FAM. PTEROPHORIDAE (Alucitidae: Plume Moths).—These insects are readily distinguishable by their deeply fissured wings; the anterior pair is longitudinally cleft into two, or more rarely three or four divisions, and the hind pair into three. There are no maxillary palpi, and all the species are extremely lightly built with very elongate fore wings, and unusually long and slender legs armed with prominent tibial spurs. The species are nowhere numerous and 32 inhabit the British Isles. *Agdistis*, and two other genera, are exceptional in possessing undivided wings. The larvae mostly feed exposed on flowers and leaves but sometimes internally in stems or seed vessels the Compositae being more frequently selected than any other order of plants. They are long and cylindrical with numerous secondary setae. The abdominal feet are long and stem-like with uniordinal crochets. The pupae (Chapman, 1896) are attached by the cremaster and occur above ground, sometimes in a slight cocoon. The body is roughened with short spines or with small groups of longer barbed spines arising from small elevations. Unlike the Pyralididae, there are no maxillary palpi, and the deep furrow between the 9th and 10th abdominal terga is likewise absent. Among British species one of the commonest is *Pterophorus pentadactylus* whose larva feeds upon *Convolvulus*: the larva of *Agdistis bennetii* selects *Statice limonium* and that of *Trichoptilus paludum* feeds upon the leaf-tentacles of *Drosera* (Chapman, 1906). (See also Lange, 1939.)

Superfamily **Bombycoidea**

Maxillary palpi and tympanal organs absent. Frenulum almost always atrophied or vestigial: proboscis rarely developed. Chaetosema absent. Antennae pectinated, especially in male. Cu_2 absent from both wings: hind wing with Sc + R_1 usually diverging from cell and Rs, or only connected with cell by a cross-vein (R_1).

Table of families:

1. Hind wing with costal area greatly widened basally and supported by usually 2 or more stout humeral veins from a subcostal cell between bases of Sc and R . LASIOCAMPIDAE (p. 552)
–. Not as above 2

2. Hind wing with Sc + R_1 diverging from cell from base. M_2 arising at or in front of middle of cell, nearer to M_1 than to Cu_{1a} 3
–. Hind wing with Sc + R_1 connected with cell by a cross-vein or basally approximated to Rs beyond the cell 5

3. Hind wing with a rudiment of Cu_2, a vestigial frenulum, and with 2 anal veins. LACOSOMIDAE (p. 554)
–. Hind wing without such vestiges 4

4. With 2 anal veins. Tibiae with spurs . . . CITHERONIIDAE (p. 553)
–. Almost always with 1 anal vein. Tibiae without spurs . SATURNIIDAE (p. 552)

5. Sc + R_1 basally approximated to Rs beyond the cell. Proboscis present . BRAHMAEIDAE (p. 553)
–. Sc + R_1 connected with cell by a cross-vein. Proboscis absent . . . 6

6. M_2 in hind wing arising behind middle of cell, nearer to Cu_{1a} than to M_1 . ENDROMIDIDAE (p. 554)
–. M_2 arising at or in front of middle of cell, nearer to M_1 than to Cu_{1a} . . 7

7. Fore wing with R_{2-5} and M_1 on a common stalk . . LEMONIIDAE (p. 554)
–. Fore wing with M_1 free or shortly stalked on Rs . . BOMBYCIDAE (p. 554)

The Bombycoidea or 'frenulum-losers' are chiefly distinguished by the loss or the absence of characters. Their main feature is the atrophy of the frenulum and, correlated with it, the basal widening of the humeral area of

the hind wing. A frenulum occurs in some Bombycidae, but elsewhere only vestiges occasionally persist in the superfamily.

FAM. LASIOCAMPIDAE (Eggars, Lappet-moths).—Usually moderate to large sized densely-scaled moths, with stout bodies, and the humeral lobe of the hind wings prominent. The proboscis is atrophied, there are no ocelli, and the antennae are bipectinated in both sexes. These insects are widely distributed but absent from New Zealand and are most abundant in the tropics. The eggs are smooth and oval, and the larvae stout with a more or less dense clothing of secondary hairs which obscure the primitive setae. They are often provided with lateral downwardly directed hair-flanges, and hairy subdorsal tufts or dorsal humps on the anterior segments. The full number of abdominal limbs is present, and the crochets are biordinal, arranged in a mesoseries. The pupae resemble those of the Bombycidae but differ in the presence of an epicranial suture and in the labial palpi being unconcealed. The body is provided with numerous setae and there is no cremaster. A dense, rather firm, oval cocoon of hair and silk is commonly present and met with above ground. *Lasiocampa* is a small genus of large moths common in Europe and its species are usually swift fliers in sunshine: most members of the family, however, are nocturnal. *Malacosoma neustria* is the Lackey Moth of Europe, whose larvae live gregariously in webs during their earlier stages, and are very destructive to the foliage of fruit trees. The larvae of *M. americana* have a similar habit and are commonly known as 'tent-caterpillars', their webs measuring 2 feet or more in length.

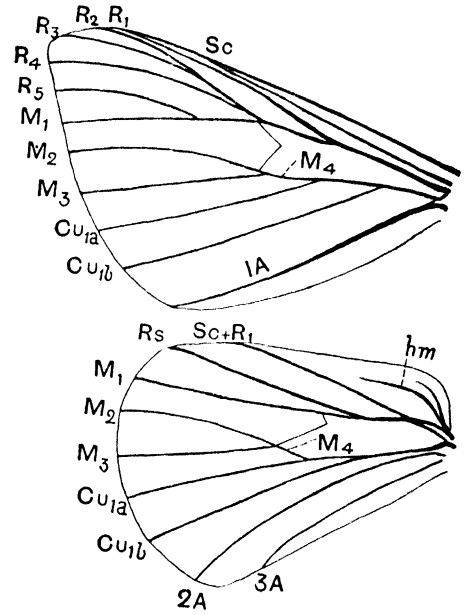


FIG. 422.—*Malacosoma neustria*, venation

FAM. SATURNIIDAE.—In this family (which includes the Hemileucidae) the antennae are prominently bipectinate in both sexes, the rami being longest in the males; the labial palpi are minute and there is no frenulum. It includes a number of large, or very large, tropical insects with but few representatives in temperate regions: almost all are characterized by a transparent eye-spot near the centre of each wing. The only British species is the Emperor moth *Saturnia pavonia*: *S. pyri* is the largest European Lepidopterous insect. *Attacus* ranges from Mexico and S. America to Africa, and throughout the Oriental region to Japan. *A. atlas* (Fig. 423) and *A. edwardsi* are among the largest moths in the world, the females having a wing-expanse of about 25 cm. Saturniid larvae are very highly specialized (Fig. 424):

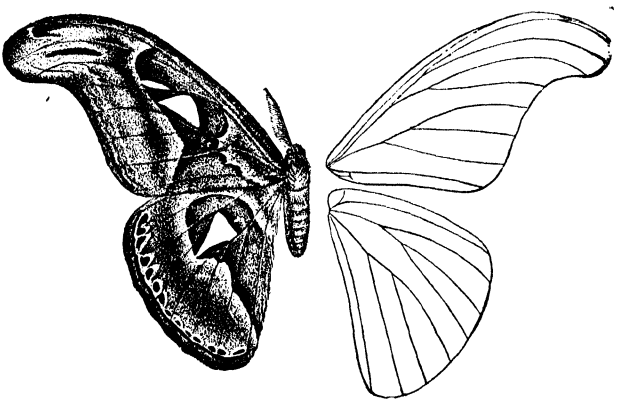


FIG. 423.—*Attacus atlas*, male, India × 23
After Hampson (F.B.I.).

they are stout and smooth and differ from most other families in possessing scoli or at least rudiments thereof. The position and number of the scoli vary very greatly in different genera, and for a detailed study of their arrangement reference should be made to Fracker's paper (1915); in *Saturnia* they are subequal in size on all the segments. The pupae have the antennae broadly pectinate in both sexes, with the axis of the flagellum very prominent. The maxillae are always short, not more than $\frac{1}{3}$ the length of the wings, and the cremaster, if present, is very short. A dense firm cocoon is always formed and is very characteristic of the family: several species yield silk of commercial value. *Antheraea yamamai* is the Japanese oak silkworm which is reared on a large scale in that country, and was introduced into Europe in 1861. *A. pernyi*, the Chinese oak silkworm, yields Shantung silk which is pale buff in colour and largely exported. *A. paphia* and *assama* are polyphagous forest-inhabiting insects. *A. paphia* is uni- or bivoltine and very distributed through the oriental region: it yields the brownish Tasar silk. *A. assama* is a multivoltine semidomesticated species chiefly found in Assam: it yields Muga silk which is mainly used locally. *Philosamia ricini* and *P. cynthia* are very closely related multivoltine species. The former is extensively domesticated and its larvae are reared on *Ricinus communis*. It yields Eri silk which is white or brick-red but not reelable, and is mainly used locally in Assam and Bengal. *P. cynthia* occurs wild in India and China but is also domesticated and has been introduced into various parts of the world including Europe and N. America. *Telea polyphemus* (N. America) also yields silk which can be commercially utilized. The biology of a number of species is described by Wailly (1896–1897) and for a full account of the Eri silkworm see Lefroy & Ghosh (1912). A good deal of information will also be found in Packard's monograph (1914) of the North America Saturniidae and in a paper by Michener (1952).

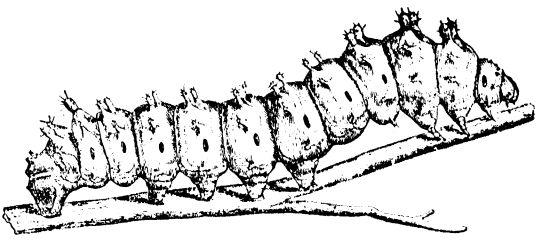


FIG. 424.—*Platysamia cecropia*, larva
After Riley.

FAM. BRAHMAEIDAE.—A very small group of tropical moths related to the Saturniidae, but readily distinguishable by the presence of a proboscis, and the large upturned labial palpi. They are large, sombre-coloured insects with very complex wing-patterns, and the antennae are bipectinated in both sexes. *Brahmaea* occurs in Africa and through southern Palaearctic Asia to China: the life-history is described by Packard (1914).

FAM. CITHERONIIDAE (Ceratocampidae).—Large or medium-sized moths

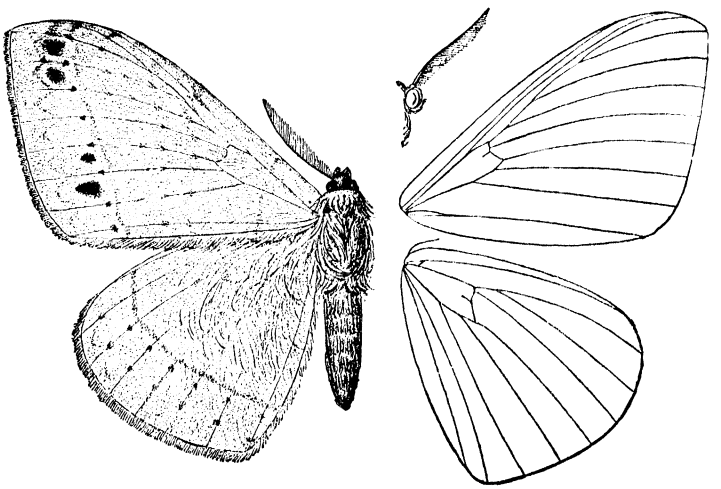


FIG. 425.—*Eupterote fabia*, male, India. ×
After Hampson (F.B.I.).

with stout hairy bodies, and powerful wings. The antennae are bipectinate for about half their length only, and both proboscis and tibial spines are present. The family is a small one, unknown in Europe, but well represented in N. America. The larvae are thinly hairy, and are armed with unbranched scoli on the 1st to 6th abdominal segments, and a large mediodorsal scolus on the 8th segment. The pupae are roughened with spines on the thorax and abdomen, the metathorax is provided with oblong lateral tubercles, and the cremaster is bifurcate. Transformation occurs in the ground, no cocoon being formed. For a monograph of the family vide Packard (1905; 1914): keys to the larva are given by Fracker (1915), and the pupae have been studied by Mosher (1914).

FAM. LACOSOMIDAE (Perophoridae).—These insects are moderate sized rather stout-bodied moths found in N. and S. America. Their affinities are doubtful and they have been placed as exceptional members of the Drepanidae or Psychidae. They are remarkable on account of the larval habit of making suspended protective cases of the leaves of the food-plants. In some instances the case is only constructed by the mature larva, the latter living previously under a web, and in at least one species the larva constructs a covering of its own excrement. There is a considerable literature on these larvae and further information is given by Sharp (1899: 378). The life-history of *Lacosoma chiridota* is described by Dyar (1900).

FAM. BOMBYCIDAE (including **Eupterotidae**).—In this group a frenulum is usually present in *Eupterote* (Fig. 425) and its allies and absent in *Bombyx* and related genera. None is British and the family is mainly Ethiopian and Oriental. The antennae are markedly pectinate in both sexes and the larvae are of two types. In *Eupterote*, etc., they are tufted with long hair and secondary setae are always numerous, but distinct verrucae are wanting. In *Bombyx* and its allies the larvae are glabrous and elongate, usually with a mediodorsal horn on the 8th abdominal segment: they form dense silken cocoons. The larva of *Bombyx mori* is the well-known silkworm, an inhabitant of China which has been introduced into many parts of the world for commercial purposes. It is now entirely domesticated and is not known in the wild state. A number of local races exist, and these have been regarded by Hutton, Cotes and others as distinct species. They differ chiefly in the number of annual broods which are largely dependent upon climate. The natural food in all cases is the leaves of mulberry, and the silk produced is white or yellow.

The **Lemoniidae** includes the genus *Lemonia* with ten Palaearctic species. In the adults, the claw of the fore leg is much enlarged. The **Endromididae** also require mention: the family includes only one species *Endromis versicolor*, which is a rather large day-flying moth, widely distributed in N. and C. Europe but extremely local in Britain. It frequents the vicinity of woods, its larvae feeding on birch and other trees. Seitz also includes with it the anomalous species *Mirina christophi* of Amurland.

Superfamily **Calliduloidea**

Maxillary palpi and tympanal organs absent. Frenulum present though small. Proboscis present. Antennae simple or pectinate. Chaetosema present. Cu_2 absent from both wings. Fore wing with M_2 basally approximated to M_3.

Table of families:

1. Moths with the appearance of a Geometrid. Hind wing with Sc + R_1 remote from Rs beyond the cell . . . . . PTEROTHYSANIDAE
–. Moths resembling small butterflies. Hind wing with Sc + R_1 approximated to Rs beyond the cell . . . . . CALLIDULIDAE

The **Pterothysanidae** include slender moths with large wing-expanse bearing a resemblance to Geometridae. They are chiefly African, but the genus *Pterothysanus* inhabits the eastern Orient and is easily recognized by the long double hair-fringe which adorns the inner margin of the hind wings. The related family **Callidulidae** are day-flying moths, bearing a close resemblance to certain Thecline or other butterflies. The family is essentially Oriental and does not occur in Europe.

Superfamily **Papilionoidea** (Fig. 400)

Antennae slender with an abrupt club. Labial palpi moderately long, more or less rough-haired, terminal segment rather pointed. Maxillary palpi obsolete.

Fore wings with Cu_2 absent, M_2 arising from or above middle of transverse vein. Hind wings without frenulum: Cu_2 absent; $Sc + R_1$ arising out of cell near base, thence strongly curved and diverging.

This and the next superfamily together include those insects commonly known as butterflies and are frequently regarded as constituting a group (Rhopalocera) of equal systematic value to the whole of the remainder of the Lepidoptera or moths (Heterocera). There is, however, no scientific justification for according to these insects any higher rank than that of two superfamilies. They are characterized by the antennae being clubbed or dilated, the absence of a frenulum and by the humeral lobe of the hind wing being greatly developed. In other Lepidoptera the antennae are not clubbed or dilated except in infrequent cases, and in such instances a frenulum is present. *Euschemon* is often regarded as a moth and either given separate family rank or placed in the Castniidae. Recent research, however, indicates that it is probably the most archaic of all butterflies and a member of the Hesperiidae. A frenulum is present in the male but absent in the female and, as Tillyard has pointed out (1918), if the nature of the wing-coupling apparatus be the criterion relied upon, the male of *Euschemon* is a frenate moth and the female a butterfly! The Papilionoidea are a tolerably natural group, but there is no general consensus of opinion as to their phylogeny. Both Hampson and Meyrick regard them as being derived from the Pyraline family Thyrididae while other authorities derive them from the Castniidae.

Key to the families:

1. Anterior legs of male useless for walking 2
–. Anterior legs of male well-developed 3

2. Anterior legs of female useless for walking . . NYMPHALIDAE (p. 555)
–. Anterior legs of female well developed . . . . RIODINIDAE (p. 557)

3. Anterior tarsi of male more or less abbreviated or with one or both claws absent LYCAENIDAE (p. 558)
–. Anterior tarsi of male normal, claws developed 4

4. Hind wing with a single anal vein . . . . . PAPILIONIDAE (p. 559)
–. Hind wing with 2 anal veins . . . . . PIERIDAE (p. 558)

FAM. NYMPHALIDAE. The dominant family of the butterflies and one of the largest of all Lepidoptera, including about 5,000 described species. The fore legs in both sexes are reduced in size, usually folded on the thorax, and functionally impotent: the tibiae are short and clothed with long hairs, hence the name of 'brush-footed' butterflies.

The Danainae (Euploeiinae, Limnadidae) have the antennal club often but little pronounced, and the whole antenna is devoid of scales: the forefeet in the female terminate in a corrugate knob. The larvae are smooth and cylindrical, with two to four pairs of fleshy processes, at least on the mesothorax, and often on one or more of the abdominal segments. They are all very strikingly marked with black and yellow, red, or green. The imagines have developed what must be, to our senses at any rate, an acrid disagreeable odour and taste, accompanied with a leathery consistency of body which evidently protects them from insectivorous enemies. In the majority of forms secondary sexual characters in the form of androconia, tufts of hairs, etc., having peculiar odours, are prominent (Bingham). The subfamily occurs in all warmer regions and well-known genera are *Danais*, *Euploea* (Fig. 427), and *Amauris*.

The Ithomiinae differ from the Danainae in that the female has a true though somewhat shortened fore tarsus. The antennae are devoid of scales and the wings are elongate, often in great part translucent, and thinly scaled. The subfamily is Neotropical, and many species exhibit colour resemblances to the Heliconiinae or to the Pieridae.

The Satyrinae (Agapetidae) are a world-wide group which includes the common 'Meadow-browns', 'Heaths', 'Graylings' and 'Marbled Whites'. They are easily

recognizable by certain of the veins at the base of the fore wings being greatly swollen, and by the strongly adpressed palpi. They are small to medium-sized butterflies, frequently some shade of brown or tawny in colour, with a variable number of eye-like or annular spots. Their powers of flight are not greatly developed, and they are largely shade-loving insects, cryptically coloured on the underside. The larvae feed mostly upon Gramineae: they are fusiform and green, yellowish, or brown marked with longitudinal lines. In appearance they bear a resemblance to Noctuid larvae. The head is often bilobed or horned, the prothorax constricted, and the body is clothed with small papillae bearing short secondary setae. The segments are divided into annulets, and the suranal plate is bifurcate, bearing a pair of short backwardly directed processes. The pupae are similar in general form to those of the Nymphalinae but are devoid of tubercles, and have few prominent ridges. They are generally suspended by the cremaster, and there is no median silken belt: a few are subterranean and, in some cases, they construct a slight cocoon or cell. *Erebia* is characteristic of the Alps

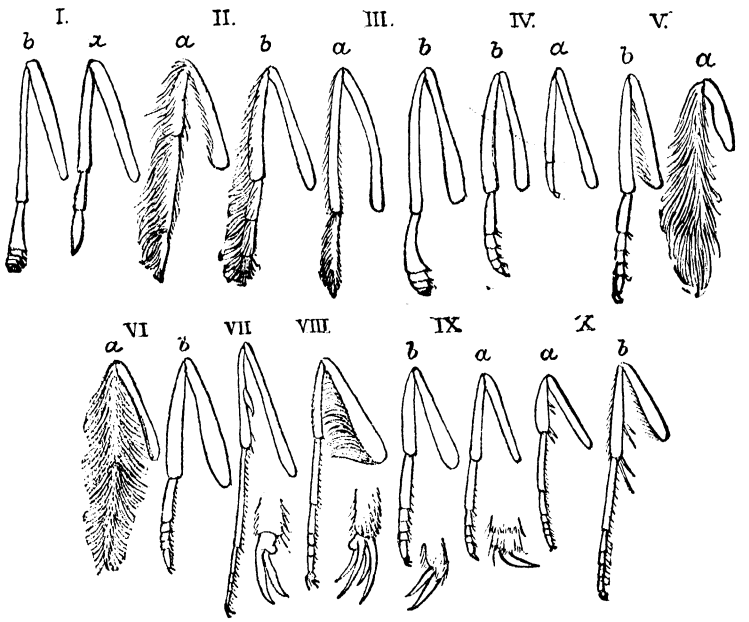


FIG. 426.—Fore legs of Papilionoidea

a, male; *b*, female. I, Danainae; II, Satyrinae; III, Nymphalinae; IV, Acraeinae; V, Libytheinae; VI, Riodinidae; VII, Papilionidae; VIII, Pieridae; IX, Lycaenidae; X, Hesperiidae. *After* Bingham (F.B.I.).

of Europe, but also occurs on the mountains of Asia, S. Africa and N. America: two species inhabit N. Britain. In *Melanitis* the bases of the veins of the fore wings are normal and not swollen. *M. ismene* extends across the southern half of Africa through the Oriental region to Australia: it has both wet and dry season forms and numerous local races. The Neotropical genera *Cithaerias* and *Haetera* have delicate transparent wings, with the scales almost wanting.

The Morphinae are exclusively tropical, and have the discal cell in the hind wings open; there is also a cradle-like depression along their inner margins for the reception of the abdomen. The species of *Morpho* are large, and have an extensive wing-expanse in proportion to the size of the body. They are brilliant metallic blue insects peculiar to the forests of tropical America. The eastern representatives of the group do not equal their S. American allies either in size or brilliancy.

The Brassolinae are likewise Neotropical, and are very large insects with the discal cell of the hind wings closed. They are deeply and richly coloured, and the under surface is marked with eye-spots and intricate lines. *Caligo* is one of the most familiar genera.

The Acraeinae are essentially African insects and the majority belong to the extensive genus *Acraea*: a few are Oriental and S. American. The wings are elongate and sparsely scaled, or more or less diaphanous. These insects appear to be largely

immune from insectivorous enemies in all stages, and the imagines readily exude a nauseous fluid. The females in certain species develop an abdominal pouch very much as in *Parnassius* (vide p. 559).

The Heliconiinae form one of the most characteristic groups of Neotropical butterflies and are peculiar to that region. The fore wings are about twice as long as broad; the fore tarsus in the male is elongate and single-segmented, and 4-segmented in the female. They are medium-sized insects, many of which are stated to be protected owing to possessing nauseous or evil-smelling properties. They are closely related to the Nymphalinae in all their stages, but the imagines are readily distinguished by the closed discal cell.

The Nymphalinae constitute the largest of the subfamilies: the discal cell in both pairs of wings is very often open or closed only by an imperfect veinlet. The palpi are large and usually broad anteriorly. The fore tarsi in the male are unjointed and in the female four or five segments are present. In Britain, as in most parts of the world, they constitute the dominant group of butterflies and include the 'Fritillaries' (*Argynnis*, *Brenthis* and *Melitaea*); the 'Tortoiseshells' and 'Peacock' (*Nymphalis*); the 'Purple Emperor' (*Apatura*) and other familiar insects. The larvae are almost always cylindrical and armed with numerous scoli. In *Apatura* and *Charaxes* they are smooth with tentacle-like processes on the head, and a pair of posteriorly directed anal processes. Müller (1886) gives a very complete account of the metamorphoses of many Brazilian species, and discusses the significance of colour pattern and its relation to the scoli. The pupae are very characteristic and are often armed with prominent tubercles on the surface of the body: there are usually seven rows on the abdomen, and there is a pointed projection on either side of the head in many species. The pupa is suspended head downwards by the cremaster, unsupported by a median girdle. Among the more notable species may be mentioned the central European *Araschnia levana* which produces two annual generations so dissimilar that they were formerly regarded as the two species, *A. levana* and *A. prorsa*. *Vanessa cardui*, the 'Painted Lady', is probably the widest distributed of all Lepidoptera. *Apatura* occurs over the northern hemisphere, and is represented in Britain by *A. iris*, which is local in oak woods of the southern counties. The Indo-Malayan *Kallima* includes the 'leaf butterflies', remarkable on account of the extraordinarily perfect resemblance to leaves which is exhibited by the under surface of the closed wings. *Charaxes* includes large butterflies very widely distributed through the eastern hemisphere to Australia, and the hind wings are produced at veins M_3 and Cu_{1b} into long slender tails.

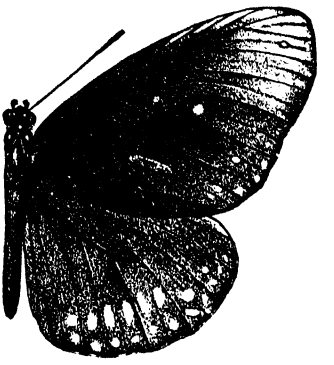


FIG. 427.—*Euploea godarti*, male. India × $\frac{1}{1}$
After Bingham (F.B.I.).

FAM. RIODINIDAE (Erycinidae, Nemeobiidae).—An extensive family comprising over 1,000 species which are characteristic of the Neotropical region. A few species are found in the United States and approximately 100 occur in the eastern hemisphere. For the most part they are small butterflies, with short broad fore wings, and the fore legs in the male are imperfect and brush-like, with one segmented tarsi devoid of claws: in the female the fore legs are functionally perfect but distinctly smaller than the remaining pairs. The vast majority of the species belong to the subfamily Nemeobiinae which has a single European representative, *Nemeobius* (= *Hamearis*) *lucina*. The latter insect extends its range into Britain where it is local but not rare. The Libytheinae may be easily recognized by the very long and closely approximated porrect palpi. The widely distributed genus *Libythea* includes a single Palaearctic species *L. celtis*, which occurs in central Europe. The affinities of this subfamily have given rise to much discussion, and certain authorities relegate it to the Nymphalidae while others regard it as forming a separate family. The Nemeobiinae on the other hand are more nearly related to the Lycaenidae. The larvae of the Libytheinae bear considerable resemblance to those of Pieridae: each segment is divided into annulets, and numerous secondary setae are present. The pupae are short and smooth and suspended perpendicularly. Larvae of the Nemeobiinae exhibit marked diversity of form: in some cases they are onisciform, attenuated at the extremities, and covered with a variable development of secondary setae. Both larvae and pupae resemble those of the Lycaenidae rather than any other family.

FAM. LYCAENIDAE (Blues, Coppers, Hair-streaks).—A family of small to moderate-sized butterflies well represented in most regions. Over 280 species are Palaearctic, and 18 have been recognized as British, though several are either no longer met with or are casual and extremely rare. The predominant colour of the upper surface of the wings is metallic blue or coppery, dark brown, or orange; on the under side coloration is more sombre, with dark-centred eye-spots or delicate streaking. The antennae are ringed with white and a rim of white scales surrounds each eye; the hind wings are frequently provided with delicate tail-like prolongations. The legs are all functional and used for walking but, in the males, the anterior tarsi are more or less abbreviated, or with one or both claws wanting. The sexes frequently exhibit great differences in coloration; thus in *Lysandra corydon*, the male is pale shining blue and the female iridescent brown. The great majority of the larvae are onisciform, tapering towards the extremities, and with broad projecting sides concealing the limbs (Fig. 428). This type of body-form resembles that of *Zygaena* more than of any other Lepidoptera. Secondary setae are usually numerous, but some larvae are smooth or dorsally corrugated; many are clothed with a short pile, others are armed with bristle-bearing verrucae and a few are hairy. The pupa is relatively short and stout, anteriorly rounded, and with little or no freedom of motion in the abdominal segments, which fit together to form a smooth surface. Generally it is attached at the anal extremity and secured by a central girth of silk: there are, however, a number of exceptions and in some cases the pupa is subterranean. For an account of the metamorphosis of several species of the family the student is referred to a series of papers by Chapman (1911–20). The larvae in some cases are known to be carnivorous: that of *Gerydus chinensis* feeds upon aphids in China (Kershaw, 1905). *Maculinea arion* (Europe) is phytophagous up to the last instar when it enters nests of *Myrmica* and becomes carnivorous preying upon the ant larvae (Chapman, 1916). The larva of the American *Feniseca tarquinius* is wholly carnivorous feeding upon woolly aphids (*Eriosoma*, etc.), while that of *Spalgis epius* is recorded by Green as preying upon coccids. Larvae of other species are frequently sought after by ants, who use their antennae to stroke them and induce them to yield drops of fluid secretion. The latter is apparently the product of a dorsal gland situated on the 7th abdominal segment (vide Hinton, 1951). The Indo-Australian *Liphyra brassolis* (Fig. 429) is the most remarkable member of the family, being totally unlike other forms in any of its stages (Chapman, 1902; 1903). Its larva is flattened, and has a very hard smooth sclerotized covering, devoid of evident segmentation: the jaws are sharply toothed and adapted for tearing and piercing rather than mastication. This curious larva is found associated with *Oecophylla smaragdina* and is believed to prey upon the brood of the latter, its hard covering serving as a protection against the ants. Pupation takes place in the larval skin: the pupa shrinks away from the cuticle and is loosely enclosed in the puparium thus formed. The newly emerged imago is covered with a number of loosely attached scales which may serve as protection against the ants, as they certainly cause the latter trouble when enveloped by them (Dodd, 1902). *Euliphyra mirifica* similarly frequents nests of the same ant in W. Africa, and its greatly modified larva has been described by Eltringham (1913).

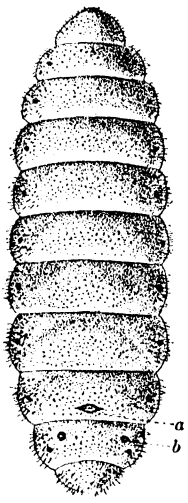


FIG. 428.—A Lycaenid larva

a, aperture of gland; *b*, one of the pairs of extensile organs. *After* Wheeler, 'Ants'.

FAM. PIERIDAE (Whites, etc.).—Included in this family are some of the very commonest of all butterflies; they are mostly of medium size and usually either white, yellow or orange marked with black. The six legs are well developed and similar in both sexes, and the claws of the feet are bifid or toothed. Several taxonomists have united this family with the Papilionidae, to form a single group, but the distinctness of the characters in the two cases does not appear to warrant this procedure. The larvae are rather elongate with the segments divided into annulets, and the body bears numerous secondary setae varying in size: the crochets are bi- or tri-ordinal arranged in a mesoseries. The larvae are further characterized by the absence of osmeteria, fleshy filaments and cephalic or anal horns.

The pupae are suspended in an upright position attached by the caudal extremity and a central band of silk: they may be readily distinguished by the single median cephalic projection or spine, and the hind wings are not visible ventrally (Mosher).

Pieris includes the common White or Cabbage butterflies whose larvae, in several species, are extremely destructive to cruciferous vegetables in Europe and N. America. In this respect *Pieris rapae* is probably the most injurious of all butterflies. Larvae of other members of the family feed chiefly on plants belonging to the Leguminosae and Capparidaceae. *Euchlöe* and *Synchlöe* include the 'Orange Tips', *Colias* the 'Clouded Yellows' and *Gonepteryx* the 'Brimstones' or 'Sulphurs': all are characteristic of the northern hemisphere. Certain species of Pieridae have the habit of migrating in large numbers, which has attracted the notice of travellers in many parts of the world. No satisfactory reason for these flights has been put forward: clouds of butterflies chiefly of *Appias* and *Catopsilia* may stream past the observer for hours at a time, all going in one direction (Bingham).

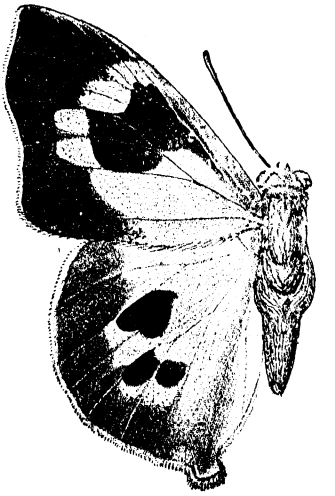


FIG. 429.—*Liphyra brassolis* × $\frac{1}{1}$
After Bingham (F.B.I.).

FAM. PAPILIONIDAE (Swallow-tails).—An extensive family of pre-eminently tropical butterflies including some of the most magnificent of all insects. About 600 species are known; less than 70 of these are Palaearctic, and about 30 range into America north of Mexico. In the British Isles the sole representative is *Papilio machaon* which is local and now restricted to certain fenny districts in East Anglia. The wings of these insects are extraordinarily variable in shape and, in the majority of species, the hind pair is provided with conspicuous tail-like prolongations which are marginal extensions in the region of vein M_3. The prevailing ground colour is generally black, strikingly marked with shades of yellow, red, green or blue. The larvae are smooth or provided with a series of fleshy dorsal tubercles or sometimes with a raised prominence on the 4th segment. Except in *Parnassius*, in which secondary setae and verrucae are evident, the body is practically devoid of setae. An osmeterium is situated on the prothorax (vide p. 526) and when retracted its presence is revealed by a dorsal groove through which it is everted. The pupae are variable in form: the head bears two lateral cephalic projections and the hind wings are visible ventrally. Suspension takes place at the caudal extremity in an upright position, and the pupa is further secured by a median silken girdle. In *Thais* there is a cephalic as well as an anal attachment and *Parnassius* is exceptional in that the pupa is not suspended but occurs in a slight silken web among leaves. The imagines of many species of the family have the sexes extraordinarily different both in form and colour, and often in habits also. In numerous instances the females are polymorphic while, in other cases, this peculiarity extends to both sexes. As examples may be mentioned the Oriental *Papilio memnon* which has three distinct forms in each sex and two of these in the

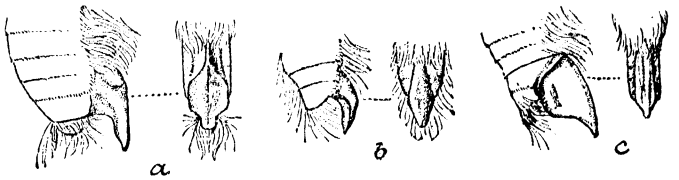


FIG. 430.—Anal pouches (ventral and lateral aspects) of three species of *Parnassius*
After Bingham (F.B.I.).

female are tailless. The North American *Iphiclides ajax* has three distinct seasonal forms, viz. those appearing in early spring, late spring and summer. The African *Papilio dardanus* is represented by different races or subspecies in various regions of that continent, and each of these possesses from one to five different forms of the female which, for the most part, are close mimics of certain Danaine butterflies. The greater number of the species of the family are included in the genus *Papilio*: those of the *Ornithoptera* group comprise the finest of all butterflies and they form the subject of a sumptuous monograph by Rippon (1890–1910). In the oriental genus

Leptocircus the fore wings have a transparent scaleless band, and the tails are exceedingly long. *Parnassius* occurs in the mountains of the Holarctic region chiefly in Central Asia. Both pairs of wings are diaphanous, with few scales, and the tails are wanting. During copulation the females develop a corneous anal pouch exhibiting specific variations in form (Fig. 430). This genus also differs from other Papilionidae in its venation and metamorphosis and, for this reason, is sometimes placed in a family of its own.

Superfamily **Hesperioidea**

Antennae dilated apically to form a gradual club which often ends in a hook, bases remote. Labial palpi more or less rough-haired, maxillary palpi wanting. Fore wing with Cu_2 wanting, M_2 arising from or below middle of transverse vein, none of the veins stalked and Rs with four branches. Hind wing with no frenulum except in male of Euschemon, *Cu_2 absent, $Sc + R_1$ arising out of cell near base, then rapidly diverging.*

FAM. HESPERIIDAE (Skippers).—These insects derive their popular name from their erratic darting flight which is different from the more sustained aerial evolutions of other butterflies. They form an extremely large family, generally distributed, but not ranging into New Zealand (vide Mabille & Boullett, 1909; also Mabille, 1903). Reuter regards this family as constituting a suborder—the Grypocera, but this view is based upon an exaggerated value ascribed to their distinguishing features. The antennae are relatively widely separated at their bases, and their apices are generally prolonged beyond the club to form a small recurved point. The abdomen is stout, the wings are proportionately less ample than in most butterflies, and the venation of a markedly distinct type. As a general rule the larvae are moderately stout and taper towards both extremities; secondary setae are small, or absent dorsally, and the crochets are tri-ordinal arranged in a circle. In the Hesperiinae the head is large and attached to a strongly constricted 'collar' while in the Megathyminae it is small and partially retractile (Fracker). They frequently live concealed, drawing together leaves by means of silk, or inhabit webs or galleries: those of the Megathyminae are borers. The pupa is devoid of angular points or projections and is usually enclosed in a slight cocoon among leaves: in other cases it is exposed and attached by the caudal extremity, and also by means of a median band of silk. The eggs are spherical or oval, flattened beneath, smooth or reticulated, and sometimes ribbed (Meyrick). The vast majority of the species belong to the Hesperiinae and eight are indigenous to Britain. The Megathyminae include the Giant Skippers which have the apex of the antennae devoid of a recurved point, and the wing-veins are peculiarly specialized and greatly strengthened in the male. The group is mainly a tropical one and unrepresented in the Palaearctic region. The Euschemoninae are often regarded as a family of moths, the males possessing a frenulum. *Euschemon* is the most archaic of all butterflies and according to Tillyard (1919) its larvae and pupae exhibit definite Hesperiid characters.

Superfamily **Geometroidea**

Maxillary palpi vestigial or atrophied. Tympanal organs in abdomen. Cu_2 absent from both wings: fore wings almost always with M_2 not nearer M_3 than M_1 at base and with $1A + 2A$ forming a basal fork.

Table of families:

1. Tympanal organs in the 7th abdominal segment . . AXIIDAE (p. 561)
–. Tympanal organs in the 1st or 2nd abdominal segment 2

2. Hind wing with Sc + R_1 approximated or partly joined to Rs beyond the cell. Tympanal organs dorsal 3
–. Hind wing with Sc + R_1 remote from Rs beyond the cell. Tympanal organs ventral, except male Uraniidae 4

3. Fore wing with M_2 basally approximated to M_3 . . DREPANIDAE (p. 561)
–. Fore wing with M_2 not nearer to M_3 than to M_1 at base CYMATOPHORIDAE (p. 561)

4. Fore wing with $R_4 + R_5$ remote from $R_2 + R_3$ and usually stalked with M_1. 5
–. Fore wing with R_{4+5} connected with $R_2 + R_3$: hind wing with Sc + R_1 furcate at extreme base . . . . . GEOMETRIDAE (p. 561)

5. Frenulum absent. Tympanum of male at sides of tergite 2 . URANIIDAE (p. 562)
–. Frenulum present . . . . . EPIPLEMIDAE (p. 562)

Note. The small family **Sematuridae** with a few, mostly Neotropical species is sometimes considered allied to the Uraniidae, although it has no tympanal organs. The **Axiidae** include about 10 Mediterranean species.

FAM. DREPANIDAE (Drepanulidae: Hook Tips).—A rather small family mainly developed in the Indo-Malayan portion of the Oriental region. Its members exhibit considerable diversity of structure and, as a rule, have the apex of the fore wing falcate. The eggs are rounded-oval with the surface finely punctured. The larvae are somewhat slender without the claspers on segment 13, and the anal extremity is prolonged into a slender projection which is raised in repose; certain of the other segments are often humped. The pupa is enclosed in a cocoon, usually among leaves above ground. *Drepana* is the chief genus with 9 Palaearctic species. *Cilix* has the fore wings non-falcate, the frenulum is vestigial and there is no proboscis; *C. glaucata* is the only species and is Holarctic in distribution.

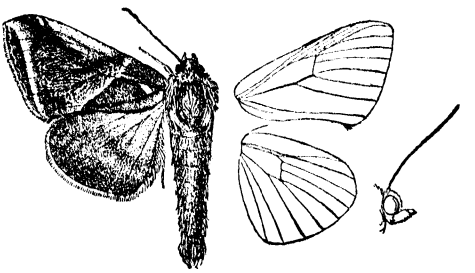


FIG. 431.—*Habrosyne derasa*, male, Palaearctic region. × $\frac{1}{1}$
After Hampson (F.B.I.).

FAM. CYMATOPHORIDAE (Polyplocidae).—A relatively small family resembling the Noctuidae and mainly restricted to the northern hemisphere. Thirteen genera are Palaearctic, four being represented by common species in the British Isles, the most familiar being the 'Buff Arches' (*Habrosyne derasa*: Fig. 431) and the 'Peach Blossom' (*Thyatira batis*). The larvae are cylindrical and bear no secondary setae: the abdominal feet carry biordinal crochets arranged in a curved mesoseries, and the claspers are reduced in size. Pupation occurs in a rather slight cocoon among leaves.

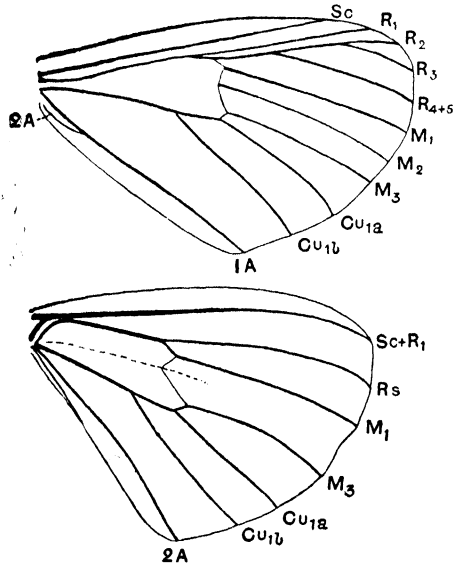


FIG. 432.—*Abraxas grossulariata*, venation

FAM. GEOMETRIDAE (Carpets, Waves, Pugs, etc.).—A very large family consisting of some 12,000 species which are almost always of slender build with relatively large wings (Fig. 432). Their flight is never strong and, when at rest, the wings are often laid horizontally. Both frenulum and proboscis are generally present, but in a few cases either the one or the other may be wanting. In some genera the females have greatly degenerate wings or are completely apterous as in *Alsophila*, *Operophtera*, *Erannis* and *Apocheima* and its allies. The larvae are elongate and usually very slender: as a rule abdominal legs are only developed on the 6th and 10th segments and progression takes place by drawing the posterior somites close to those of the thorax, the body thus forming a loop. The whole body is then extended in the direction desired and the looping action repeated. In some instances abdominal legs appear on segments other than those normally carrying them. Thus in *Colotois pennaria* a pair is present on the 5th segment but disappears with the fourth moult while in *Alsophila*

aescularia they are developed on the same segment and persist throughout the larval period. In *Brephos notha* Sharp states that rudimentary abdominal feet are present on the 3rd to 5th segments in the newly hatched larva, but attain greater development when the latter is fully grown. It is evident that in this species the larva is much more a Noctuid than a Geometrid in its morphology. The vast majority of the larvae of the family bear an exceedingly close resemblance to twigs, or the thicker veins of leaves, and can only be detected with difficulty when at rest. In the pupa there are no maxillary palpi, the first two pairs of legs are longer than in most other Lepidoptera, and there is often a deep dorsal furrow between the 9th and 10th abdominal segments. A slight cocoon is spun between leaves or the pupa is subterranean. The family is divided into six subfamilies by Hampson while Meyrick (1928) regards each division as constituting a separate family under a different name. Over 3,000 species occur in the Palaearctic region and, of these, about 270 are British. In *Boarmia*, and its allies, a fovea is present on the underside of the fore wing at the base of the anal region; it is generally confined to the male, is often hyaline and sometimes glandular. This structure is present in many species, and it is suggested by Meyrick that it may be a scent-producing organ. The posterior tibiae, also in the male, are often enlarged and contain an expansible tuft of hairs. *Brephos*, *Alsophila* and a few other genera are regarded by Meyrick as being the most primitive of all Geometers and constitute his family Monocteniadae. *Brephos* has also been referred to a family of its own, while other authorities have regarded it as a Noctuid. The larvae of *Paleacrita* are known as Canker Worms which are pests of fruit and shade trees in N. America. Those of the Winter Moth (*Operophtera brumata*) and of species of *Erannis* are well-known defoliators of similar trees in Europe.

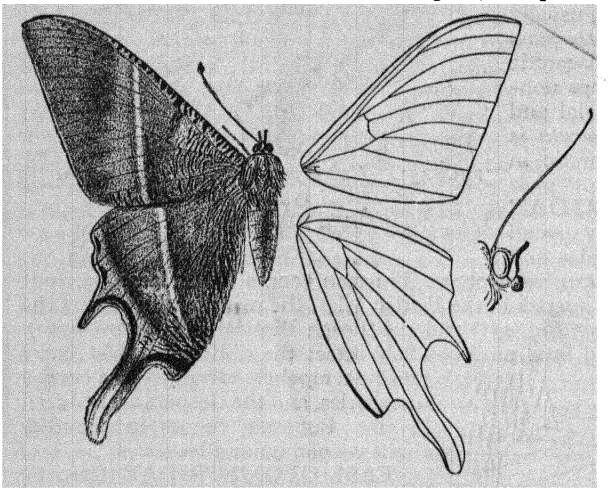


FIG. 433.—*Nyctalaemon patroclus*, male, India. × ½
After Hampson (F.B.I.).

FAM. URANIIDAE.—A very widely distributed but exclusively tropical family occurring in both the old and new worlds. They are often large slender-bodied moths, many of which are diurnal in habit. *Chrysiridia*, *Nyctalaemon* (Fig. 433) and *Urania* include exquisitely coloured insects resembling Papilionid butterflies: others bear a likeness to Geometrid moths. The larvae exhibit great diversity of structure but have the full number of abdominal limbs (Hampson, 1895; Gosse, 1881): in two genera they are known to feed on Euphorbiaceae. Those of *Nyctalaemon* and *Epicopeia* are figured by Hampson: in *E. polydora* (Himalaya) the body is invested with a thick covering of long white cottony filaments. In *Chrysiridia ripheus* there is an armature of black spatulate processes (Eltringham, 1924). The pupae are enclosed in loosely woven, silken cocoons. The Asiatic genus *Epicopeia* has a vestigial frenulum and is often relegated to a separate family—the Epicopeiidae—which has been monographed by Janet & Wytsmann (1903).

FAM. EPIPLEMIDAE.—A group of about 550 inconspicuous species, only doubtfully separate from the Uraniidae. They occur on all continents but are best developed in Papua and adjacent islands. They commonly rest during the day with the fore wings rolled up in a peculiar manner while the hind pair is applied to the sides of the body: in this attitude they resemble spiders.

Superfamily **Sphingoidea**

Antennae gradually thickened into a club with the apex pointed and usually hooked. Proboscis and frenulum almost always strongly developed. Cu_2 absent

from both wings. Fore wing with M_1 from stem of R_{3-5} or basally approximated to it. Hind wing with $Sc + R_1$ connected with cell by a cross-vein (R_1) and approximated to Rs beyond the cell. Tympanal organs absent.

A somewhat isolated group with a single family whose affinities lie toward the Notodontidae.

FAM. SPHINGIDAE (Hawk Moths).—An important family of moderate-sized to very large moths, including at least 1,000 species, which are distributed over almost the whole world. It is essentially a tropical group which is represented in the British Isles by 8 genera and 17 species. *Celerio lineata* is cosmopolitan and others such as *Acherontia atropos*, *Daphnis nerii* and *Herse convolvuli* (Fig. 434) have a very wide geographical range. The imagines are easily recognizable by the elongate fore wings and their very oblique outer margin. The antennae are thickened towards or beyond the middle and are pointed at the apices which are nearly always hooked: in the male the antennae are ciliated with partial whorls. The proboscis may be developed to a length which is not attained by any other Lepidoptera, but it is very variable. In *Cocytius* (tropical America) it measures 25 cm. long while the opposite extreme is found in *Polyptychus* in which it is reduced to a pair of tubercles. The frenulum and retinaculum are present in all generalized forms, but in some instances they are reduced or vestigial. In the Humming Bird Moths (*Macroglossa*) and the Bee Hawk Moths (*Hemaris*) the apex of the abdomen is provided with an expansile, truncated tuft of hairs. In the latter genus the disc of the wings is transparent, the fugitive scales present on newly-emerged specimens being very quickly lost. Sphingidae have an exceptionally powerful flight and hover over flowers as they feed on the wing: most are crepuscular and nocturnal but a few (*Macroglossa*, *Hemaris*, etc.) are diurnal.

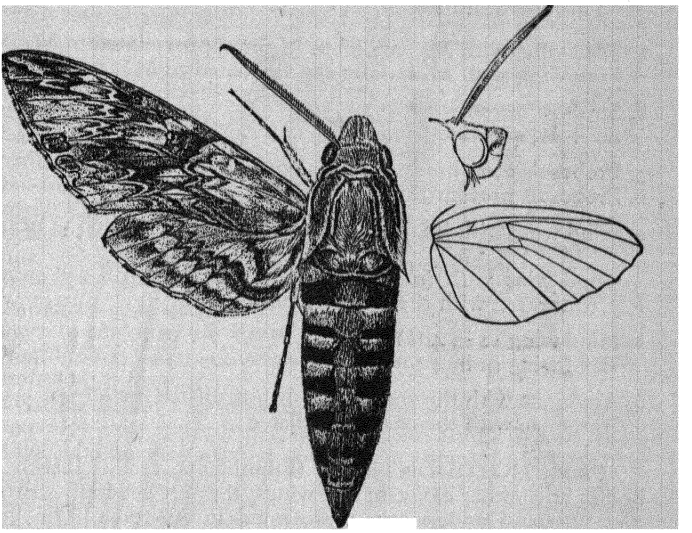


FIG. 434.—*Herse convolvuli*, male and venation of hind wing. × ½
After Hampson (F.B.I.).

The larvae are smooth, or with a granulated skin, but the latter feature is often only present in the first instar. The 8th abdominal segment almost always bears an obliquely projecting dorsal horn—relatively longer in the first than the later instars. The pupa occurs free in a cell in the ground, or in a very loose cocoon on the surface, between leaves, etc. The 5th and 6th abdominal segments are free and there is always a cremaster. Various methods of accommodating the proboscis are noticeable in the pupa and in some genera this organ projects from the body in a conspicuous manner so as to resemble the handle of a pitcher.

The Death's Head moths (*Acherontia*) are remarkable in several respects: the imagines have been noted to enter beehives to rob them of honey, and they possess the faculty of sound production. The note emitted is a shrill chirping sound and many hypotheses have been advanced to account for it. The literature thereon is fully discussed by Tutt (1899); the sound was originally attributed to friction but it seems probable that the real cause is the forcing of air through the proboscis, though the source of the air has not been ascertained (Rothschild & Jordan). The imago is occasionally audible before emergence from the pupa, but the larva emits a different

type of sound. Most observers agree that when irritated it produces a series of rapidly repeated 'cracking' notes resembling those emitted during the discharge of successive electric sparks, and the sounds are made by the mandibles when sharply brought together. The principal works on the family are those of Rothschild & Jordan (1903; 1907). For a general study of the larvae, consult Forbes (1911), while the larval colour changes and their significance are discussed by Piepers (1897); for the life-history of *H. convolvuli*, vide Poulton (1888).

Superfamily **Noctuoidea**

Maxillary palpi minute. Tympanal organs present in metathorax. Cu_2 *absent from both wings; fore wing usually with* M_2 *basally approximated to* M_3 *and with* $1A + 2A$ *not forming a definite basal fork.*

Table of families:

1. Fore wing with M_2 parallel to M_3 or approximated to M_1 . . . . . NOTODONTIDAE (p. 564)
–. Fore wing with M_2 basally approximated to M_3 2

2. Sc + R_1 fused with Rs . . . . . AMATIDAE (p. 565)
–. Sc + R_1 separate from Rs 3

3. Proboscis atrophied . . . . . LYMANTRIIDAE (p. 567)
–. Proboscis present 4

4. Hind wing with Sc + R_1 anastomosing with the cell to near or beyond the middle . . . . . ARCTIIDAE (p. 565)
–. Hind wing with (*a*) Sc + R_1 anastomosing with cell near the base only or (*b*) connected with the cell by a bar 5

5. Hind wing as in 4 (*b*) . . . . . HYPSIDAE (p. 568)
–. Hind wing as in 4 (*a*) 6

6. Antennae with the shaft more or less dilated distally . . . . AGARISTIDAE (p. 565)
–. Antennae with the shaft not dilated . . . . . NOCTUIDAE (p. 566)

FAM. NOTODONTIDAE (Prominents, etc.).—Insects with moderately stout bodies and rather elongate fore wings: they are generally distributed but absent from New Zealand and poorly represented in Australia. The imagines are exclusively nocturnal, and are often attracted to a light, otherwise the various species are usually only obtained as larvae. A large number of the larvae of this family are well figured by Packard (1896); they mostly feed exposed on trees and shrubs, seldom affecting herbaceous plants. According to Fracker all exhibit secondary setae on the abdominal limbs and, in some genera (*Phalera*, etc.), these setae are present on the body also. The anal claspers are frequently modified into slender processes which are erected when in repose: the latter habit is also exhibited by *Notodonta* which has the claspers unmodified. The pupa only exhibits a small proximal portion of the labial palpi, maxillary palpi are absent, and the maxillae do not reach the caudal margin of the wings: the abdomen is punctate and a cremaster usually present (Mosher). *Notodonta* is characteristic of the temperate regions of the northern hemisphere and in this genus, *Lophopteryx*, and others there is a tuft of projecting scales on the middle of the hind margin of the fore wings. *Stauropus* is Indo-Malayan with a single European species *S. fagi*: its larva is very remarkable on account of the great length of the 2nd and 3rd pairs of thoracic legs. The anal extremity is inflated and claspers are replaced by two slender processes. In repose both extremities are abruptly erected, and in the curious attitude thus presented the larva, when irritated, has been regarded by Müller as resembling a spider; when at rest it was compared by Birchall to a twig with unopened buds, and by other observers to a dead and crumpled leaf. The larva of *Dicranura vinula* is a very striking and familiar object: it is provided with a pair of roughened tubercles on the prothorax, and a prominent fleshy protuberance on the metathorax. The anal claspers are modified into a pair of long slender processes containing extensible filaments, and the histology and mechanism of these organs have been investigated by Poulton (1887). This larva, and also those of other members of the family, is provided with a ventral prothoracic gland (Latter, 1897) having the power of ejecting an irritating fluid. The latter in the case of *D. vinula*, has been found to

consist of formic acid. The pupa in this species, and in those of *Cerura*, is enclosed in a hard wood-like cocoon on the bark of trees. The escape of the imago is facilitated by the cocoon being thinner anteriorly and the labrum of the imago bears two sharply pointed processes used for scraping the inner surface of the cocoon, in order to break a way through. At the same time, a secretion of potassium hydroxide is produced from the mouth in order to soften the cocoon. The eyes, and median portion of the head of the pupa, persist as a shield protecting those same parts in the imago until emergence is effected (Latter, 1892; 1895).

FAM. AMATIDAE (Syntomidae).—This family comprises about 2,000 species and is most abundant in the tropics; no representatives are indigenous to the British Isles and *Syntomis phegea* is the commonest of the few European forms. They are small to medium-sized moths (Fig. 435), usually inactive and largely diurnal in habit. The proboscis is generally well developed, the labial palpi are small and porrect and the retinaculum bar-shaped. Although often included among the Zygaenidae, they appear to be nearest related to the Arctiidae. Many are brilliantly coloured, and a number of species bear a striking resemblance to Aculeata, Tenthredinidae and other insects (Kaye, 1913). The resemblance is heightened by the frequently basally constricted abdomen and the general shape and coloration; in many cases the wings have transparent areas devoid of scales. In the Neotropical genus *Trichura* the males of certain species are provided with a long filamentous appendage arising from the terminal abdominal segment. This structure attains a length equal to that of the whole body of the insect, but its significance appears to be unexplained. The larvae are short, and armed with verrucae bearing numerous setae and they closely resemble those of the Arctiidae. Pupation takes place in a cocoon of silk and felted hairs: according to Mosher the pupa of *Ctenucha* is indistinguishable from that of an Arctiid.

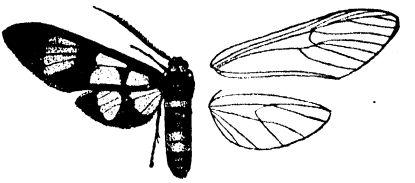


FIG. 435.—*Euchromia polymena*, male, India. × $\frac{1}{1}$

After Hampson (F.B.I.).

FAM. ARCTIIDAE (Lithosiidae: Tiger Moths, etc.).—An assemblage of usually stout-bodied moths, often with moderately broad wings, which are frequently conspicuously spotted, banded or otherwise marked with bright colours. Most species are nocturnal in habit and are attracted to a light. The family is tolerably well represented in nearly all zoogeographical regions, but attains its greatest development in the tropics. Over 3,500 species are known and, of these, 40 inhabit the British Isles. According to Meyrick *Callimorpha* (= *Panaxia*) is the most ancestral form, but it is placed by Hampson in the Hypsidae. In its general affinities the family comes nearest to the Noctuidae. It is noteworthy that species of several genera are known to be capable of sound-production, but the mechanism thereof has not been adequately studied.

The Arctiinae comprise the 'Tiger' and 'Ermine' moths with their allies. They are brightly coloured insects with extremely diverse patterns, and individual species exhibit an extraordinarily wide range of variation with respect to the latter. The extensive genus *Arctia* includes the common 'Tiger' Moth (*A. caia*) which extends through the northern Palaearctic region to Japan. *Utetheisa pulchella*, although casual in Britain, occurs through the greater part of the Old World including Australia. The larvae are clothed with dense long hairs which they utilize along with silk to construct their cocoons; those of the Palaearctic species hibernate and feed principally upon low herbaceous plants. The Lithosiinae include those moths which are popularly termed 'Footmen'; they are diurnal or crepuscular in habit and, in typical genera, the fore wings are long and very narrow. The larvae are sparsely hairy, and commonly feed upon lichens growing about tree trunks and in other situations. The Nycteolinae are a very small group which is sometimes regarded as a separate family (Cymbidae): they are frequently green insects found among the herbage of trees and shrubs. The larvae are never prominently hairy and the cocoon is boat-shaped. In *Pseudoips* (*Halias*) the larva is smooth and feeds in the open while in *Earias* it is hirsute and lives among rolled leaves, etc.; that of *E. insulana* is the destructive Egyptian Cotton Boll-worm, widely distributed in the tropics. The New World subfamilies Dioptinae and Pericopinae are regarded as constituting separate families by American entomologists.

FAM. AGARISTIDAE (Phalaenoididae).—A small family absent from Europe

and including over 60 genera embracing about 300 species. They are largely tropical, only two Palaearctic species being listed by Staudinger & Rebel; others occur in N. America and Australia. In general facies and vivid coloration they resemble the Arctiinae and many are diurnal in habit (Fig. 436). They are very similar to the Noctuidae in structure, and also in larval features, but their type of coloration and

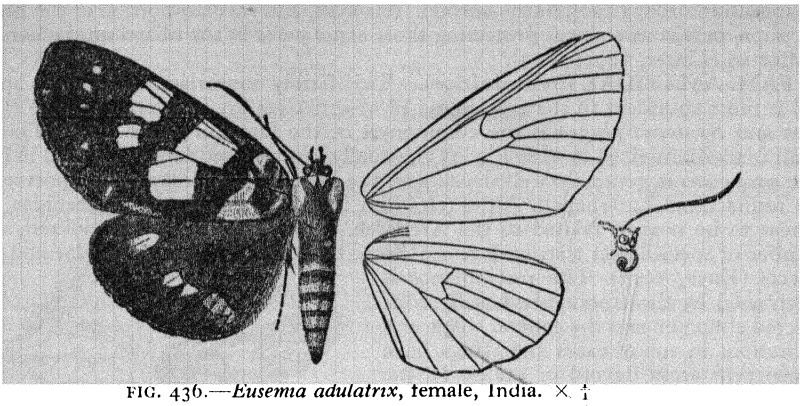


FIG. 436.—*Eusemia adulatrix*, female, India. × ½
After Hampson (F.B.I.).

antennal characters serve to distinguish them. According to Hampson (1892) in *Aegocera tripartita* a portion of the membrane of the anterior wing is dilated and ribbed; a clicking sound is produced during flight probably by friction on the greatly enlarged mid-tarsal spines.

FAM. NOCTUIDAE (Agrotidae).—This family includes a larger number of described species than any other group of Lepidoptera; about 1,800 are Palaearctic (cf., Kozhantshikov, 1937) and approximately 3,500 are known from N. America. They are eminently nocturnal insects attracted to a light and to the collector's sugar mixture, while *Plusia* and its allies frequent flowers at dusk. The family exhibits a monotonous similarity of structure particularly with regard to the venation and labial palpi; except in the Hyblaeinae maxillary palpi are vestigial. A frenulum is always present and the proboscis very rarely atrophied. The colour of the fore wings is nearly always cryptic and sombre, thus assimilating the insect to its surroundings (Figs. 437, 438). Being protected in this manner it passes the day resting with folded wings on tree-trunks, etc., to a large extent concealed from its enemies. In the larvae of the majority of species primary setae only are present, and the crochets are generally in a uniordinal mesoseries. There are usually four pairs of abdominal feet, but among the Catocalinae, Plusiinae, and Hypeninae the 1st pair, or the 1st and 2nd pairs, are more or less aborted and the larvae are semiloopers. Most of the larva feed upon foliage; they are often polyphagous and many are nocturnal while a few are stem-borers and live concealed. Among the more exceptional instances are the larvae of *Eublemma* which are predacious upon Coccoidea, those of *E. amabilis* being one of the most important enemies of *Laccifer lacca*. Species of *Cryphia* feed upon lichens; *Nonagria* lives in stems of marsh plants; *Parascotia fuliginaria* utilizes fungi growing on rotting wood; and larvae of *Hadena* often select the seed capsules of Caryophyllaceae. According to Mosher the pupae, with few exceptions, are characterized by the presence of labial palpi and of maxillae which extend to the caudal margin of the wings. Numerous genera have the prothoracic epimera exposed, and those lacking labial palpi possess

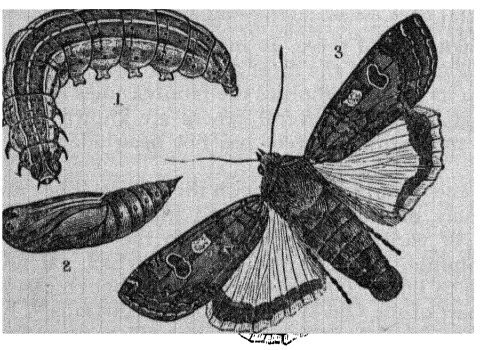


FIG. 437.—*Triphaena promba*, Europe
1, larva; 2, pupa; 3, imago × ½. *After* Curtis, 'Farm Insects'.

setae arranged around the scars of the larval verrucae as in Arctiidae. They differ from the latter, however, in that the cremaster bears hooked setae. Pupation takes place as a rule in an earthen cell below ground, and the pupal cuticle is retained within the latter by the cremaster: in *Plusia* and its allies a cocoon is usually present and is spun between leaves, etc. The eggs of Noctuidae are spherical and generally ribbed and reticulated.

Certain Noctuid larvae (*Agrotis*, etc.) are known as 'Cut-worms'; they are more or less abundant every year and in N. America rank among the worst of insect pests (vide Gibson, 1915a). The larva of *Leucania unipuncta* is the notorious and almost cosmopolitan 'Army Worm' so called from its habit of appearing in enormous numbers; as food becomes exhausted these larvae assume a gregarious marching habit seeking fresh fields. It is particularly injurious to cereals in the United States and Canada, and for a full account of its habits vide Gibson (1915). Some of these larvae exhibit a 'phase' variation in colour analogous to that seen in locusts (Faure, 1943). The larvae of the Antler Moth *Charaeas graminis* are periodically exceedingly destructive to upland pastures in N.W. Europe; a severe outbreak in Britain took place in 1917. Among other destructive species is *Aletia argillacea* whose larva is the well-known Cotton Worm of N. America; that of *Heliothis armigera* is the Boll-worm which is injurious to cotton bolls and the fruit of other economic plants on that same continent. *Diataraxia oleracea* is a serious pest in tomato houses in England (Lloyd, 1920).

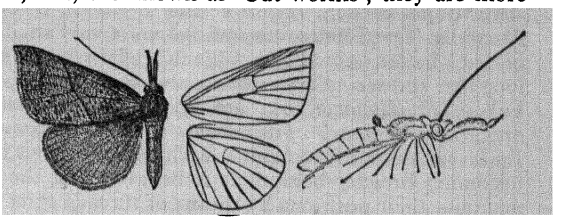


FIG. 438.—*Hypena proboscidalis*, male, Palaearctic region. × $\frac{1}{1}$

After Hampson (F.B.I.).

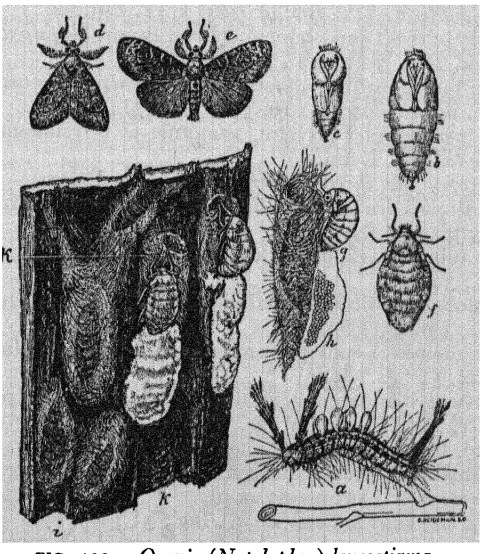


FIG. 439.—*Orgyia* (*Notolophus*) *leucostigma*

a, larva; *b*, female pupa; *c*, male pupa; *d*, *e*, male imagines; *f*, female imago; *g*, same ovipositing; *h*, egg-mass; *i*, male cocoons: *k*, female imagines ovipositing. Reduced from Howard, *Yearbook U.S. Dept. Agr.*, 1895.

FAM. LYMANTRIIDAE (Liparidae, Ocneriidae: Tussock Moths).—The Lymantriidae are mostly moderate-sized insects, rarely brilliantly coloured, and the antennae of the males are very prominently bipectinate to the apex. The family is hardly distinguishable from the Noctuidae on any venational feature: as a rule the bipectinate male antennae, and the absence of ocelli, afford more easily recognizable characters. The caudal extremity of the female is often provided with a large tuft of anal hairs which are deposited as a covering for the egg-masses. The larvae are hairy, generally densely so, often with thick compact dorsal tufts on certain segments (Fig. 439). Osmeteria are frequently present on the 6th and 7th abdominal segments. Larvae of the common European Gold Tail (*Euproctis chrysorrhoea*) are provided with urticating hairs composed of barbed spicules. It appears uncertain whether their irritating properties are mechanical only, or are partly due to a poisonous secretion bathing these spicules. Eltringham (1913) has shown that the female collects the spicules, which are present on the cocoon, by brushing the latter with the anal tuft, and subsequently distributes them over the egg-mass. The pupae are enclosed in cocoons above ground, and are characterized by the presence of very evident setae arranged around the scars of the larval verrucae. The best known member of this family is *Lymantria dispar*, the common Gipsy Moth

of Europe, which was introduced into N. America about 1868 along with the Brown Tail (*Euproctis phaeorrhoea*). These species have now become serious pests of shade and foliage trees on that continent. *Lymantria monacha* is the Nun Moth whose larvae are often a serious pest in the forests of Germany. In *Orgyia* wings are vestigial or absent in the female (Fig. 439).

The **Hypsidae** differ from the preceding family in the presence of a well-developed proboscis. The larvae are thickly covered with long hairs and construct a slight pupal cocoon. *Hypsa* occurs in Africa, throughout the Orient and in tropical Australia. The **Thaumetopoeidae** are a very small Palaearctic family of few species, perhaps better treated as a subfamily of the Notodontidae. The larvae are tufted with long hair and secondary setae are always numerous, but distinct verrucae are wanting. Larvae of *Thaumetopoea* are known as processionary caterpillars which exhibit gregarious habits. *T. processionea* is the well-known European processionary moth. Its larvae march in columns, each being headed by a leader, the column gradually becoming broader behind. It is believed that the individuals guide themselves and maintain their positions by means of threads spun by the leaders of each of the files. Brindley (1910) has observed these columns in the case of *T. pinivora* and conducted a series of experiments. He concludes, however, that the threads secreted by individuals on the march are of very slight importance either in forming the procession or maintaining its integrity. The larvae endeavour to maintain head and tail contact with the members of their file and this appears to be of primary significance in forming the procession.

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Order 24. **TRICHOPTERA** (Caddis Flies)

Small to moderate-sized moth-like insects with setaceous antennae. Mandibles vestigial or absent: maxillae single-lobed with elongate palpi: labium with a median glossa and well-developed palpi. Wings membranous, more or less densely hairy, and held roof-like over the back in repose. Fore wings elongate, hind wings broader with a folding anal area: venation generalized: cross-veins few. Tarsi 5-segmented. Larvae aquatic, more or less eruciform and usually living in cases: body terminated by hooked caudal appendages. Pupae exarate with strong mandibles: wing tracheation reduced.

The Trichoptera are weakly flying insects of moth-like appearance found in the vicinity of water (Figs. 40, 41). They are unfamiliar to the general student, whose acquaintance with the order is usually restricted to the case-bearing larvae which frequent ponds and streams. The imagines are mostly obscurely coloured, being generally some shade of brown, often with darker markings. They are not often seen on the wing unless disturbed, and they rest on herbage, trees, or stones: their flight is of short and uncertain duration. Many species are nocturnal: some are attracted to a light, others to the moth-collector's saccharine mixture, and a few visit flowers. They have seldom been observed in the act of feeding: the mouthparts are adapted for licking fluid nourishment, but probably a number of species take no food at all. In their general affinities they are allied to the Lepidoptera and are only separable from the latter upon comparatively slight characters. In the Trichoptera, however, a thyridium is generally present on each wing, M_4 is separate from Cu_{1a} in the fore wing and broad scales are universally wanting. About 3,000 species of the order are known and, of these, 188 inhabit the British Isles. The principal work on the European forms is that of McLachlan (1870–80), and Mosely (1939) has monographed the British species. The best modern introductions to the order are by Ulmer (1909) and by Betten (1934).



FIG. 440.—*Hydroptila angustella.* × 5
After McLachlan.

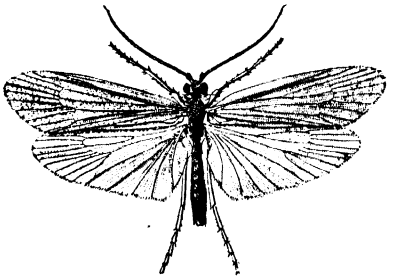


FIG. 441.—*Halesus guttatipennis* × circa 2
After McLachlan.

Anatomy (Fig. 442).—The antennae are multi-articulate and setaceous, frequently several times the length of the wings: when in repose they are

held closely porrected in front of the head. The compound eyes are usually small, but occasionally they occupy nearly the whole of the head in the male. Ocelli are either three in number or wanting. The structure of the mouthparts needs comparative study among representative genera. The clypeus is narrow and transverse, while the labrum is generally somewhat elongated. The mandibles are atrophied, or vestigial, in many genera such as *Phryganea*, *Limnephilus*, *Anabolia*, etc. (Lucas, 1893), but are better developed in certain others. The maxillae are small and closely associated with the labium: they are ordinarily provided with a single lobe or mala, the palpi are elongated and 5-, rarely 6-segmented in the females, but in the males the segments are more variable. The labium consists of a well-developed mentum, a median glossa, and usually 3-segmented palpi. There is a prominent hypopharynx which bears the aperture of the salivary glands. In the Australian *Plectrotarsus* the labrum and labium are greatly elongated, forming a kind of rostrum, and the two pairs of palpi are carried forwards. According to Cummings (1913) in *Dipseudopsis* each maxillary lobe is in the form of a pendulous, annulated half-tube recalling the condition found in certain archaic Lepidoptera in which the two elements of the proboscis are not coadapted.

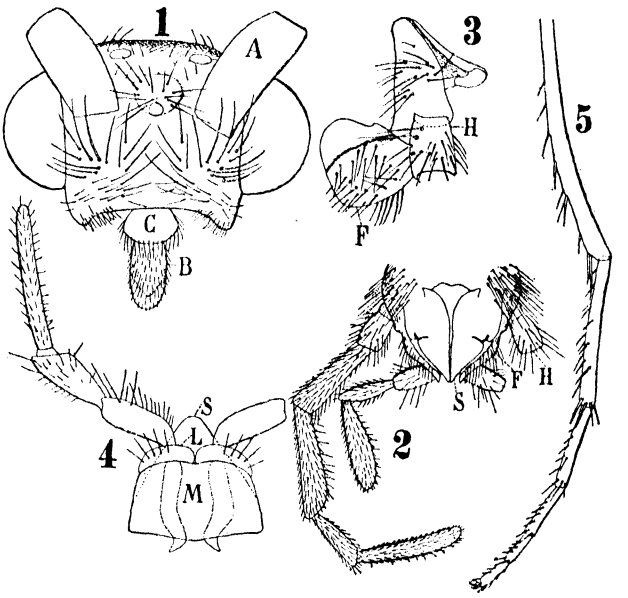


FIG. 442.—*Limnephilus*. 1, head, frontal view. 2, maxillae and labium (inner aspect). 3, maxilla. 4, labium. 5, tarsus and apex of tibia of 3rd leg

A, base of antennae; *B*, labrum; *C*, clypeus; *F*, galea; *H*, base of maxillary palp; *L*, prementum; *M*, mentum; *S*, glossa. *After* Silvestri.

The prothorax is small and ring-like; the mesothorax is the largest segment and the metathorax is somewhat shorter. The legs are long and slender with large, strong coxae: a meron is present in relation to the two hind pairs of coxae, but is less completely developed than in most Lepidoptera. The tibiae are often furnished with spines and movable spurs, the tarsi are 5-segmented, and between the claws there is either a pair of pulvilli or a cushion-like empodium. The wings are almost always fully developed, but the females of *Enoicyla* and *Philopotamus distinctus* are practically apterous. In *Anomalopteryx* (male) and *Thamastes* (both sexes) the hind wings are reduced to scale-like rudiments. The extremely hairy nature of the wings, which is especially characteristic of the order, is due to the presence of macrotrichia both on the veins and wing-membrane. Certain genera, however, exhibit a tendency to a reduction of this clothing, and in some forms there is an almost general absence of hairs. Scattered scales of a primitive type are found on the wings

of certain Trichoptera, but are narrow and acuminate, with few striae, and do not assume the broadened form so characteristic of Lepidoptera. The fore wings are denser than the hind wings, and are often slightly more coriaceous. The wing-coupling apparatus is exhibited in a primitive condition in *Rhyacophila* in which there is a jugal lobe on the fore wing resting on the costa of the hind wing. There are neither jugal bristles nor frenulum, and the humeral lobe is suppressed or vestigial. In the majority of genera the jugal lobe is rudimentary or wanting, and an amplexiform type of coupling apparatus is developed. This is brought about by a fold along the whole length of the anal area of the fore wing engaging the costa of the hind wing. In some forms a row of costal hooks along the hind wing grapple the anal margin of the fore wing, and thus securely interlock the two wings of the side. The

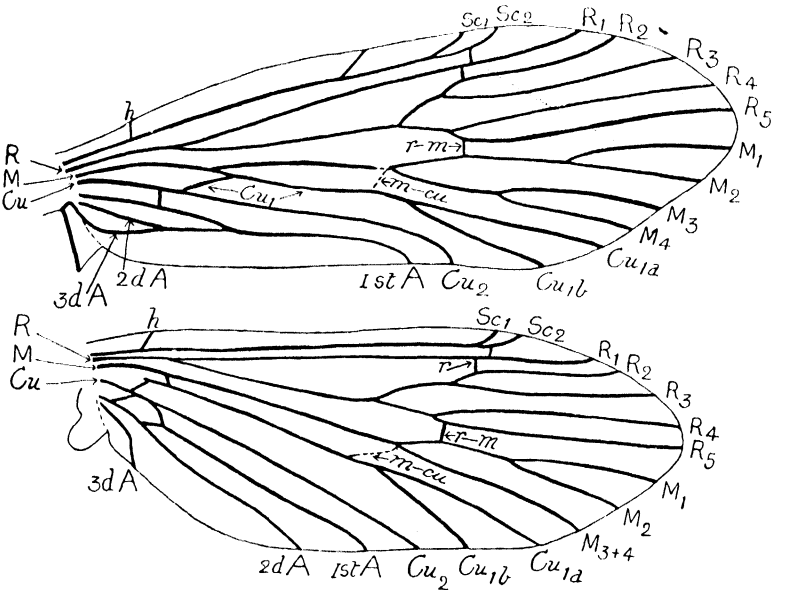


FIG. 443.—*Rhyacophila fuscula*, venation

After Comstock, with legend slightly altered.

venation, as exemplified by *Rhyacophila fuscula*, is of an extremely generalized type (Fig. 443) and closely resembles that of the most primitive Lepidoptera. Almost all the veins are longitudinal, not more than two veinlets in the costal series are retained, and the cross-veins are reduced in number. Unlike the Lepidoptera, M_4 of the fore wing is not fused with Cu_{1a}. Near the fork of vein R_{4+5} on both pairs of wings there is, ordinarily, a semi-transparent whitish spot generally devoid of hairs and known as the *thyridium*. It is possibly due to the presence of a gland or sensory organ and is wanting in Lepidoptera. The usual number of abdominal segments is apparently 10. The genitalia in the male (Zander, 1901) consist in more primitive forms of a pair of claspers and two lobes (parameres?) of the aedeagus, but in such genera as *Limnephilus* the claspers are absent: in the female the terminal segments are sometimes retractile and tubular, thus functioning as an ovipositor. The genital aperture is usually on the 9th sternite. The sperms are sometimes transferred to the female in a spermatophore (Khalifa, 1949).

In the males of species of *Hydroptila* there is an elaborate apparatus of scent-brushes and scent-scales situated at the hinder region of the head and attached to tubes or membranes which are capable of being everted, presumably by means of blood pressure. When not in use these organs are withdrawn into the head (Eltringham, 1920).

The internal anatomy of Trichoptera has been very little investigated and only fragmentary accounts exist. The alimentary canal is relatively short with a small stomach, a tubular and slightly coiled intestine, and an expanded rectal chamber: six Malpighian tubes are present. The nervous system, in addition to the usual cephalic centres, consists of 3 thoracic and 7 abdominal ganglia, but the 3rd thoracic and true 1st abdominal ganglia are indistinguishably fused (Glasgow, 1936). The testes are simple ovoid sacs and the ovaries consist of numerous polytrophic ovarioles (Stitz, 1904).

Biology and Metamorphoses.—The early stages of Trichoptera, almost without exception, are passed in fresh water. One or two species develop in brackish or salt water (e.g. *Philanisus*) while the larva of *Enoicyla* is terrestrial, living among moss at the bases of trees in woods (Rathjen, 1939). The eggs of caddis flies are laid in water, on aquatic vegetation, on overhanging trees or occasionally far from water (McLachlan). They are deposited in masses covered by a mucilage which rapidly swells when wetted. The larvae are the familiar objects known as 'caddis worms' and those of the greater number of species form cases or shelters within which they reside. These structures are composed of a basis of silk to which various foreign materials are added. They are commonly tubular in form with an opening at either end. The anterior aperture is wide and through it the head and legs of the contained insect can be protruded. The posterior aperture is usually smaller and is frequently protected by a perforated silken plate. As a rule the larva performs undulatory movements with the abdomen which maintain a current of water in contact with the body, flowing out through the posterior opening of the case. At its hinder extremity the larva is provided with a pair of grappling hooks and it is by means of these organs that it is able to maintain a firm hold of its case, dragging the latter along with it while it crawls about. The variety of cases made by caddis larvae is very great (Fig. 444) and their form and the materials used in their construction are in some cases characteristic of particular species, in others of genera or families. Almost all kinds of material which can be found in the water are utilized by one or other of the species. Leaves, pieces of leaves or stalks, straws, pieces of stick, etc., are often employed while other species select seeds, sand, particles of gravel or the shells of small molluscs. In addition to the case-bearing forms certain other Trichopterous larvae come under a different category and are, furthermore, structurally different in themselves. In these instances either no habitation is formed at all (e.g. *Rhyacophila*) or a silken retreat is formed which is fixed and not portable. These retreats are often common to several larvae and may be

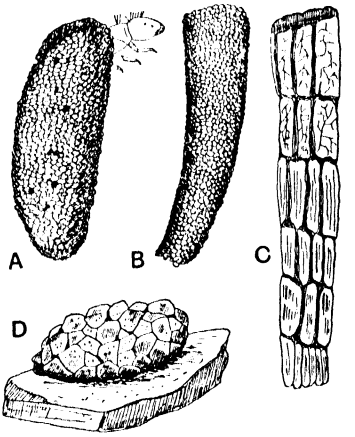


FIG. 444.—Cases of Trichoptera, magnified

A, *Hydroptila maclachlani*, case with larva —*after* Klapalek. B, *Odontocerum*, larval case. C, *Phryganea*, larva case. D, *Hydropsyche*, pupal shelter.

coated with mud or particles of gravel. Species of *Hydropsyche*, *Philopotamus*, *Plectrocnemia*, etc., which are carnivorous in habit, obtain their food by constructing nets or snares in the water around the mouths of their habitations (Wesenberg-Lund, 1911; Noyes, 1914). Such nets are composed of strong silken threads which are supported on some available framework such as fragments of leaves or twigs. Water flows freely through the net, but the latter holds back the organisms which serve as food for the caddis larvae.

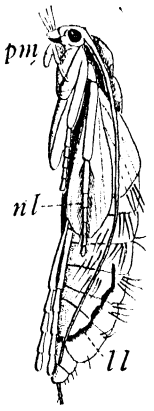


FIG. 445.—A typical Trichopterous Pupa.

ll, lateral line; *nl*, swimming leg; *pm*, provisional mandibles.

A typical Trichopterous larva has a well-developed sclerotized head and very short antennae (Fig. 446A). Biting mandibles are present and the maxillae are single-lobed with short 4- or 5-segmented palpi. The labium bears a small terminal median lobe and very much abbreviated palpi. The thoracic terga vary with regard to their degree of sclerotization and, in case-bearing larvae, one or more of the segments bear sclerotized dorsal plates. The legs are long and well developed with 1-segmented tarsi, each being terminated by a single claw. The abdomen is typically 10-segmented and generally covered with a membranous cuticle. The first segment, in many species, carries three prominent retractile papillae, one being dorsal and the remaining two lateral in position. They serve to maintain the insect in position in its case and thereby allow of an even flow of water through the latter. The anal segment in all larvae bears a pair of short and sometimes jointed appendages: each is terminated by a strong grappling hook and long flexible setae. The larvae are apneustic and live submerged, breathing, in most cases, by means of filamentous tracheal gills. The latter are arranged in segmental groups which are commonly disposed in dorsal, lateral, and ventral series along either side of the abdomen. Gills are wanting in newly hatched larvae and are not acquired until later. More rarely gills are absent throughout life and respiration is cutaneous: in some genera a tuft of anal blood gills is present. Most case-bearing larvae bear a delicate longitudinal cuticular fold on either side of the abdomen: it is beset with fine hairs and is known as the lateral line.

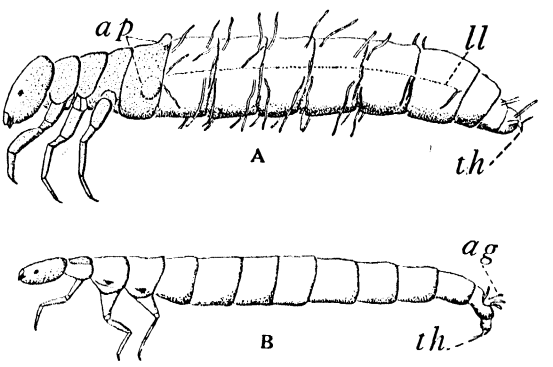


FIG. 446.—Trichopterous larvae

A, Eruciform or case-bearing type. B, Campodeoid or non-case-bearing. *ag*, anal gills; *ap*, abdominal papillae; *ll*, lateral line; *th*, terminal hooks.

Trichopterous larvae are divisible into two general types. In the first type of larva (campodeoid larva of Ulmer) the body is compressed and the head not inclined at an angle. These larvae seldom construct transportable cases and both the lateral line and abdominal papillae are wanting: tracheal gills are seldom present. In the second type (eruciform larva of Ulmer) the head is inclined at a marked angle with the rest of the body. Such larvae are

cylindrical in form and construct portable cases. Papillae are developed on the 1st abdominal segment and the lateral line and tracheal gills are present.

The digestive system in Trichopterous larvae forms a straight tube from the mouth to the anus (Betten, 1902; Russ, 1908). The oesophagus leads into a muscular crop which is followed by the stomach: the latter is the most extensive region of the gut and extends from the metathorax into the 6th abdominal segment. The hind intestine is extremely short and is divided into two successive, more or less globular chambers: six Malpighian tubes are present. There are two pairs of salivary glands belonging to the mandibular and maxillary segments respectively (Lucas, 1893): a pair of silk glands open on to the labium and these alone persist in the imago, becoming modified during pupation into salivary glands. According to Gilson (1894) the silk glands and associated structures closely resemble those of Lepidopterous larvae and the silk is produced in a similar manner. Metameric thoracic glands, known as Gilson's glands, occur in many larvae (Henseval, 1896). In *Phryganea* they take the form of a pair of branched tubes in each segment of the thorax: the ducts of a pair unite and open by means of a cannula-like papilla on the mid-ventral line of their segment (Fig. 447). In *Limnephilus* there is a single pair of unbranched glands in the prothorax, those of the other segments being wanting. The thoracic glands have been variously homologized with coxal glands and with nephridia: functionally they are regarded as being accessory organs of excretion. The nervous system is very simple: there are 3 thoracic ganglia and 6 to 8 ganglia are mentioned as being found in the abdominal nerve-cord.

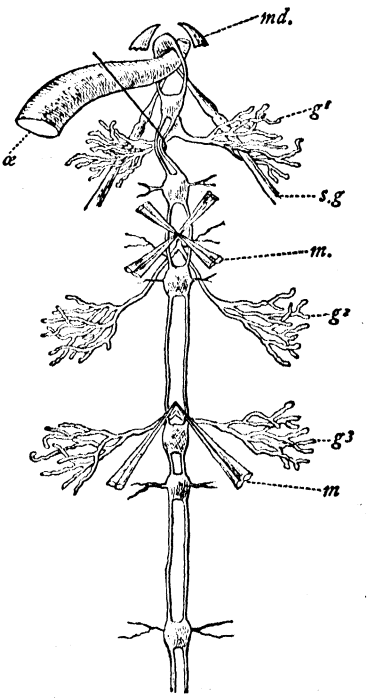


FIG. 447.—Thoracic glands (g^1–g^3) of the larva of *Phryganea grandis*

sg, silk gland; *m*, muscles; *oe*, oesophagus; *md*, mandibles. *After* Gilson, *J. Linn. Soc.*, 25.

Two distinct types of pupal shelter are prevalent (Hickin, 1949). Before pupation a case-bearing larva shortens its habitation when necessary and fixes it to some object in the water. A silken wall is constructed across either end and these partitions are sometimes strengthened by the addition of minute stones or plant fragments. Due provision is always made for the ingress and egress of the water. The pupa lies free within the case, no cocoon being formed. Most caseless larvae (*Rhyacophila*, etc.) construct special pupal shelters which take the form of oval cavern-like structures constructed of small stones, sand or other particles. The pupae in these instances are enclosed in brownish cocoons.

A Trichopterous pupa (Fig. 445) breathes by means of the persistent larval gills or through the general body surface. It is provided with strong mandibles which are used for biting through the case to allow of the pupa reaching the atmosphere prior to the emergence of the imago. The antennae, wings and legs are quite free from the body, and the abdomen is armed with dorsal

crochets or spines which enable the pupa to work its way out of its habitation. When the time for the emergence of the imago approaches, the pupa makes an upward passage through the water either by crawling or by swimming. In the former method the legs are clawed and the pupa is enabled to cling to vegetation or other objects. In the case of swimming pupae a degree of mobility is exhibited which is not attained by the pupae of any other insects. The middle pair of legs form oars and are provided with hair fringes adapting them to that usage. In some species the pupae are able to swim freely about at the surface until they find suitable objects to crawl out upon: with the inhabitants of swift streams the imago emerges almost as soon as the pupa reaches the surface.

Certain of the more important features in the biology of the different families may be summarized as follows:—

A. Larvae of the first type (campodeoid)

RHYACOPHILIDAE.—Larvae in swiftly flowing water: those of *Rhyacophila* live free beneath stones and are often provided with tracheal gills. In *Glossosoma* gills are wanting and the larvae live in transportable cases of small stones. The pupae in this family are enclosed in cocoons protected by a shelter composed of gravel or sand particles.

HYDROPTILIDAE.—Larvae devoid of tracheal gills and living in standing or flowing water, feeding with modified mouthparts on the juices of *Spirogyra*, etc. There is no case in the first four instars, but the last instar which is of very different appearance, constructs a transportable, seed-like, silken case, sometimes with sand or plant particles attached (Nielsen, 1948).

PHILOPOTAMIDAE, POLYCENTROPIDAE, PSYCHOMYIIDAE, HYDROPSYCHIDAE.—In these families, the larvae live in silken non-portable retreats. Tracheal gills are wanting, but anal blood-gills are commonly present. Certain of these larvae are carnivorous and construct silken snares to secure their prey. The pupae are protected by cavern-like shelters composed of gravel or sand particles.

B. Larvae of the second type (eruciform)

PHRYGANEIDAE.—Larvae mostly in standing water. Cases long and cylindrical, formed of fragments of leaves or fibres arranged in a spiral manner, and open at both ends.

MOLANNIDAE.—Larvae in ponds, lakes or streams, living in shield-like or conical cases composed of sand particles.

LEPTOCERIDAE.—Larvae in standing or running water, living in straight or slightly curved cylindrical cases of fine sand, vegetable debris, etc.

ODONTOCERIDAE.—Larvae in mountain streams, living in slightly curved cylindrical cases of sand. Hind extremity of case closed by a blackish membrane with a central slit: before pupation the mouth is closed by a single stone.

LIMNEPHILIDAE.—Larvae of varied habits, living in both standing and running water. Cases of sand, sticks, leaves or shells, or of a mixture of several materials.

SERICOSTOMATIDAE.—Larvae chiefly in running water: in cases of sand or stones.

Among the chief writings on the metamorphoses of Trichoptera are papers

by Thienemann (1905), Siltala (1907), Lübben (1907), Barnard (1934), Ulmer (1901), Lestage (1921) and Hickin (1946). The last three papers give keys for the identification of the early stages.

Classification.—The following key to the families is modified from Mosely & Kimmins (1953). Ross's work (1944) on the North American fauna contains valuable suggestions but cannot yet be extended to the world fauna.

1. Insects minute, very strongly pubescent, fringes of hind wing longer than greatest width of wing; antennae short and stout; maxillary palpi with 5 segments, last simple . . . . . HYDROPTILIDAE
–. Insects usually much larger and less pubescent, fringes of hind wing shorter than its greatest width 2

2. Maxillary palpi with 5 or 6 segments 3
–. Maxillary palpi with fewer than 5 segments 22

3. Last segment of maxillary palpi generally much longer than all others together, annulated, flexible 4
–. Last segment of maxillary palpi not or little longer than all others together, not annulated, usually not flexible 8

4. Ocelli present . . . . . PHILOPOTAMIDAE
–. Ocelli absent 5

5. Anterior tibia with 3 spurs 6
–. Anterior tibia with fewer than 3 spurs 7

6. Fore wing with R_1 forked . . . . . PSYCHOMYIIDAE (part)
–. Fore wing with R_1 simple . . . . . POLYCENTROPIDAE

7. Fore wing with R_2 and R_3 on a common stem. . . HYDROPSYCHIDAE
–. Fore wing with R_2 and R_3 coincident . . . . PSYCHOMYIIDAE (part)

8. Ocelli present 9
–. Ocelli absent 13

9. First 2 segments of maxillary palpi short and thick, 3 longer and thinner. Tibial spurs, 1, 2 or 3, 4, 4. . . . . RHYACOPHILIDAE
–. Segment 2 of maxillary palpi longer than 1 10

10. Anterior tibia with 2 or more, mid tibia with 4 spurs . PHRYGANEIDAE ♀
–. Anterior tibia with 1 or no spurs 11

11. Mid tibia with 4 spurs. Mouthparts elongate. R_2 ends in R_1 in hind wing . PLECTROTARSIDAE ♀
—. Mid tibia with 1–3 spurs. Mouthparts not elongate. R_2 not ending in R_1 in hind wing 12

12. Hind wing with R_2 and R_3 forming a fork, Cu_1 forked . LIMNEPHILIDAE ♀
—. Hind wing with R_2 and R_3 not forming a fork, Cu_1 simple SERICOSTOMATIDAE (part) ♀

13. Fore wing with a closed cell between the branches of M . CALAMOCERATIDAE
—. No such closed cell 14

14. Fore wing with no closed cell between branches of Rs 15
—. Fore wing with such closed cell 16

15. Tibial spurs, 2, 2, 4 . . . . . BERAEIDAE
—. Tibial spurs, 2, 4, 4 . . . . . MOLANNIDAE

16. A small, strongly sclerotized jugal lobe on fore wing. First segment of maxillary palp with a basal nodule . . . . . PHILORHEITHRIDAE
—. These modifications absent 17

17. Fore wing with R_4 and R_5 coincident 18
—. Fore wing with R_4 and R_5 separate 19

18. Hind wing with Rs and M each with two branches only ODONTOCERIDAE (part)
—. Hind wing with either Rs or M, or both, with more than two branches . LEPTOCERIDAE

19. Fore wing with vein M anastomosing with R_{4+5} for a short distance . PHILANISIDAE
—. Fore wing with vein M not anastomosing with R_{4+5} 20

20. Hind wing with veins R_{2+3} and M not forked . . HELICOPHIDAE
—. Hind wing with one or both these veins forked 21

21. Fore wing in anal area with an impressed line or furrow, simulating a vein, and bearing on its lower surface a row of stiff setae, forming a wing-coupling device ODONTOCERIDAE
—. Fore wing without this structure SERICOSTOMATIDAE and ODONTOCERIDAE . (genus *Caloca*)

22. Mouthparts elongate to form a rostrum. Ocelli present. Tibial spurs, 1, 4, 4. Maxillary palpi with 3 segments . . . PLECTROTARSIDAE ♂
—. Mouthparts not elongate 23

23. A small, strongly sclerotized jugal lobe on fore wing. Maxillary palpi with 3 or 4 segments, basal one with a nodule. Ocelli absent. Spars, 2, 4, 4, . . PHILORHEITHRIDAE ♂
—. Jugal lobe absent. Maxillary palpi with no basal nodule 24

24. Maxillary palpi with 1–4 segments, more or less thickened and hairy, masking the face. Ocelli absent, except in the Thremminae. Tibial spurs, 2, 2, 2; 2, 2, 4; or 2, 4, 4 . . . . . SERICOSTOMATIDAE ♂
—. Maxillary palpi not thickened and masking the face. Ocelli present . . 25

25. Maxillary palpi with 4 segments. Tibial spurs 2, 4, 4 . PHRYGANEIDAE ♂
—. Maxillary palpi with 3 segments. Tibial spurs variable . LIMNEPHILIDAE ♂

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Order 25. **DIPTERA** (Two-winged or True Flies)

Insects with a single pair of membranous wings, the hind pair modified into halteres. Mouthparts suctorial, usually forming a proboscis and sometimes adapted for piercing: mandibles rarely present: labium usually distally expanded into a pair of fleshy lobes. Prothorax and metathorax small and fused with the large mesothorax: tarsi commonly 5-segmented. Metamorphosis complete, larvae eruciform and apodous, frequently with the head reduced and retracted: tracheal system variable, most often amphipneustic, pupa either free or enclosed in the hardened larval cuticle or puparium: wing-tracheation reduced.

The Diptera are one of the largest orders of insects including over 64,000 described species, and approximately 5,200 species are known from the British Isles. Structurally Diptera are among the most highly specialized members of their class. The imagines of almost all the species are diurnal and the majority are either flower-lovers, which feed upon nectar, etc., or frequent decaying organic matter of various kinds. Although these two habits predominate, a considerable number of flies are predacious and live on various insects. In addition to the foregoing, there are other Diptera which have acquired blood-sucking habits, and besides man many other vertebrates, excepting fishes, may be resorted to by one or other species. Excluding the Muscidae and Pupipara, this habit is largely confined to the female. The blood-sucking forms include almost the whole of the Culicidae, besides the Simuliidae, Tabanidae and Pupipara, also certain members of the Ceratopogonidae, Psychodidae and Muscidae. In virtue of this propensity the order has acquired great significance in relation to medical science. The pathogenic organisms of some of the most virulent diseases such as malaria, sleeping sickness, elephantiasis, and yellow fever are transmitted to man through the intermediary of blood-sucking Diptera.

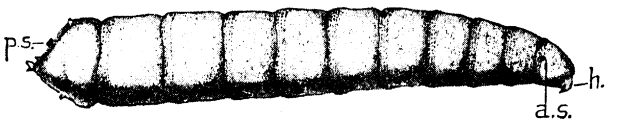


FIG. 448.—A typical Cyclorrhaphous larva (*Hylemyia*)
h, head; *a.s*, *p.s*, anterior and posterior spiracles.

External Anatomy

The work of Crampton (1942) forms a useful introduction to the external anatomy of the Diptera.

The **Head** (Fig. 449) is remarkable on account of its mobility and is usually of relatively large size. An extensive portion of its area is occupied by the *compound eyes* which, as a rule, are considerably larger in the male than the female. When the eyes of the two sides are contiguous they are

stated to be *holoptic*, and when markedly separated *dichoptic*; very occasionally the holoptic condition is found in the female as well as the male. In some species the upper facets are larger and more conspicuous than the lower, a peculiarity rarely seen in the female. It assumes its most extreme development in the Bibionidae where the two areas of different facets are sharply defined (Fig. 87). Between or slightly behind the eyes are the *ocelli*: the latter are usually three in number and are generally arranged in the form of a triangle: in some families ocelli are wanting. A complete Y-shaped epicranial suture has been described in *Mycetophila* but this is a secondary structure. The terminology of the regions of the head in general use is confusing owing to the multiplicity of names which have been employed: many do not admit of wide application and are often devoid of morphological value. In a Muscoid fly the 'front' [1] is regarded as the region between the eyes, and is limited by a line drawn through the bases of the antennae and by the upper margin of the head. In holoptic flies the space between the eyes and the basal line of the antennae is the *frontal triangle*: the triangular region bearing the ocelli and often bounded by grooves or depressions is the *ocellar triangle*. The region enclosed by the frontal suture is the *face* which is demarcated laterally by the *facial ridges* (facialia or vibrissal ridges) and distally by the epistoma. At the lower extremities of the facial ridges are two prominences or *vibrissal angles* carrying the vibrissae. The antennae are frequently lodged in *antennal grooves* or foveae which may be separated by a median *facial carina*. The *genae* (parafacials or cheeks) comprise the region lying between the face and the anterior margin of the eye on either side, while the *jowls* are the lower portions of the genae below the eyes. The upward continuations of the genae, along the inner border of the eyes, are known as the *orbits* or *parafrontals*. The *epistoma* is the distal border of the face and, in front of it, is a sclerite which is here regarded as the *clypeus* (or frontoclypeus). In many Nematocera the frontoclypeus is a well-defined region, but in some Brachycera and all Cyclorrhapha the clypeus (tormae of Peterson) appears to be separated off as a distinct sclerite. The latter is frequently a crescentic or semilunar plate, lying in the membrane of the rostrum, and forming the anterior or dorsal wall of the fulcrum.

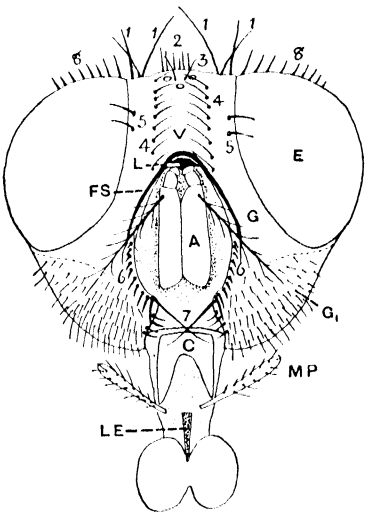


FIG. 449.—Frontal view of head of a Cyclorrhaphous fly (Schizophora)

A, antenna; *C*, clypeus; *E*, eye; *FS*, frontal suture; *G*, gena and lower portion G_1 or jowl; *L*, lunule; *LE*, labrum; *MP*, maxillary palp; *V*, vertex. The numerals refer to the chaetotaxy (p. 594).

The **Ptilinum** or frontal sac is a characteristic cephalic organ of Cyclorrhapha and its presence is indicated externally by the arched *frontal* or *ptilinal suture*. The latter lies transversely above the antennae and extends downwards on each side of them, thus presenting a ∩-shaped form. The suture is of the nature of an extremely narrow slit, along the margins of which the wall of the head is invaginated to form a membranous sac or ptilinum, and

[1] In most Diptera almost the whole of the anterior surface of the head appears to be formed by the vertex: the true frons is either of very limited extent or merged with the clypeus.

the walls of the latter are seen to consist of the same layers as the integument. The outer surface of the ptilinum is roughened owing to the presence of minute scales or spines of various forms. When viewed in sections taken through the head, the ptilinum is seen lying in the cavity of the latter in front of the brain. Attached to its inner surface in certain positions, are groups of slender muscle-fibres which apparently aid in retracting the organ (Laing, 1935). The function of the ptilinum is to thrust off the anterior end of the puparium at the time when the contained imago is ready to emerge and to force the fly through soil, etc. (Fraenkel, 1936). This is accomplished by the sac being exserted and distended in front of the head, under pressure from within (Fig. 450). When fully protruded it is in the form of a bladder, which presses upon the wall of the puparium until the latter ruptures. After the emergence of the fly, the ptilinum is withdrawn into the head-cavity and is no longer functional. The only outward manifestation of its existence is seen in the presence of the frontal suture. The ptilinum, however, offers a field for investigation both from the developmental and physiological points of view: there is also a great deal of doubt as to its presence or absence in certain families. In the Aschiza the frontal suture is vestigial or absent and no trace of the ptilinum can be detected. Just above the bases of the antennae in the Cyclorrhapha is a small crescentic sclerite known as the *frontal lunule*: in the Schizophora it is separated by the frontal suture from the part of the head immediately above.

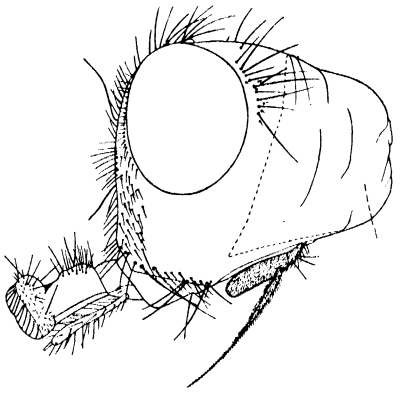


FIG. 450.—Head of *Calliphora* (seen immediately after emergence from pupa) with ptilinum *p* inflated

The **Antennae** (Fig. 451) furnish some of the most important characters in the classification of Diptera. They are seen in the least modified condition among the Nematocera, where the flagellum consists typically of a variable number of cylindrical segments similar to one another. In the Brachycera the antennae are composed, as a rule, of a smaller number of dissimilar elements. They consist of 2 or 3 evident basal segments carrying a terminal appendage, which corresponds to the greater part of the flagellum in Nematocera. This appendage may be distinctly annulated or jointed, or very much attentuated when it is known as a *style*. If it is still more slender and bristle-like it is termed an *arista*, which is a characteristic feature of the Cyclorrhapha. Morphologically, there is no clearly marked distinction between a style and an arista: the former, however, is

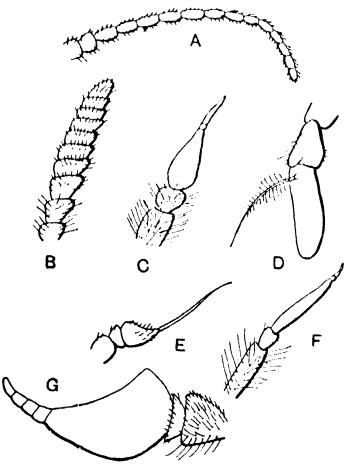


FIG. 451.—Antennae. A, Mycetophilid. B, *Bibio*. C, *Empis*. D, *Sarcophaga*. E, *Rhagio*. F, *Bombylius*. G, *Tabanus*

always terminal while the latter is usually dorsal and rarely terminal. In the Cyclorrhapha the antennae similarly consist of three basal segments of which the third is the largest and most complex and carries the arista. The various forms of the arista are of classificatory value, and they may be either bare, plumose, or pectinate.

The **Mouthparts** of Diptera exhibit a wide range of structure in adaptation to diverse habits, and there are many differences of opinion in interpreting the morphology of certain of the component parts. The generally accepted homologies as presented by Dimmock (1881) are confirmed by Kellogg (1899) who, from a study of the larval head in Nematocera, observed that the developing imaginal mouthparts are found in unmistakable correspondence or homologous relations with the larval counterparts. A similar conclusion was arrived at by Miall in his study of the head of *Chironomus*. There is, however, some diversity of opinion with reference to the homologies of the maxillae and their palpi (see Imms, 1944; Hoyt, 1952).

Although the most generalized type of mouthparts in Diptera is far removed from the orthopterous condition, the following features can be recognized. (1) The *labrum* which is dorsally well sclerotized but ventrally more membranous, this surface sometimes being termed the epipharynx. (2) *Mandibles* are absent except in many of the blood-sucking forms. (3) The *maxillae* are very rarely if ever complete: the basal sclerites may be separate and distinct, or either the cardo or stipes may be wanting. A single maxillary lobe or lacinia (Imms, 1944) is generally evident among Orthorrhapha. It is very variable in development and may be almost filiform (*Exoprosopa*), rod-like (*Sciara*, *Trichocera*), or totally wanting (*Tipula*, *Dolichopus*). The maxillary palpi are particularly important for classificatory purposes: they may consist of four complete segments, but in the more highly specialized forms they are reduced to single-segmented organs. (4) The *labium* forms the proboscis which is usually expanded distally to form a pair of prominent fleshy lobes or *labella*. Crampton (1921) brought forward evidence which suggests that the latter organs are the reduced and modified labial palpi. In most Nematocera the labella are free, but in the higher Diptera coalescence takes place to a greater or lesser degree. With the beginning of coalescence fine trachea-like food channels or *pseudotracheae* become evident: they attain their most complete development in the Calyptratae where the fusion reaches its maximum. In the majority of Diptera a posterior sclerotized plate is present near the base of the labella and is probably the counterpart of the prementum (Fig. 454), the rest of the mentum being represented by the median membranous area behind. (5) The *hypopharynx* is probably universally present and is either in the form of a lanceolate organ or a greatly attenuated stylet. It is perforated by the salivary duct and is frequently considerably developed.

The mouthparts attain their fullest development in those Nematocera and Brachycera with blood-sucking habits (Snodgrass, 1943). In these forms the trophi, with the exception of the palpi and labium, are either stylet-like or blade-like, and adapted for piercing. The females, moreover, are unique among Diptera in possessing mandibles. In the males the latter organs are rarely present and are usually atrophied, except in the Tabanidae, the Simuliidae and the Ceratopogonidae. The labrum in these blood-sucking forms is grooved or ∩-shaped, and the hypopharynx flattened: when apposed, the two elements constitute a closed channel through which the blood is drawn by the pumping action of the cibarium. The hypopharynx conveys the saliva

to the distal orifice of the channel where it mixes with the blood. The wound on the host is made either by the mandibles alone, or in conjunction with the laciniae of the maxillae. The labium takes no part in piercing: it is grooved dorsally and serves as a sheath retaining the other appendages when at rest (Fig. 452). In the Tabanidae (Fig. 453) both mandibles and maxillae are flattened and blade-like, minutely serrated distally: the labrum is shaped like a double-edged sword, and overlies a similar but more slender hypopharynx. In addition to functioning as a sheath for the other mouth-organs, the labium in Tabanids is also an organ for imbibing liquid matter from moist surfaces, which is absorbed by the pseudotracheae present on the labella. In the Culicidae (Fig. 452) specialization has been carried a step further, all the mouthparts are more elongated and the piercing organs are modified into extremely fine needle-like stylets. The labella have many sensory hairs on their distal margins and are mainly tactile in function: the method of feeding in this family is dealt with on p. 613. In the predacious Brachycera (Asilidae and Empididae) the labium is hardened and horny with the labella small, and usually with poorly developed pseudotracheae. The laciniae are rigid and blade-like, being seemingly adapted for perforating the prey: both the labrum and hypopharynx are large and strong.

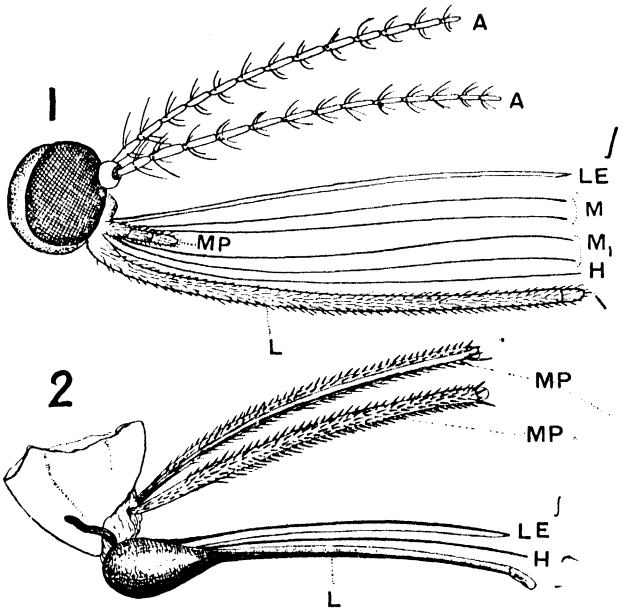


FIG. 452.—Mouthparts of 1, *Culex*; 2, *Glossina palpalis*
A, antenna; *H*, hypopharynx; *L*, labium; *LE*, labrum; *M*, mandibles; M_1, maxillae and *MP*, palpi; (2 *after* Stephens & Newstead).

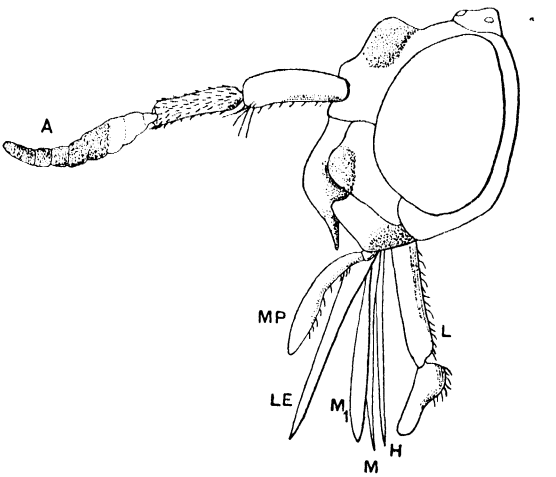


FIG. 453.—*Chrysops*, lateral view of head × 15
A, antenna; other lettering as in Fig. 452. *After* Surcouf & Gonzalez-Rincones.

In most Cyclorrhapha all the mouth-organs contribute to the formation of the proboscis. Its morphology is difficult to appreciate owing to the modification which has

resulted through the reduction of the maxillae, and the increased development of membranous areas, in order to impart to the organ the maximum flexibility. The anatomy of the proboscis has been most fully studied in *Calliphora* (Fig. 454). In this genus (Graham-Smith, 1930) it consists of a proximal and somewhat cone-shaped basal portion or *rostrum*, and a distal portion or *haustellum*. Morphologically the rostrum belongs to the head and carries anteriorly the *maxillary palpi*. Situated within this region is a complex cuticular framework known as the *fulcrum*. According to Snodgrass (1943; 1953), the fulcrum is derived from the inflected margins of

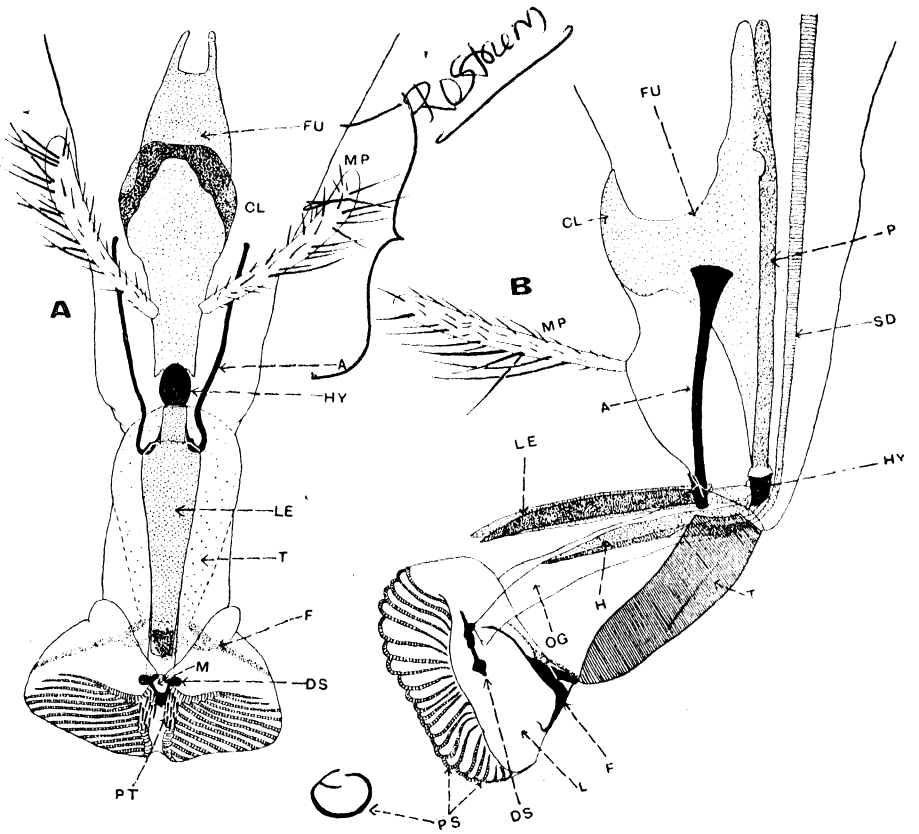


FIG. 454.—Proboscis of *Calliphora*. A, frontal; B, lateral view

A, apodeme (stipes); *CL*, clypeus; *DS*, discal sclerite; *F*, furca; *FU*, fulcrum; *H*, hypopharynx; *HY*, theca, *L*, labellum; *LE*, labrum; *M*, mouth; *MP*, maxillary palpi; *OG*, oral groove; *P*, course of pharynx; *PS*, pseudotracheae; *PT*, prestomal teeth; *SD*, salivary duct; *T*, prementum.

the clypeus to which its anterior portion is hinged. The proximal portion of the fulcrum is quadrangular in section, and the distal portion U-shaped, the anterior or roof-like portion being wanting in this region. Between the lower end of the fulcrum and the base of the labrum is a small U-shaped *theca* which lies on the pharyngeal wall, and serves to keep the lumen of the cibarium distended. The haustellum carries the labrum and the hypopharynx on its anterior (or dorsal) face, and these organs are situated in a furrow formed by its projecting membranous sides. The haustellum is continuous with the apex of the rostrum and, on its posterior aspect, it is strengthened by the *prementum*. The latter articulates distally with a short

rod or *furca*, and arising therefrom are two divergent arms which form the principal skeleton of the oral lobes. The membrane investing the oral or distal surface of the labella contains a series of food channels or *pseudotracheae* which pass from its outer edges to the inner margins. These channels are kept open by a framework consisting of a series of incomplete sclerotized rings which impart to them an appearance resembling tracheae. Each ring is bifurcate at one end and single at the other—the single and bifurcate extremities alternating. The pseudotracheae open on the external surface of the oral lobes by means of the space which lie between the forked extremities of the rings: inwardly they communicate with the oral aperture. The latter is situated in a small oral pit between the labella: the sides of the depression are bordered by a row of prestomal teeth which are greatly developed in *Ochromyia* and blood-sucking Muscids. The proboscis is adapted for sucking up liquids, and none but the most minute solid particles are able to enter the food channels. Under certain conditions the labella may be strongly reflected which allows of the protrusion of the prestomal teeth and their use as rasping organs. When this occurs food can be sucked directly through the oral aperture which admits particles of larger size than could traverse the pseudotracheae. When the proboscis is protruded, the rostrum is extended by means of the distension of the lateral air-sacs at its base, and probably of certain of the cephalic air-sacs also. The haustellum, on the other hand, is brought into use by means of the contraction of its extensor muscles and, finally, the labella are extended and rendered turgid by means of blood-pressure. The retraction of the proboscis is brought about by the contraction of its numerous muscles.

In the blood-sucking Muscidae and the Pupipara the proboscis itself has become modified to form the principal organ of penetration. It differs from that of most Cyclorrhapha in its horny consistency and swollen bulbous base: owing to the elongation of the haustellum the proboscis can no longer be concealed when retracted. In *Stomoxys* the labella are small oval lobes, devoid of pseudotracheae, and have their outer membrane provided with plate-like teeth adapted for cutting. The labrum and hypopharynx are shorter than the proboscis and, consequently, do not perform any part in the making of the wound: they have, furthermore, thin and flaccid distal extremities. In *Glossina* (Fig. 452) the proboscis is embraced by the elongate palpi when at rest, and specialization has proceeded still further. The labella are even less evident, and the slender labrum lies throughout in close contact with the labial groove and, for this reason, has lost much of its rigidity. In *Hippobosca*, *Olfersia* and their allies the basal portion of the proboscis is sunk within the head, the distal part of the organ alone being visible. It bears no labella but the cutting teeth exhibit a bilateral arrangement. The labrum is much stouter than in the preceding genera and, instead of lying within the labial groove, it forms the roof of the latter. The hypopharynx in *Hippobosca* is a slender flattened organ containing the salivary duct between its two layers: at its upper end the dorsal lamina fuses with the labrum and the ventral lamina merges into the lining of the labial groove.

The principal general papers regarding the mouthparts of Diptera are those of Dimmock (1881), Kellogg (1899), Peterson (1916), Frey (1921), Snodgrass (1943), Imms (1944), and Hoyt (1952): for the Pupipara and *Glossina* the reader is referred to papers by Jobling (1926–33).

The **Tentorium** is characterized by three pairs of arms and a reduced body: the primitive invaginations persist to a greater or less degree in most

Diptera as intracranial tunnels. As a rule the most prominent invaginations are those of the anterior arms (well seen in *Chironomus* and *Anopheles*) which are situated some distance below the antennae, and are often located within the arms of the V-shaped suture. The invaginations of the dorsal arms lie just below the bases of the antennae, but as a rule they are wanting: those of the posterior arms are situated near the ventrolateral margins of the occiput (Peterson, 1916).

The **Thorax** (Fig. 455) is characterized by the great development of its median segment which carries the wings, and the correlated reduction of the segments in front and behind it (Young, 1921). The two latter regions are little more than anterior and posterior bands, whose active function is the support of the fore and hind legs. The sclerites are well exhibited for preliminary study in Tipulidae, but among Cyclorrhapha real difficulty will be experienced owing to the specialization which has resulted.

The *pronotum* in Tipulids is represented by a band-like scutum and scutellum, but is still more reduced in the higher Diptera. The *mesonotum* forms the greater part of the dorsal aspect of the thorax and is clearly divisible into prescutum, scutum and scutellum: the postnotum of this segment is well developed in Tipulidae, Culicidae and other Nematocera, but is subdivided among the higher Diptera. The boundary between the prescutum and scutum is known as the *transverse suture* and, although complete and V-shaped in Tipulids, it is generally incomplete in the middle line in other Diptera. On the mesonotum are certain more or less prominent lateral swellings on either side, which are recognized by systematists, and known as calli or callosities. The *prealar callus* is situated just above the root of the wing, while the *humeral callus* forms the anterodorsal angle of the prescutum, and the *postalar callus* constitutes the prominent posterodorsal angle of the scutum. The *metanotum* is always reduced and band-like, and is continuous laterally with the epimera.

The pleura do not present any serious difficulties among typical Nematocera and Brachycera, and both episterna and epimera can be recognized in each segment. Among Cyclorrhapha, however, the interpretation of the pleurites is in a far from satisfactory condition, and the extensive use of chaetotaxy for classificatory purposes demands the definition of these plates with precision. The terminology of Osten-Sacken, although of limited application, has much to recommend it for the somewhat paradoxical reason that it has no strict morphological value. In cases where homologies are uncertain, a purely conventional terminology presents more chances of fixity, and can coexist with the growth of a more scientific system, based upon increasing knowledge of comparative morphology. In Osten-Sacken's nomenclature the pleural regions are identified in relation to certain well-defined sutures. (1) The *notopleural suture*, running from the humeral callus to the wing-base, thus separating the mesonotum from the pleuron: (2) the *sternopleural suture*, running below the notopleural suture and separating the mesopleura from the sternopleura: (3) the *mesopleural suture*, passing downwards from the wing-base to the middle coxa. The *mesopleuron* (= dorsal part of mesepisternum) is the area in front of the root of the wing between the noto- and sternopleural sutures: the *pteropleuron* (= dorsal part of mesepimeron) lies below the root of the wing and behind suture 3: the *sternopleuron* (= ventral part of mesepisternum) is situated below suture 2 and above the anterior coxa: the *metapleuron* (= lateral part of mesopostnotum) lies behind the pteropleura and to the outside of the metanotum: the *hypopleuron* (= meropleurite,

composed of ventral part of the mesepimeron and the meron) is the region above the middle and posterior coxae and below the metapleuron (vide Fig. 455). For further information on the thorax of Diptera vide Osten-Sacken (1884), Edwards (1925) and Crampton (1942).

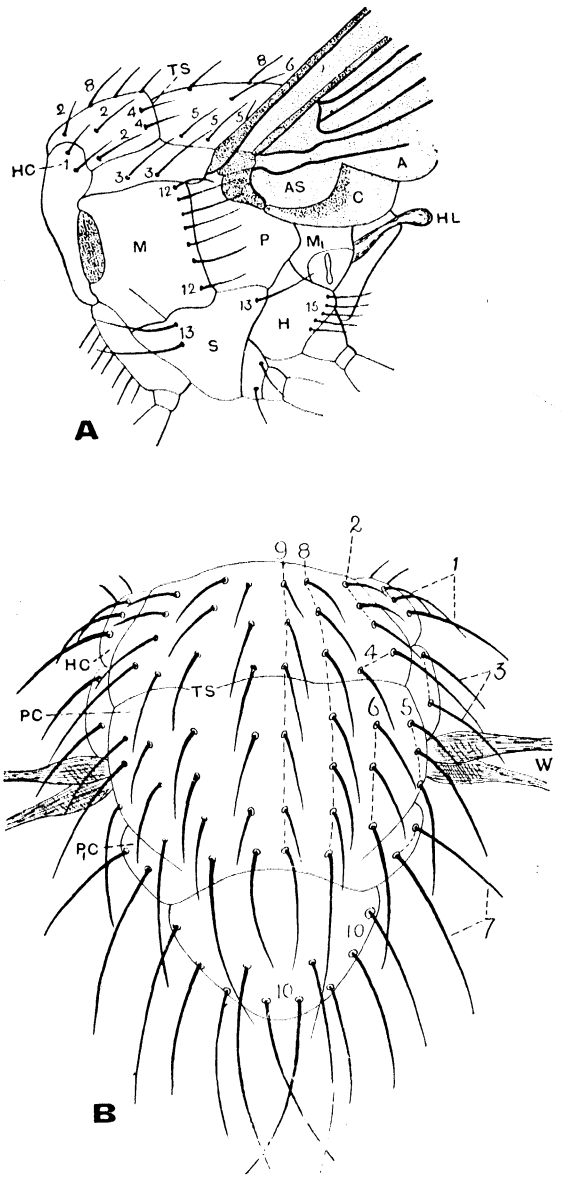


FIG. 455.—Thorax of A, *Lucilia caesar* × 11; B, *Compsilura concinnata*, dorsal view × 11

A, alula; *AS*, antisquama; *C*, calyptra; *H*, hypopleuron; *HC*, humeral callus; *HL*, haltere; *M*, mesopleuron; M_1, metapleuron; *P*, pteropleuron; *PC*, prealar callus; P_1C, postalar callus; *S*, sternopleuron; *TS*, transverse suture; *W*, wing-base. The numerals refer to the chaetotaxy, vide pp. 594–5. Adapted from Surcouf & Gonzalez-Rincones.

Chaetotaxy.—The study of the arrangement of the *macrochaetae* or differentiated bristles of flies is termed by Osten-Sacken *chaetotaxy*. His important paper (1884) emphasized the value of these structures for classificatory purposes, and their application has been greatly extended by more recent writers, notably Girschner. A knowledge of chaetotaxy is essential for the systematic study of Diptera and the following are the most important of the macrochaetae (Figs. 449, 455).

A. CEPHALIC BRISTLES.—1. *Vertical:* inner and outer pairs situated close to and rather behind the upper inner corner of the eye. 2. *Postvertical:* just behind the ocelli. 3. *Ocellar:* one pair in the ocellar triangle. 4. *Interfrontal:* a double row in front of the ocelli, external to the frontal suture, often descending to the base of the antennae. 5. *Orbital:* one or more on each side of the front near the orbit, behind 4, and immediately below 1. 6. *Facial:* a series above 7, on either side of the face external to the antennae. 7. *Vibrissae:* stout, placed close to the sides of the epistoma. 8. *Postorbital:* a row nearly parallel with the posterior margin of the eye.

B. THORACIC BRISTLES.—1. *Humeral:* one or more on the humeral callus. 2. *Posthumeral:* near the inner edge of the humeral callus. 3. *Notopleural:* one pair between the humeral callus and the base of the wing. 4. *Presutural:* one or more immediately in front of the transverse suture on either side. 5. *Supra-alar:* between 3 and 7, above the root of the wing. 6. *Intra-alar:* several between 5 and 8 7. *Postalar:* behind 5, on postalar callus.

8. *Dorsocentral:* a row on either side of 9, on the inner part of the mesoscutum. 9. *Acrostichal:* a row along each side of median line. 10. *Scutellar:* along the margin of the scutellum.

C. LATERAL THORACIC BRISTLES.—11. *Propleural:* immediately above coxae of fore legs. 12. *Mesopleural:* on the mesopleura. 13. *Sternopleural:* on the sternopleuron. 14. *Metapleural:* on the metapleura. 15. *Hypopleural:* on the hypopleura.

D. ABDOMINAL BRISTLES.—1. *Marginal:* inserted dorsally on the margins of the segments (Tachinidae). 2. *Discal:* one or more pairs near the middle of the segments. 3. *Lateral:* one or more near the lateral margins of the segments.

The **Legs** do not call for any detailed mention and, except in a few abnormal forms, the tarsi are 5-segmented. In many Acalyptratae a differentiated bristle is present on the outer border of the tibiae, a short distance below the apex, and quite distinct from the tibial spurs. It is known as the *preapical bristle* and considerable importance has been ascribed to it for classificatory purposes. For the same reason the pads of the feet are noteworthy: thus, pulvilli may be wanting or vestigial in many Nematocera, or may be replaced by a single pad-like arolium (Scatopsinae). In the Stratiomyidae, Tabanidae, etc., both the pulvilli and the arolium are pad-like, while among the Asilidae there is a stiff and bristle-like empodium. Two pad-like pulvilli are the rule among Cyclorrhapha.

Wings are usually present but are wanting or vestigial in a certain number of forms. Apterous or sub-apterous species are principally found in maritime and insular genera (Clunioninae, Ephydridae, etc.), parasites (Pupipara), and among species inhabiting ants' and termites' nests (Phoridae, *Termitomastus*). Occasional apterous species, not associated with the above modes of life, occur in various families, notably *Chionea*, *Epidapus* (female) and certain Sphaeroceridae.

The venation of the more generalized members of the order shows a tolerably close approximation to the hypothetical primitive type, the chief differences being the atrophy of Cu_1 and the vestigial condition of 2A and 3A. Neither accessory nor intercalary veins are developed, and only the chief cross-veins are present. A very primitive dipterous wing is seen in the Tanyderid *Protoplasa* which exhibits all four branches of Rs and M, while there is no tendency towards the apical coalescence of adjacent veins. It has been pointed out by Comstock that in all Nematocera, in which Rs is 3-branched, R_2 and R_3 remain distinct: while in those Brachycera that have Rs 3-branched (Fig. 457) R_4 and R_5 are separate. Among certain other of the Brachycera Rs is 2-branched only, and this condition obtains among the Cyclorrhapha. According to Tillyard Cu_1 of Comstock is in reality M_4, while its basal section is Comstock's *m-cu* cross-vein. The lettering of the venational figures is in accordance with this interpretation.

On the posterior margin of the wing, near the base, there is frequently a free lobe or *alula*, and on the inner side of the latter there are often one or two additional lobes or *squamae*. When two squamae are present, the one nearest the alula is known as the *antisquama*, the squama being the lobe nearest the thorax (Fig. 455). In the Calyptratae the squama is large, usually covering the haltere, and is often referred to as the *calyptron* (or calypter). All three lobes are well seen in *Musca* and *Calliphora*.

With the exception of a few degenerate apterous forms (e.g. *Melophagus*, *Braula*, etc.), *halteres* (balancers) are universally present among Diptera. They develop from the dorsal metathoracic wing-buds, and are consequently the highly modified counterparts of the posterior wings. Further proof of their alary origin is also afforded by certain mutations described by Morgan in

Drosophila in one of which the halteres are replaced by hind wings with clearly recognizable venation (Fig. 456). Each haltere consists of a dilated basal portion or *scabellum*, which supports a delicate *pedicel* or stalk, surmounted by a knob-like extremity or *capitellum*. The scabellum articulates freely with the metathorax, and is moved by four muscles arising from its proximal border (Lowne): the halteres are, therefore, freely movable and are capable of vibration. It is in the scabellum that the principal sensory structures of the haltere are located. These consist in *Calliphora* of three groups of minute so-called chordotonal organs invested by a thin integument, and three highly sculptured elevations of the cuticle containing larger and more complex structures—the two *scapal organs* (scalae of Lowne) and the *basal organ* (cupola of Lowne). Both scapal and basal organs exhibit thin transparent areas, each of which overlies a minute vesicle enclosing a central refractive spot. The cavity of the haltere contains blood and a fine tracheal branch. The nerve supplying this appendage is the largest in the thorax. Binet (1894) has demonstrated that the majority of its fibres arise from the brain, and traverse the thoracic ganglia on their course to the metathoracic centre; from there they pass onwards to the scabellum, and are distributed to the several sense organs (Lowne, 1890; Weinland, 1890). Pringle (1948) has shown that the halteres, which during flight are rapidly oscillated, function as gyroscopic organs and allow the fly to control any tendency to roll or yaw. Experiments conducted with certain species show that, if the capitellum and part of the pedicel of a haltere be amputated, flight becomes clumsy and difficult: if both halteres be treated alike the

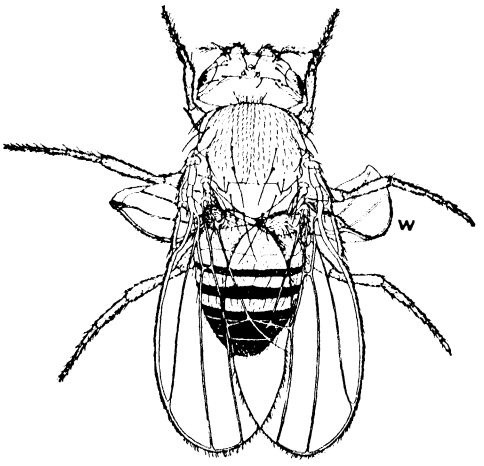


FIG. 456.—*Drosophila melanogaster:* Mutant with halteres replaced by hind wings *W*
After T. H. Morgan, *Publ. Carnegie Inst.*, 327, 1923.

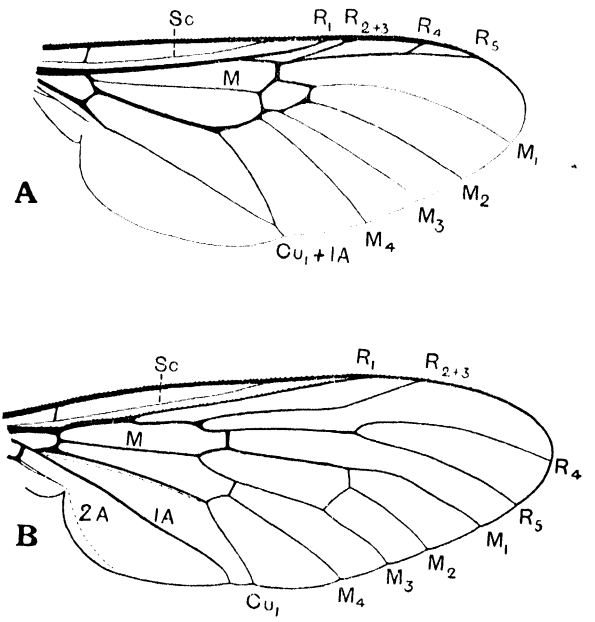


FIG. 457.—Venation of Brachycera. A, *Geosargus*; B, *Rhagio*

power of flight is almost entirely lost, and insects so mutilated can only fly a few centimetres, and usually fall vertically when thrown into the air.

In the **Abdomen** the first segment is much reduced. Of the segments that follow the 2nd–11th are present in *Tipula*, but among the Cyclorrhapha the number is difficult to ascertain, and rarely more than 4 or 5 are evident without dissection. In *Dacus* Miyake (1919) finds 11 segments present in both sexes, the 1st segment being represented by its reduced sternum. In the female *Musca* the visible segments are the 2nd to the 5th, while the 6th to 10th segments form the retractile ovipositor. The latter organ is formed in this manner in the majority of Diptera, but in the Tipulidae a valvular ovipositor may be present (Snodgrass, 1903). In the male, the 9th and 10th segments are often curved ventrally and with the genitalia form the *hypopygium*. In a number of families, the hypopygium is twisted through 180°, so that the anus may become ventral to the genital aperture (*hypopygium inversum*). Segments 6–8 may in such cases become much modified and asymmetrical; the structures found in the Cyclorrhapha are still very difficult to interpret (Lamb, 1922; Feuerborn, 1922; Crampton, 1944; Hardy, 1944). They have a *hypopygium circumversum* in which after inversion the anus has apparently moved back into a position dorsal to the genitalia. The genitalia include *claspers*, made up of a movable coxite and style, and an aedeagus with accessory structures lying between sternites 8 and 9 (Edwards, 1920).

There are two *spiracles* in the thorax and may be eight in the abdomen. Their position in the latter and the number which remain functional is modified in higher groups. Their regulatory mechanism is discussed by Hassan (1944).

Internal Anatomy

The **Alimentary Canal** is generally but little convoluted among Nematocera, but is more coiled among Brachycera. In the Cyclorrhapha it exhibits greater complexity, its length being much increased mainly owing to the greater extension of the mid intestine (Fig. 104).

The cibarium forms the sucking apparatus by means of which the food is drawn up through the proboscis and passed into the oesophagus. The original circular lumen in these parts becomes modified, and the sclerotized lining is developed as two or three hardened plates. The latter afford a basis for the attachment of dilator muscles, and are capable of being drawn apart by their contractions. In this manner the lumen is increased, and the food sucked up through the siphon formed by the mouthparts. In the Brachycera, the anterior part of the pharynx is also furnished with muscles and forms a second pump. In Culicidae the cibarium is provided with dilator muscles but the principal pumping apparatus is pharyngeal. The blood is first pumped into the cibarium and from thence it passes into the pharynx, a valve situated between these two regions precluding a return flow.

The *oesophagus* passes through the neck into the thorax where it divides. One branch enters the proventriculus and the other is continued backwards as the slender duct of the food reservoir. The *proventriculus* is the homologue of the gizzard and has a well-marked musculature: it never contains denticles and a valve is usually present. The proventriculus is wanting in *Phlebotomus*, *Simulium* and *Culicoides*, is elongate and tubular in *Tabanus* and in Cyclorrhapha it is much reduced and disc-like, mainly consisting of its valvular portion. The *food-reservoir* (or crop) is the most characteristic

feature of the digestive canal. It is situated in the anterior region of the abdomen and is, morphologically, a diverticulum of the oesophagus. Although present in most families it is wanting in certain Asilidae, Oestridae and in *Hippobosca* and *Melophagus*. In *Musca* it is a bilobed sac with very thin walls composed of a single layer of small flattened cells, external to which is a network of muscle fibres; internally it is lined by a delicate cuticle. The usual position of the food reservoir and its duct is ventral, but in *Tabanus* these parts are dorsal. In the Culicidae, instead of a single sac, three oesophageal diverticula are present, of which two are dorsolateral, while a third and larger sac is ventral. The function of the food reservoir is that of a storage chamber into which the nutriment is passed as it is sucked up: its contents then become gradually emptied into the mid gut. The time the food remains in the reservoir varies greatly: thus in *Musca* it may not be emptied for several days, while in *Tabanus* it is usually empty and possibly its contents are quickly regurgitated into the mid gut (Patton & Cragg). As a rule, after a meal the reservoir is distended with food, as has been demonstrated by allowing flies to feed upon a coloured liquid.

The *mid intestine* in Nematocera is a pyriform or fusiform sac: in the Culicidae its anterior region, or cardia, is elongate and tubular, and leads into a dilated chamber or stomach. Among Cyclorrhapha the mid gut is no longer dilated but is tubular throughout, and thrown into numerous convolutions. It is divisible into an anterior region—the *ventriculus* or *chyle stomach*, followed by a narrower and much longer *proximal intestine*. The *Malpighian tubes* are generally four in number: in most Cyclorrhapha they arise in pairs from a common duct on either side. *Psychoda* and the Culicidae are exceptional in possessing five Malpighian tubes: in *Culicoides* there are only two (Bugnion).

The *hind intestine* is divisible into the *distal intestine* and *rectum*. The former, in many Diptera, is naturally separable into a narrow coiled *ileum* and a wider region or *colon*. The rectum is a pyriform or rounded chamber provided with a variable number of papillae which may be either two (*Chironomus*), four (*Musca*, *Calliphora*, etc.) or six (*Anopheles* and *Tabanus*).

The **Salivary Glands** are usually elongate and tubular but exhibit great variation in length. In the Culicidae they are situated in the thorax and each gland is trilobed: a layer of secretory cells surrounds the cavity of each lobe, and the smaller central lobe (formerly known as the poison gland) differs somewhat in histological features. The common salivary duct passes to the base of the hypopharynx, where it expels the secretion down the salivary groove to the apex of that organ. In the Tabanidae the glands extend into the anterior part of the abdomen, while in *Musca* they are considerably longer than the total length of the body.

Labial Glands are frequently present on the proboscis at the bases of the labella. In *Musca* they are spherical aggregations of gland cells. According to Hewitt (1914) the ducts are intracellular, each arising from a vacuole. They pass outwards from the gland to form a number of larger ducts which unite and open into the oral pit by means of a pair of median pores. The secretion of the labial glands serves to moisten the surface of the labella.

The **Nervous System** (Brandt, 1879; Künckel d'Herculais, 1879) presents many modifications, almost every transition being found between the Nematocera, with 3 thoracic and 7 abdominal ganglia, and the Calyptratae in which all of the ganglia of the ventral chain are fused into a single thoracic mass (Fig. 68). There is, furthermore, a marked relation between the degree

of concentration of the nervous system and specialization in other directions. A graduated series illustrating the progressive concentration of the nervous system may be exemplified as follows.

1. Two or three thoracic centres and always six abdominal centres: 1st abdominal ganglion united with the metathoracic and the 7th and 8th abdominal ganglia fused (most Nematocera also Asilidae, Empididae, Bombyliidae and *Xylophagus*). 2. Three thoracic and five abdominal centres (Scenopinidae). 3. Two thoracic and four abdominal centres (Therevidae). 4. Two thoracic and no abdominal centres (Dolichopodidae). 5. One thoracic and five abdominal centres (Tabanidae, Stratiomyidae). 6. One thoracic and two abdominal centres (Syrphidae). 7. One thoracic and one abdominal centre (Conopidae and most Acalyptratae). 8. A single thoracic centre (Calyptratae and Pupipara).

In the Nematocera, and also the Rhagionidae and Asilidae, the nervous system of the imagines exhibits only a slightly greater concentration than in their larvae. Stratiomyidae, Syrphidae, Conopidae and certain Acalyptratae exhibit decentralization in the imago compared with the larva. In the Calyptratae and Pupipara the concentration of the larval nervous system is persistent in the imago. In *Musca* and other Calyptratae the nervous system exhibits the highest stage of concentration. The brain and infra-oesophageal ganglion are closely united to form a compact mass perforated by a foramen for the oesophagus. The thoracic and abdominal ganglia are intimately fused to form a common ganglionic mass situated in the thorax. Posteriorly, the nervous system is prolonged as a median abdominal nerve giving off lateral segmental nerves, two pairs in the thorax, and the remainder in the abdomen (Fig. 68D).

In the **Female Reproductive System** there is a variable number of polytrophic ovarioles (Fig. 458). The latter are fewest in number in larviparous species: thus in *Glossina*, *Musca bezzii* and *Termitoxenia*, a single ovariole is present on each side, while in *Melophagus* and *Hippobosca* there are two. The majority of Diptera, however, are oviparous and the ovarioles are much more numerous, their number varying from about 5 to over 100. In *Chironomus* the morphology of the ovaries is peculiar: each consists of a central axis radiating out from which is a large number of short ovarioles, the whole being enclosed in a delicate membrane (Miall & Hammond).

Spermathecae are universally present: they are usually conspicuous dark brown or black globular sacs, lined with thick cuticle. There may be a single spermatheca present (*Anopheles*, *Simulium*), or two (*Mansonia*, *Phlebotomus*, *Dacus*), or three (*Culex*, *Aedes aegypti*, the Tabanids and most Calyptratae). A pair of tubular accessory glands is usually present opening into the dorsal region of the vagina. Small and unpaired in *Anopheles*, they are large in Tabanids, elongate and filiform in *Musca*, *Hypoderma* and most other Calyptratae. Their normal function apparently is to secrete a viscid substance which enables the eggs to adhere to one another or to the substratum upon which they are laid. In *Glossina* and the Pupipara they secrete a milky fluid which serves to nourish the intra-uterine larva.

Viviparity is not infrequent among Calyptratae and is of general occurrence in the Pupipara: among other Diptera it is exceedingly rare but occurs in *Chironomus stercorarius*. Viviparous Diptera may be divided into two main groups as follows (Keilin, 1916):

GROUP 1.—Species whose larvae hatch from the eggs in the uterus of the parent but exhibit no special adaptations to an intra-uterine life. Included in this group are numerous Tachinidae which produce a large number of minute eggs and the larvae emerge within the uterus which is greatly elongated for their reception. In some

species the larvae hatch outside the parent, immediately after the eggs have been laid. Larviparity is characteristic of the Sarcophagidae, but in this group the eggs are larger and fewer: usually 40 to 80 are produced at a time and the larvae are deposited in their first instar. In a number of other species (*Theria muscaria* = *Helicobosca distinguenda*, *Mesembrina meridiana*, *Hylemyia strigosa* = *strenua*, *Musca larvipara*, *Dasyphora pratorum*, etc.) a single very large egg is produced at a time and the parental uterus is enlarged to form an incubatory pouch. In these instances the larva is retained for a variable time within the parent before deposition and the extreme condition is

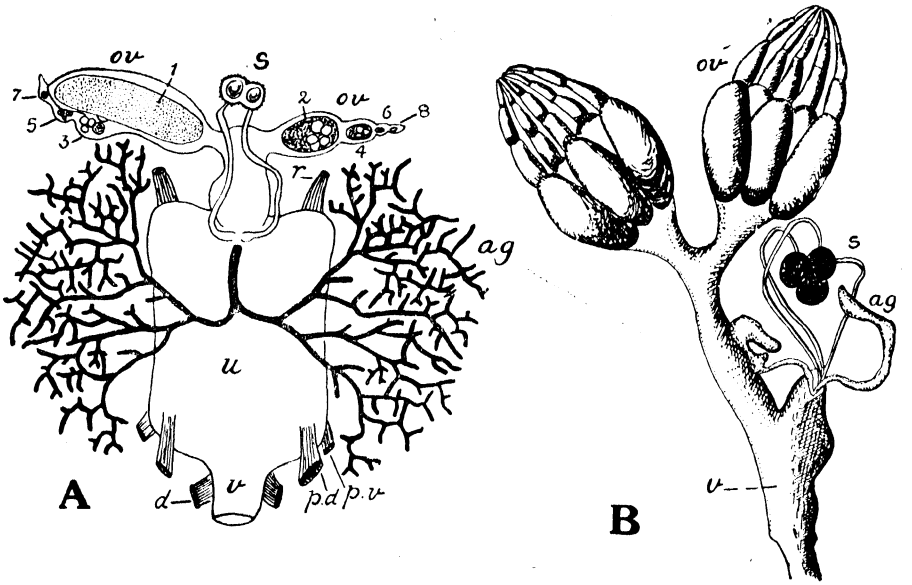


FIG. 458.—Female reproductive organs. A, *Glossina palpalis*, adapted from Roubaud, 1908; B, *Limnophora* (*Melanochelia*) *riparia*, after Keilin, 1917

ag, accessory glands; *d*, dilator muscle of vagina, *v*; *pd*, *pv*, dorsal and ventral protractor muscles of uterus, *u*; *r*, retractors of same; *ov*, ovary; *s*, spermatheca. The numerals in A refer to the relative ages of the oocytes.

afforded by *Dasyphora pratorum* in which it has attained its 3rd instar at the time of extrusion.

GROUP II includes *Glossina* and the Pupipara. The larva lies in the uterus of the parent and is nourished by the product of special nutritive glands. The secretion is discharged at the apex of a papilla and absorbed directly through the mouth of the larva. The following special adaptations to an intra-uterine life are exhibited. The buccal apparatus is reduced to a single basal sclerite: the mid gut is a closed sac which does not communicate with the hind intestine and, moreover, is greatly elongated to form a food-reservoir; there are no salivary glands. The hind intestine is greatly shortened and forms a receptacle for the accumulation of waste products excreted by the Malpighian tubes. The larvae when deposited are mature and shortly afterwards pupate.

In the **Male Reproductive System** (Keuchenius, 1913) the *testes* are, as a rule, ovoid or pyriform and frequently pigmented. The vasa deferentia are generally short and become confluent distally to form a common ejaculatory duct. In association with the latter, in many Diptera, is a muscular *ejaculatory sac* probably concerned with regulating the discharge of the seminal fluid. Paired accessory glands are often present.

In *Chironomus*, *Phlebotomus* and *Tabanus* the first portion of the common genital canal is enlarged and functions as a *vesicula seminalis* from which a narrow ejaculatory duct leads to the aedeagus; in these genera accessory glands are wanting. In *Culex* each vas deferens enlarges distally to form a

vesicula seminalis, and two pyriform accessory glands open into a very short ejaculatory duct. In *Musca* there are no accessory glands and the ejaculatory duct is a long winding canal: *Calliphora* (Graham-Smith, 1939) (Fig. 154) resembles *Musca* but differs in the presence of accessory glands. In *Dacus* the latter consist of about 16 blind tubules (Miyake, 1919), while in *Hypoderma* there is a small unpaired globular gland. In the Pupipara the genital organs attain their greatest complexity, and the testes are in the form of compactly coiled tubules resembling balls of thread. The reproductive organs of *Glossina* resemble those of Pupipara rather than of Muscidae, the testes being similar densely coiled tubes. The ejaculatory sac is an organ of variable structure: in *Musca* it contains a sclerotized, phylliform *ejaculatory apodeme* which aids in propelling the seminal fluid along the genital canal during copulation (Hewitt). In *Dacus* the ejaculatory sac is very large, while in *Phlebotomus* its place appears to be taken by an organ termed by Grassi the 'pompetta'—a piston-like chamber provided with a movable rod: since the opening of the ductus ejaculatorius is near the lower end of this chamber, the latter is believed to regulate the seminal flow after the manner of a pump.

The **Heart** has been very little investigated: in *Musca* (Hewitt) and *Calliphora* (Lowne) it is divided into four large chambers, corresponding to the visible abdominal segments, and a small anterior chamber: each chamber in *Musca* has a pair of dorsolateral ostia at its posterior end. Anteriorly the heart is prolonged as a tube of narrow calibre.

The most important feature of the **Tracheal System** is the great development of air-sacs, particularly among Cyclorrhapha. In *Musca* and *Volucella* the air-sacs occupy more space than any other organs, and the haemocoele is consequently much reduced. The largest and most prominent of the air-sacs are the abdominal: numerous sacs are also present in the thorax and head (Hewitt, 1914; Künckel d'Herculais, 1879).

Literature.—General works on the anatomy of adult Diptera are extremely few: a good deal of information will be found in the writings of Dufour (1851) and the textbook of Patton & Cragg (1913). For the detailed structure of individual types vide Miall & Hammond (1892) for *Chironomus*; Nuttall & Shipley (1901–03) for *Anopheles*; Künckel d'Herculais (1875) for *Volucella*; Hewitt (1914) for *Musca*; Lowne (1890) for *Calliphora*; Tulloch (1906) for *Stomoxys*; Cragg (1912) for *Haematopota*; and Roubaud (1909) for *Glossina*; Owsley (1946) for Asilidae.

Metamorphoses

No other order of insects presents so great a diversity of larval habits as the Diptera. Four families only have the great majority of their species phytophagous in the larval state, i.e. Cecidomyidae, Trypetidae, Agromyzidae and Chloropidae, while the Mycetophilidae and Platypezidae are fungivorous. The saprophagous habit is largely in evidence among the Anthomyinae. Other notable scavengers are the Bibionidae, Sepsidae, Phoridae, Helomyzidae and Cordilurinae. True parasitism, either internal or external, obtains in the Tachinidae (s.l.), Oestridae, Pipunculidae, Conopidae, Bombyliidae, Acroceridae, Nemestrinidae and in a few Acalyptrates. Next to the parasitic Hymenoptera, the Diptera constitute the most important natural controlling agency over the increase of other insects. The predacious habit occurs in many families, particularly among the Brachycera, and in numerous members of the Syrphidae and Muscidae. With the exception of many

Sciomyzidae and Ephydridae, the truly aquatic larvae belong mostly to the Nematocera and to the Stratiomyidae and Tabanidae among the Brachycera.

In their larval instars many Diptera affect the operations of man or his person. The four phytophagous families enumerated above include some of the most serious pests the agriculturist and fruit grower have to contend with. The larvae of the pear and wheat midges, of the Mediterranean fruit fly, the frit and gout flies are cases in point. Among the Muscidae, the larvae of the cabbage root fly and onion fly bring about great losses to growers of those vegetables.

The science of parasitology is concerned with many Dipterous larvae which directly affect the bodies of man and domestic animals. Under the term *myiasis* are included all affections produced by Dipterous larvae among vertebrates, and more particularly mammals. The species concerned are either parasitic or saprophagous, and it is frequently possible to distinguish between primary myiasis, which is induced by true parasites, and secondary myiasis which is brought about by saprophagous larvae. The latter only follows on diseased conditions or wounds, and usually where there is microbic infection.

From the clinical standpoint myiasis in man may be grouped as follows :—

1. CUTANEOUS MYIASIS: the larvae primarily concerned are those of *Dermatobia*, *Cordylobia* and *Bengalia*. Species of *Hypoderma* and *Gasterophilus* also occasionally induce myiasis. 2. MYIASIS OF THE CRANIAL CAVITIES (orbital, nasal and auditory): caused by larvae of *Oestrus*, *Rhinoestrus*, *Gasterophilus* and *Dermatobia*. When of a secondary nature it is commonly due to larvae of *Sarcophaga*, *Musca*, or *Callitroga*: auditory myiasis appears to be always of a secondary nature and follows some purulent affection of the ear. 3. MYIASIS OF THE DIGESTIVE CANAL: larvae of at least 18 genera have occurred in the alimentary tract, but probably many pass through without causing recognizable symptoms.

In almost all cases of human myiasis the occurrence of Dipterous larvae is occasional and their presence is a departure from their normal host or mode of life.

Dipterous *larvae* (Fig. 448) are devoid of true legs, locomotion often either taking place by means of pseudopods, or by the aid of groups of shagreen-like spinules, frequently located on swellings of the body-wall. The greatest number of undoubted segments present is twelve, e.g. three thoracic and nine abdominal. Departures from this generalized condition are not infrequent: thus in some larvae the number is less than twelve, atrophy or fusion of one or more of the somites having taken place. In larvae possessing more than twelve apparent segments (Anisopodidae and Therevidae) two explanations have been offered. Either certain segments have undergone secondary division, or the intersegments have become greatly enlarged so as to assume the appearance of true segments. Keilin (1915) has shown that six groups of sensory organs are present in all Dipterous larvae, and are in direct relation with the imaginal leg-buds, thus occupying the positions of the ancestral thoracic limbs.

The number of families in which a well-developed *head* is present is small; it is fully formed in the Culicidae, which are described as being 'eucephalous', as well as in most other Nematocerous larvae (except Cecidomyidae and Tipulidae). At the opposite extreme is the so-called 'acephalous' condition present in the Cyclorrhapha, where the head is vestigial (Fig. 448). Many Dipterous larvae (e.g. Brachycera) are in a 'hemicephalous' or intermediate condition, a reduced head or 'jaw-capsule' being present.

This type of head is incomplete posteriorly and can be withdrawn into the thorax. A similar condition is found in the Tipulidae, the skin of the neck being attached to the middle region of the head with the result that the latter is incomplete posteriorly, and permanently imbedded within the body.

The *antennae* are variously formed, very rarely prominent, and are composed of 1 to 6 segments. They are best developed in active larvae which need to seek out their food (Nematocera). In the Mycetophilidae, many Brachycera and most Cyclorrhapha they are reduced to the condition of small papillae.

The *mouthparts* are variable in character in different groups and are exhibited in their least modified condition in certain families of Nematocera. Thus, in *Bibio* (Fig. 459) there is a definite labrum, mandibles are well developed and move in the horizontal plane and the maxillae are represented by a single lobe or mala and an evident palpus on either side. The labium is in the form of a median plate with a strongly sclerotized hypopharynx

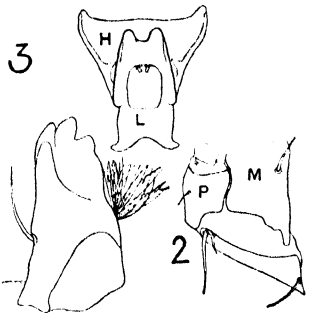


FIG. 459.—Mouthparts of larvae of *Bibio marci*

1, mandible. 2, maxilla. *P*, palp; *M*, mala. 3, *L*, labium; *H*, hypopharynx. *After* Morris.

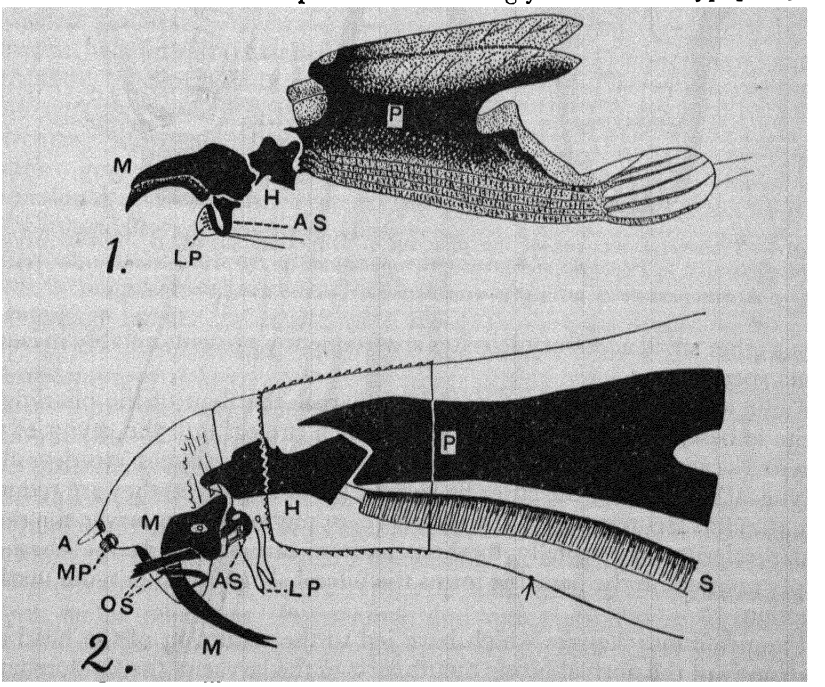


FIG. 460.—Cephalopharyngeal skeleton of larvae of 1, *Musca domestica* and 2, *Limnophora* (= *Melanochelia*) *riparia*

A, antenna; *AS*, dentate sclerite; *H*, hypostomal sclerite; *LP*, labial palp; *M*, mandibular sclerites; *MP*, maxillary palp; *OS*, accessory oral sclerites; *P*, pharyngeal sclerite; *S*, salivary duct. Adapted from Keilin, *Parasitology*, 9, 1917.

lying above it on the pharyngeal aspect: labial palpi are wanting. Among the Brachycera the same parts, although variously modified, are more or less evident but the mandibles, on the other hand, work in the vertical plane. In

the Cyclorrhapha the typical mouthparts have undergone atrophy in correlation with the reduction of the head: the maxillae and labium are scarcely recognizable other than by the papillae representing their palpi. In this group of Diptera there is a very characteristic framework of articulated sclerites, the whole being known as the *cephalopharyngeal skeleton* (Fig. 460) (Muirhead-Thomson, 1937). This structure is a secondary development and is composed of the following principal sclerites. The most anterior are the *mouth-hooks* or *mandibular sclerites* which articulate basally with the hypostomal or *intermediate sclerite*. The latter is H-shaped, its halves being joined by a transverse bar: the hypostomal sclerites receives the opening of the salivary duct. Behind this sclerite is the much larger *basal* or *pharyngeal sclerite*. The latter is formed of two lateral, vertical lamellae which unite ventrally forming a trough in which is lodged the pharynx. In many species a cuticular arc (*dentate sclerite*) unites the bases of the mandibular sclerites:

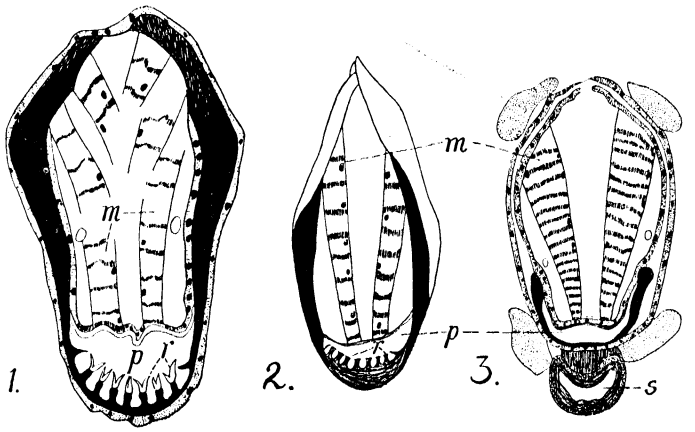


FIG. 461.—Transverse sections of the pharynx of Dipterous larvae. 1, *Muscina assimilis* (saprophagous). 2, *Pegomyia nigritarsis* (phytophagous). 3, *Syrphus ribesii* (carnivorous) *m*, dilator muscles; *p*, cavity of pharynx; *r*, ridges; *s*, salivary duct. *After* Keilin, 1915.

various other small accessory sclerites are frequently present, notably in carnivorous species.

Keilin has shown that in saprophagous larvae the floor of the pharyngeal sclerite is beset with longitudinal ridges which project into the cavity of the pharynx: larvae feeding on living animal or vegetable tissues are devoid of pharyngeal ridges or, if the latter be present (as in *Pegomyia*) they are reduced (Fig. 461) (cf. Hennig, 1935). Furthermore, in phytophagous larvae the mandibular sclerites are usually toothed, and in carnivorous larvae they are sharply pointed: in the parasitic forms the buccal armature undergoes marked reduction.

The profound changes which have led to the reduction of the head and the atrophy of the normal biting mouthparts in the larvae of the Cyclorrhapha appear to be correlated with the two series of factors. Firstly, degeneration consequent upon a life passed in the immediate proximity of an abundance of food, and also a change in the manner of feeding. Secondly, to the backward shifting of the brain and the development of the imaginal head within the larval metathorax. For a general discussion of the head and its modifications among Dipterous larvae, and the structure of the mouthparts, the student is referred to the writings of Holmgren (1904), Becker (1910), de

Meijere (1916), Keilin (1915), Keilin & Tate (1940), Anthon (1943), Cook (1949) and Hennig (1948–52).

Although Dipterous larvae are apodous in the true sense of the term pseudopods are present in numerous genera. Thus in *Chironomus*, *Thaumalea* and *Simulium* a pair is present on the prothoracic and anal segments. In *Dicranota* five pairs are evident on segments 6 to 10: in *Eristalis* there are 7 pairs while in *Atherix* and *Clinocera* there are 8. Circlets of pseudopods are present in the abdominal region in *Laphria* and the Tabanidae.

The *tracheal system* (Keilin, 1944) presents features of great systematic value and the most prevalent type is the amphipneustic one (Fig. 462). The primitive or peripneustic condition is almost entirely confined to Nematocera: the maximum number of pairs of spiracles present is 10 (*Bibio*) while 9 pairs occur in Scatopsinae, Cecidomyidae and a few others. Indications of a former peripneustic condition are seen in other forms in the presence of solid stigmatic cords leading from spiracular scars to adjacent tracheae. The larvae of Cyclorrhapha, when newly hatched, are metapneustic, becoming amphipneustic in the 2nd and 3rd instars. Among the Aschiza, the prothoracic spiracles in some genera are apparently nonfunctional, the tracheal system being physiologically metapneustic. The propneustic condition is extremely rare but is stated to obtain in *Polylepta*. Apneustic larvae are found in *Chaoborus*, in Chironomidae, and also in *Ceroplatus* and *Atherix*.

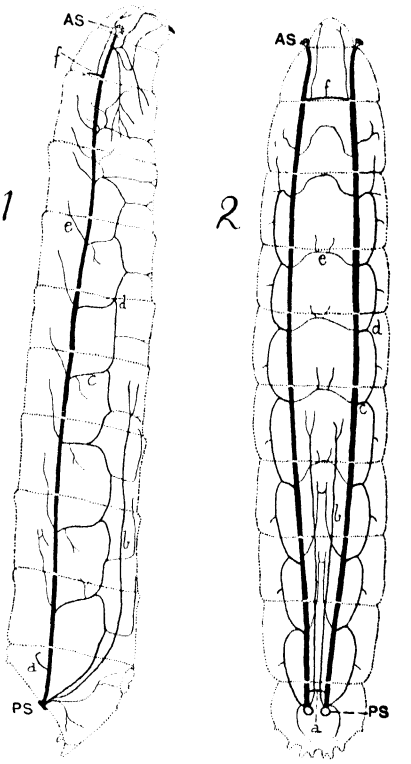


FIG. 462.—Amphipneustic tracheal system of 3rd instar larva of *Hylemyia* (Muscidae)

1, lateral; 2, dorsal view. *AS*, anterior spiracle; *PS*, posterior do.

In peri- and amphipneustic larvae the 1st pair of spiracles is carried on the prothorax: in the former condition the 2nd pair is borne on the metathorax or 1st abdominal segment, never on the mesothorax. The segmental position of the posterior pair of spiracles is variable: it is frequently on the last segment whether it be the 11th, as in many Brachycera, or the 12th segment, as in *Dicranota*, *Ptychoptera*, and numerous Cyclorrhapha. In the Culicidae and certain Brachycera the spiracles are situated on the penultimate segment, and in the Therevidae and Scenopinidae on the ante-penultimate segment. In certain metapneustic larvae (Culicidae, *Dixa*, *Psychoda*, some Tipulidae, etc.) the two main tracheal trunks give off a plexus of fine tracheal branches in the neighbourhood of the spiracles, and pass to the walls of the posterior region of the heart. These branches are very thin walled, and it appears probable that the blood is brought into close contact with the oxygen contained therein, and in this way they function as a kind of lung (Imms, 1907).

Accessory respiratory organs in the form of gills are found among aquatic larvae. In certain Chironomids two pairs of 'blood-gills' are situated on the 11th segment, and a similar number of smaller blood-gills are present around the anus. In Culicidae (Wigglesworth, 1933), these structures have been shown to extract chloride ions from the water. Tracheal gills are much more frequent than blood-gills: they may be ventral as in the two pairs on the last segment of *Dicranota*, segmental as in *Phalacrocera*, caudal as in Culicidae, or rectal as in *Simulium* and *Eristalis*. The caudal retractile processes of *Pedicia* and other aquatic Tipulid larvae are probably of a similar nature.

The *alimentary canal* in larvae of the Nematocera, and certain Brachycera, is a short tube but little convoluted. In most Cyclorrhapha (Guyénot, 1907) it is greatly lengthened and complexly coiled upon itself. The oesophagus is prolonged backwards into the mid gut to form an oesophageal valve, or cardia, of varying complexity. In many Cyclorrhapha a food reservoir is present as in the adult. The usual number of Malpighian tubes is four, which may arise separately from the hind gut, as in *Tabanus* and *Stomoxys*. In *Musca* and most other Cyclorrhapha they united basally in pairs, each pair communicating with the hind gut by means of a short duct. In the Culicidae, *Psychoda*, *Ptychoptera*, and the Blepharoceridae five Malpighian tubes are present.

Salivary glands are found in all Dipterous larvae and generally take the form of hollow vesicles lined with a single layer of cells. *Mandibular glands* occur in *Sciara* and extend almost the whole length of the body (Keilin, 1913). Metamerically arranged *hypodermal glands* are found in Tipulid larvae (Fig. 138), and small *peristigmatic glands* are found in association with the spiracles of many Dipterous larvae.

The *heart* consists of a series of eight chambers in *Anopheles* and other Nematocera. In species of *Chironomus* it is formed of a single enlarged chamber situated in the 11th segment and provided with two pairs of ostia. In *Musca* it comprises three chambers situated in the terminal segments, while in *Dicranota* no distinct chambers are evident (Miall). In all cases the heart is prolonged through the thorax as the aorta, which terminates in the head near the brain. A short distance behind the latter is a glandular structure, generally forming a ring (Weismann's ring) around the aorta (Thomsen, 1951; cf. p. 175).

The nervous system in Nematocerous larvae (Brandt, 1882; Brauer, 1884) consists of the usual supra- and infra-oesophageal ganglia and, as a rule, 3 thoracic and 8 abdominal ganglia. Among the Brachycera this generalized condition of 11 postcephalic ganglia is present in the Rhagionidae, Asilidae, Therevidae, and Dolichopodidae. The Tabanidae are intermediate between these families and the Cyclorrhapha, reduction and concentration resulting in only 1 thoracic and 5 abdominal ganglia being present. In *Stratiomyia* all the ganglia are fused into a single ovoid ganglionic mass and a similar condition is the rule throughout the Cyclorrhapha (Fig. 135). The position of the brain varies among Nematocera; although usually present in the head as in *Culex*, in *Tipula* and *Ptychoptera* it is situated partially in the head and prothorax, while in *Dicranota*, *Psychoda* and certain Chironomidae it lies wholly in the prothorax. In *Calliphora* and other Cyclorrhapha it is situated in the metathorax.

The **Pupa.**—Most Nematocera have 4 larval instars (6 in Simuliidae); in the Brachycera the number varies as a rule between 5 and 8; in the Cyclorrhapha there are only 3 instars but a fourth moult, not always complete, occurs within the puparium (Fraenkel, 1938). Pupation takes place by one of

two methods. In the Nematocera and Brachycera the skin is normally cast at pupation but in the Stratiomyidae the exuviae persist and loosely enclose the pupa. In the Cyclorrhapha the pupa is enclosed in the larval skin which hardens forming an outer shell or puparium. The puparium is ovoid or barrel-shaped and quite immobile (Fig. 197). A pupal shelter is formed in several Nematocerous families and among the Brachycera a cocoon is present in certain Dolichopodidae. Among Cyclorrhapha it is very rare but is found in a few genera of Muscidae. In the lower Diptera prothoracic and 7 pairs of abdominal spiracles are usually evident; aquatic Nematocera, however, are propneustic. In the puparia of the Cyclorrhapha remains of the larval spiracles can be seen. In *Musca* communication with the air is maintained by means of a pair of pupal spiracles in the form of small spine-like projections between the 5th and 6th segments of the puparium (Hewitt). Similar, though more prominent, respiratory structures are prevalent in other Cyclorrhapha.

Literature on the Larval and Pupal Stages.—Malloch (1917) and Verrall (1909) give much information about Dipterous larvae and the first author keys to the early stages of Nematocera and Brachycera. Recently, a very complete tabulation and summary has been published by Hennig (1948–52). Aquatic Dipterous larvae have been much studied notably by Meinert (1886), Miall (1895), Grünberg (1910), Williams (1939), Johannsen (1937), Johannsen & Thomsen (1937), Lenz (1941) and Thienemann (1944). Other studies of Nematocera are those of Mayer (1934) (Ceratopogonidae), Madwar (1937) (Mycetophilidae), Sellke (1936) (Tipulidae), and Keilin & Tate (1940) (Trichoceridae, Anisopodidae). For larvae of Cyclorrhapha the works of Banks (1912), Keilin (1915; 1917) may be referred to and for particular families—Heiss (1938) and Bhatia (1939) (Syrphidae), Muirhead-Thomson (1937) (Muscidae Anthomyinae), and Butt (1937), Phillips (1946) and Keilin & Tate (1943) (Trypetidae). Hayes (1938) has published a list of published keys for identification of larvae and Séguy (1950) a review of the biology of the order.

Classification of Diptera

The Diptera may be classified into three suborders, viz. the Nematocera, Brachycera and Cyclorrhapha. The first mentioned include the most primitive forms, the Cyclorrhapha comprise the most highly specialized while the Brachycera occupy in some respects a position intermediate between these two groups. In the time-honoured classification of Brauer two suborders are recognized, viz. the Orthorrhapha (including the Nematocera and Brachycera) and the Cyclorrhapha. These differ rather in the absence or development of a puparium than in the method by which the imago escapes from the pupa, the feature stressed by Brauer. The characters of the suborders are as given below.

Suborder I. NEMATOCERA

Larvae with a well-developed exserted head and horizontally biting mandibles; pupa free except in some Cecidomyidae. Antennae of imago many-segmented (except in Nymphomyidae), usually longer than the head and thorax, the majority of the segments usually alike; arista wanting. Palpi usually 4 or 5-segmented, pendulous. Pleural suture of mesothorax straight (except in the Psychodidae). Discal cell generally absent, cubital cell when present widely open.

Suborder II. BRACHYCERA

Larvae with an incomplete head, usually retractile, and with vertically biting mandibles; pupa free except in the Stratiomyidae. Antennae of imago shorter than the thorax, very variable, generally 3-segmented with the last elongate; arista or style when present terminal. Palpi porrect, 1 or 2-segmented. Pleural suture twice bent (except in the Acroceridae). Discal cell almost always present, cubital cell contracted before the wing-margin or closed.

Suborder III. CYCLORRHAPHA

Larva with a vestigial head: pupation in a puparium. Antennae of imago 3-segmented with an arista usually dorsal in position. Palpi 1-segmented. Discal cell almost always present. Pleural suture twice bent. Cubital cell contracted or closed. Head with a frontal lunule and usually a ptilinum (absent in suborders I and II).

Literature.—General accounts of the order include those by Hendel (1928; 1936–37) and Crampton *et al.* (1942). A handbook on the British fauna is in the course of publication (Oldroyd *et al.*, 1949–50). Lundbeck's incomplete work (1907–27) on the Danish species is also valuable and Curran (1934) has dealt with the American families and genera. Verrall's standard work (1909) deals with the British Brachycera. Among the Cyclorrhapha, Verrall (1901) has dealt with the Aschiza and Townsend's work (1934–44) on the Muscoid flies contains much information. The monograph of the Palaearctic Diptera, edited by Lindner (1924–51), is still in the course of publication. Becker *et al.* (1903–17) issued a catalogue of the Palaearctic Diptera, Aldrich (1905) of the N. American, and Kertész (1902–10) of the world (incomplete).

Suborder I. NEMATOCERA

A certain number of members of this section exhibit exceptional morphological characters. Thus, among the Culicidae the palpi are stiff and-projecting, not pendulous as in other families. When the antennae are short, and apparently only annulated (Simuliidae and Bibionidae), the widened cubital cell and pendulous palpi indicate their affinities with this suborder. The anomalous Nymphomyidae with a Brachycera-like antennae, have characteristic venation and long fringes to the wings. When the palpi are 1- or 2-segmented (certain Cecidomyidae) the antennal and venational characters remove all doubts.

The following key will serve for the identification of the families:

1. Costa extending right round the wing, though weaker along posterior margin. 2
–. Costa confined to the anterior margin of the wing 13

2. Wings with 9 veins reaching the margin. 3
–. Wings with fewer than 9 veins reaching the margin 10

3. Thorax with a V-shaped suture on the mesonotum. Female with a horny ovipositor. Intermedian cell usually present 4
–. Thorax without a V-shaped suture. Female without a horny ovipositor. Intermedian cell absent 7

4. 2 anal veins reach the margin 5
–. Only 1 anal vein reaching the margin. Ocelli absent 6

5. 2 or 3 ocelli present. Vein 2A short and strongly curved TRICHOCERIDAE (p. 610)
–. Ocelli absent. Vein 2A longer and straighter . . . TIPULIDAE (p. 609)

6. Intermedian cell present. Vein R_2 reaches the margin TANYDERIDAE (p. 610)
–. Intermedian cell absent. Vein R_2 runs into R_1. . PTYCHOPTERIDAE (p. 610)

7. Ocelli present. Antennae with 10 segments, the 2nd strongly elongate. . BIBIONIDAE (Hesperininae) (p. 617)
–. Ocelli absent or vestigial 8

8. Wings not specially hairy or scaly. 2nd antennal segment short and thick, distal segments filamentous . . . . . DIXIDAE (p. 610)
—. Wings scaly or densely hairy 9

9. Vein Sc short, wings usually ovate and held roof-like over the body. 2nd antennal segment small . . . . . PSYCHODIDAE (p. 610)
–. Vein Sc long, wings longer and narrower, not held roof-like over the body. 2nd antennal segment globose . . . . . CULICIDAE (p. 611)

10. Wings with a network of vein-like creases 11
—. Wings without this secondary network 12

11. Ocelli and mouthparts absent. Antennae very elongate DEUTEROPHLEBIIDAE (p. 614)
—. Ocelli and mouthparts present. Thorax with a V-shaped suture on the mesonotum . . . . . BLEPHAROCERIDAE (p. 614)

12. Proximal antennal segments thickened, distal ones much thinner. 7 veins reaching the margin, cross-vein m-cu present . . . THAUMALEIDAE (p. 615)
—. Antennal segments of more uniform thickness. At most 6 veins reaching the margin, cross-vein m-cu absent . . . . CECIDOMYIDAE (p. 615)

13. Wings with an intermedian cell . . . ANISOPODIDAE (part) (p. 616)
—. Wings with no intermedian cell 14

14. Ocelli distinctly present 15
—. Ocelli absent or very indistinct 18

15. Venation confined to the base of the wings which are fringed by dense hairs; these on the posterior margin are much longer than breadth of wing. Eyes connected ventrally. Antennae with 3 segments and a short 2-segmented style NYMPHOMYIDAE (p. 619)
—. Venation less restricted, wing-fringe shorter. Eyes sometimes connected dorsally but not ventrally. Antennae normal 16

16. Coxae not specially elongate, or if somewhat so, pulvilli large and the male holoptic. Tibial spurs present or absent . . . BIBIONIDAE (p. 617)
—. Coxae elongate. Pulvilli small or absent 17

17. Eyes not connected by a dorsal bridge of facets. Cross-vein m-cu present, Rs present distally and appearing like a fork of R_1, Sc short and ending free. Pronotum without long bristles . . ANISOPODIDAE (*Mycetobia*) (p. 616)
—. This combination of characters not present . . MYCETOPHILIDAE (p. 617)

18. Cu_1 and M_{3+4} separate. Mandibles developed . . SIMULIIDAE (p. 619)
—. Cu_1 and M_{3+4} on a common stalk. 19

19. Vein M_{1+2} forked. Mandibles present. Fore legs normal CERATOPOGONIDAE (p. 621)
—. Vein M_{1+2} simple. Mandibles absent. Fore legs elongate CHIRONOMIDAE (p. 620)

FAM. TIPULIDAE (Daddy-long-legs or Crane Flies).—*Antennae long* 6- *to many-segmented, ocelli wanting. Legs always long and deciduous, mesonotum with* V*-shaped transverse suture, discal cell present. Ovipositor valvular, horny. Larvae metapneustic, anal extremity with fleshy retractile processes.* The Tipulidae include some of the largest species of Nematocera. The number of antennal segments is extremely variable and they are occasionally pectinate or serrate in the male, but not plumose. The front of the head is prolonged forwards to a greater or lesser degree, and in a few genera an elongate proboscis is present: throughout the family ocelli are absent. The V-shaped mesonotal suture is characteristic but it is wanting in the apterous genus *Chionea*.

The larvae are hemicephalous, the head being deeply imbedded in the prothorax and incomplete posteriorly. The antennae are well developed, the labium is large and toothed anteriorly, and there is usually a large and heavily sclerotized hypopharynx. The body is elongate-cylindrical, either with or without pseudopods,

11 or 12-segmented, and usually ashy grey or brownish in colour. Frequently the first 6 abdominal segments are subdivided and, as a rule, the anal segment is truncated, and bears the spiracles. Around the latter is a series of fleshy retractile processes; in aquatic species these processes are often fringed with hairs and protrusible blood-gills are present. In the terrestrial forms the hair fringes and gills are usually greatly reduced. The pupae are very elongate, and the thoracic respiratory horns are either slender or plate-like.

The larvae of *Tipula* may be taken as representative of the family, and live among grass, roots, etc., decaying vegetation, or are aquatic (Bodenheimer, 1924; Sellke, 1936). The larva of *Dicranota* lives in the beds of ponds and streams where it preys upon the worm *Tubifex*. It is characterized by paired retractile pseudopods on segments 6–10, and on the 12th segment there are 3 pairs of outgrowths of the nature of gills (Miall, 1893). The larva of *Ctenophora* and its anatomy has been studied by Anthon (1908) and that of *Holorusia* by Kellogg (1901): descriptions of the larvae and pupae of many other genera are given by Malloch (1917) and Alexander (1920).

The larvae of the Cylindrotomina group are very remarkable: they are green in colour, and aquatic or terrestrial, feeding upon mosses or Angiosperms. The body is provided either with filaments or leaf-like outgrowths: Miall & Shelford (1897) have made a detailed study of the larva of *Phalacrocera* which is aquatic, feeding upon mosses, and the whole body is invested with numerous elongate filamentous processes. In *Cylindrotoma* (Cameron, 1918) the larva is terrestrial with lateral plate-like outgrowths: it feeds openly like a caterpillar on various phanerogamic plants, and the pupa is attached to the food-plant by means of the partially cast exuviae. Among the Limnobiinae the larvae of some *Limnobia* are fungivorous, while those of *Dicranomyia* are mostly aquatic or semi-aquatic. A single species of the latter genus is exceptional in having a leaf-mining larva in the Hawaiian Islands.

FAM. TRICHOCERIDAE (Winter Gnats).—*Small, Tipulid-like flies, but legs not deciduous and ocelli present.* The adult flies commonly dance in swarms during the winter, or more rarely during the summer at high altitudes. The eucephalous, amphipneustic larvae are much more like those of the Anisopodidae than those of the Tipulidae, which the adults resemble. They develop in humus, often in groups. The larva is described by Keilin & Tate (1940).

FAM. PTYCHOPTERIDAE.—*Moderate-sized flies resembling Tipulids, but legs not deciduous and a characteristic vena spuria between R and M.* The adult flies of this small family are usually found at the edges of streams or ditches. The larvae (Miall, 1895) are found in damp situations, usually in muddy water where they feed upon the vegetable matter contained therein. They are long and slender with well-developed pseudopods armed with spinules: the spiracles are minute, and are borne at the apex of an extremely slender tube formed by the greatly prolonged terminal segments of the body. The pupal respiratory organs are unequal in length, one being many times longer than the other.

FAM. TANYDERIDAE.—*Flies of rather small size, Rs and M both 4-branched.* The flies of this family are regarded as the most primitive of all living Diptera (Williams, 1933). The larva which is aquatic somewhat resembles those of *Ptychoptera* (Alexander, 1930). There are about 30 species; one in the U.S.A., a few oriental and African, and a number in New Zealand (Alexander, 1927).

FAM. DIXIDAE.—*Insects almost devoid of hairs and scales, antennae elongate, about 16-segmented, filiform apically. Venation as in Culicidae; proboscis somewhat projecting, not adapted for piercing; ocelli absent. Larvae metapneustic and aquatic, usually assuming a U-shaped attitude.* A small family comprising the genera *Dixa* and *Neodixa* with more than 100 widely distributed species. These insects have been variously included in the Culicidae and Tipulidae. They are readily separable from most of the latter by the absence of the discal cell and the V-shaped thoracic suture: the filiform non-plumose antennae are totally different from those organs in the Culicidae, and find their parallel in *Trichocera*. They closely resemble the Culicidae, however, in their venation but differ therefrom in the absence of scales from the wings. The larva of *Dixa* frequents shady, weedy pools or streams and might be mistaken for that of *Anopheles*. It is eucephalous with 12 trunk segments, the 4th and 5th each bearing a pair of ventral pseudopods armed with curved spinules: segments 5–10 in certain species carry a dorsal shield fringed by setae. The pupa closely resembles that of the Culicidae.

FAM. PSYCHODIDAE (Moth-flies, Sand-flies). *Minute moth-like flies, the legs, body and wings clothed with long coarse hairs, often admixed with scales. No ocelli; wings with Rs 4-branched and no obvious cross-veins. Larvae usually aquatic or sapro-*

phagous, of variable structure, generally amphipneustic. These fragile insects are to be found in close proximity to the larval habitat and are commonly met with in dark or shaded damp situations; some are frequent on windows and are often attracted to a light at night. Females of the genus *Phlebotomus* (Fig. 463) feed by sucking the blood of vertebrates and in some species the male has this habit also. In addition to man, reptiles are used as hosts; and in the case of *P. minutus* lizards and geckos are probably the principal animals preyed upon. The well-known 'Pappataci' or 'three-day' fever was proved in 1908 by Doerr, in Herzegovina, to be carried by *P. papatasii*; possibly other species of the genus also function as carriers. In the Oriental region, other species are carriers of Kala-azar. Townsend has brought forward evidence indicating that the disease known as Verruga in Peru is transmitted by a species of *Phlebotomus*. The eggs in this genus are elongate and dark brown; the larvae have mostly been found in damp, dark places such as crevices in rocks and stone walls, in drains, unclean cellars, moist earth, etc. Their minute size, however, renders them extremely difficult to discover and further information is greatly needed with reference to their habitat. When fully grown the larva is about 2 mm. long, and provided with elongate caudal bristles which may be almost as long as the body. Decaying vegetable matter appears to be their chief food. The pupa is found in similar situations and usually carries the larval exuviae at its anal extremity. For further information on this genus reference should be made to papers by Grassi (1907), Newstead (1911), Perfil'ev (1937) and Raynal (1934).

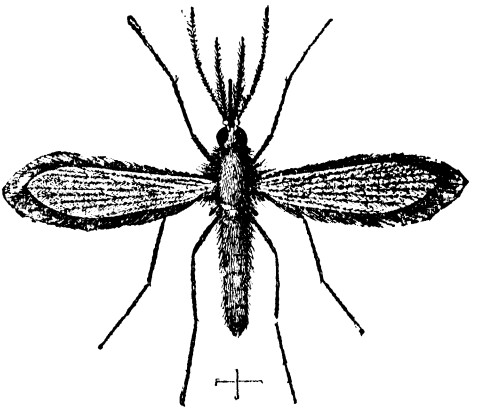


FIG. 463.—*Phlebotomus sp.*, female, Sudan. × 12

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The Psychodinae (for British species see Tonnoir, 1940) have very doubtfully been accused of the blood-sucking habit which, at any rate, is extremely rare in this subfamily. Many of the adults have remarkable secondary sexual characters (Feuerborn, 1922a). Their larvae possess a well-developed head and 12 trunk segments, the first and last carrying a pair of spiracles (Dell, 1905; Malloch, 1917; and Miall, 1895). The last segment is drawn out and provided with 4 fleshy outgrowths clothed with elongate hairs. By this means it forms a kind of siphon surrounding the posterior spiracles, and is protruded to the surface of the water. The thoracic and 1st abdominal segments are transversely divided, the remaining abdominal segments being triannulate. Dorsally, the larva carries a series of strongly sclerotized plates bearing sensory hairs. These plates are present on each segment (*Pericoma*) or only on the posterior segments (*Psychoda*). The larvae are aquatic, or live in fluid organic matter of various kinds, including sewage filter-beds. Those of *Ulomyia* and *Maruina* live in cascades. In the latter genus they are provided with ventral sucker discs as in Blepharocerid larvae, and moreover are metapneustic (Müller, 1895). The larvae of *Trichomyia* lives in decaying wood (Keilin, 1914). It is narrowly cylindrical, smooth, and devoid of dorsal plates and setae; the segments are undivided, and the tracheal system is amphipneustic with no respiratory siphon. In the remarkable genus *Termitomastus* found in the nests of Neotropical termites, the wings are reduced to strap-like rudiments: two other termitophilous genera, *Termitodipteron* and *Termitadelphos*, occur in the nests of *Eutermes* in Peru.

FAM. CULICIDAE (Mosquitoes).—*Very slender flies, generally with an elongate piercing proboscis and no ocelli: the palpi stiff and not pendulous. Legs long, antennae densely plumose in the males, pilose in the females. Wings fringed with scales along the posterior margin and the veins. Larvae and pupae aquatic and very active: the former metapneustic, with an enlarged thoracic mass.* The remarkable discoveries in their life-histories, and the part played by the adults as disease carriers, has given an enormous stimulus to the study of mosquitoes. More than 1,600 species have been described and at least 36 species occur in Britain. Culicidae are almost world-wide in distribution, but the tropics are much richer in genera and species than northern latitudes. In arctic

regions they are extremely abundant during the short summer, though few in species. In these parts they often occur far from the haunts of man and frequently in regions uninhabited by quadrupeds. In Lapland their numbers even exceed those of most tropical regions. For a full account of the biology of the family the student is referred to the standard treatise by Howard, Dyar & Knab (1912). For the anatomy of mosquitoes vide Nuttall & Shipley (1901–03), and Christophers (1901). For the larval anatomy of *Anopheles* vide Imms (1907–08) and of *Culex* vide Raschke (1887). The mouthparts of a mosquito have already been described (p. 590): in the Chaoborinae they are very short, concealed, and not adapted for piercing. Except in a few genera the whole body, legs and wings are in part, or entirely, clothed with scales.

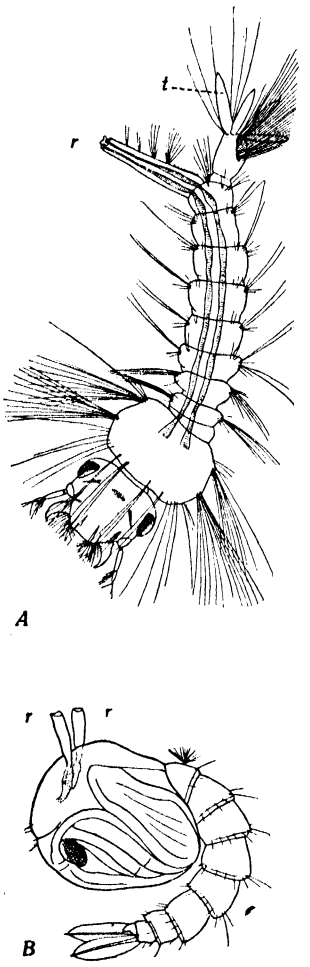


FIG. 464.—*Culex pipiens*

A, larva; B, pupa. *r*, respiratory siphon; *t*, tracheal gills. From Folsom's 'Entomology'.

The eggs are deposited on or near the surface of the water, and the number laid by a single individual varies from 40–100 (*Anopheles maculipennis*) up to 300 or more (*Culex pipiens*). They may occur singly, as in *Anopheles* or *Aëdes*, or collectively to form a compact mass or egg-raft as in *Culex* (Bates, 1949) and other genera. The eggs vary in shape in different genera: those of *Anopheles* are boat-shaped with a conspicuous float on either side: in *Culex* they are fusiform, in *Megarhinus* somewhat club-shaped, while those of *Aëdes* are ovoid and surrounded by a series of small air-chambers which aid in floating.

Mosquito larvae have a well-developed mobile head: the eyes vary according to the age of the larva and, as a rule, both the primitive larval eyes and the developing compound organs of the imago are present. A pair of dense tufts of long hair, or feeding brushes, are present over the mouth on either side of the head. By means of the movement of these brushes a current is set in motion which wafts microscopic food-particles towards the mouth. The thoracic segments are fused to form a single broad, rounded region. Nine abdominal segments are present, and the anal somite is surrounded at its apex by four tracheal gills. These organs are small in surface feeders such as *Anopheles*, but larger in *Aëdes* which is a bottom feeder. The respiratory system is metapneustic, and opens on the dorsal surface of the 8th segment. The spiracles are placed either on a quadrilateral area raised slightly above the preceding segment (Anophelinae), or more usually at the apex of a respiratory siphon. The larvae of *Chaoborus* (Peus, 1934) is a highly specialized type, being almost completely transparent and apneustic. It is provided with a pair of pigmented air-sacs in the thorax and a second pair in the 7th abdominal segment: these structures act as organs of flotation, respiration being cutaneous.

When at rest, and during feeding, the larvae of Anophelines float horizontally just beneath the surface-film with the palmate hairs and spiracular area in contact with the latter. In the Culicines the larvae bring the apex of the siphon in contact with the surface and hang head downwards, inclined at an angle with the surface film.

In their feeding habits, mosquito larvae may be phytophagous or carnivorous. As a rule they feed upon minute algae and other particles contained in the water. Certain forms, however, are carnivorous. These may be readily recognized either by the mouth-brushes being replaced by stout spines, which serve to seize the prey, or by the prehensile antennae (Chaoborinae). The organisms most frequently preyed upon are other mosquito larvae.

As a rule, mosquito larvae are only able to exist in small numbers in permanent waters on account of the presence of predators, such as fish and insect larvae. Their habitat is extremely varied, thus *Anopheles lutzi* breeds in the cups of epiphytic and

pitcher plants. The larvae of *A. rossi* frequent shallow rain-filled pools such as abound in India during the monsoon. *A. ludlowi* occurs in pools flooded by the sea at high tides: larvae of *Taeniorhynchus* live at the roots of aquatic plants in swamps, inserting their modified siphons into the tissues, and thus deriving their supply of oxygen. *A. listoni* frequents sub-Himalayan hill streams; *A. chaudoyei* lives in the waters of Saharan oases containing 40 gm. of chlorides per litre and *A. stephensi* abounds in Bombay, living in the waters of wells and cisterns. The pupae are very active, and respire by means of a pair of breathing trumpets communicating with the anterior spiracles. They float at the top of the water with their trumpets attached to the surface film.

When at rest Anophelines can usually be distinguished from other mosquitoes by the fact that they settle with the proboscis and the long axis of the body in one straight line, while in the Culicines the abdomen is usually parallel with, or inclined towards, the surface upon which the insect rests (Fig. 465). The length of the life-cycle of mosquitoes is primarily dependent upon temperature: thus, that of *A. aegypti* is normally 15–20 days, but may be as short as 11 days. The adult refuses to feed below 23° C. and is quite inactive at 20° C.

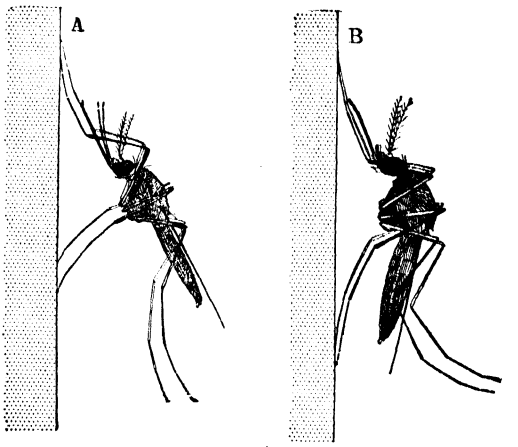


FIG. 465.—Resting attitudes of A, *Anopheles*, B, *Culex*

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Economically mosquitoes are of the utmost significance owing to their functioning as the intermediary hosts of malaria, yellow fever, filariasis, dengue and other diseases. Increased knowledge of these insects, and the diseases transmitted by them, has rendered vast areas of tropical countries no longer a menace to the life of the European. The experimental researches of Ross, on the malaria *Plasmodium*, have conclusively proved that this parasite passes through two periods of multiplication during its life-cycle: the first is one of asexual reproduction (schizogony) and occurs mainly in the blood of man. The second or sexual cycle (sporogony) takes place in the mosquito, and commences with the entry of blood containing suitable forms of the parasite into the stomach of the insect. After fertilization the zygote bores into the gut-wall where it becomes encysted. The cyst increases enormously in size, and eventually ruptures, liberating great numbers of sporozoites into the haemocoelic cavity of the insect. Those sporozoites, which bore their way into the salivary glands, are then able to be transmitted to another human being through the punctures of the mosquito, and there continue their development.

When the female mosquito feeds the tip of the labium is first brought against the skin, and then the pointed mandibles and maxillae are inserted. The labrum is also inserted into the puncture along with the hypopharynx. The labium is then doubled back in the form of a loop as the mouthparts become more deeply inserted. According to Macgregor (1931) two methods of feeding occur. In the method just described the ingested food is drawn continuously into the stomach. In the second method, termed 'discontinuous feeding', the mouthparts are not disengaged from the labium and the tip of the proboscis is merely dipped from time to time below the surface of the fluid to be imbibed. The ingested food then passes first to the oesophageal diverticula which act as food reservoirs. These organs also function as air separators in which 'air locks', between discontinuous sections of fluid, are removed before such fluid passes into the stomach. Control is exercised over ingested foods to the extent that blood is allowed to pass to the stomach and sugary solutions into the diverticula. It appears that in *Aëdes* the entry and digestion of blood in the stomach is a necessary condition for ovulation.

A number of Anopheline mosquitoes are now known to be carriers of the plasmodia of one or more forms of malaria and, as the habits of these species greatly vary, a knowledge of their bionomics is of the highest importance from the standpoint of

public health. Among the more important carriers are *Anopheles maculipennis* (Europe, parts of United States), *A. culicifacies* (India), *A. costalis* and *A. funestus* (Africa), *A. albimanus* (Central and S. America), *A. quadrimaculatus* (U.S.). An important recent development is the recognition within many of the older species of 'micro-species' with substantial differences in their biology and efficacy as vectors (Bates, 1949).

Aëdes aegypti is one of the commonest mosquitoes of the tropics and subtropics of the world, and occurs largely along coasts and the courses of the larger rivers. In 1881 Finlay observed the incidence of this mosquito and yellow fever in Cuba, and succeeded in transmitting the disease through the agency of its punctures. In 1899 an American commission sent to Cuba definitely proved that yellow fever is carried by *A. aegypti*. As the result of anti-*Aëdes* measures in the Panama Canal zone, which was at one time a notorious region for this disease, yellow fever has become non-existent there. The eggs of this mosquito are laid upon any accumulation of stagnant water however small, old tins, broken bottles, holes in trees often being utilized. The larva of this species may be recognized by its comparatively colourless appearance, and the short black respiratory siphon, $\frac{1}{4}$ the length of the abdomen. The adult is most easily identified by the lyre-shaped white mark on the thorax: it is essentially a domestic species rarely found away from towns and villages.

Culex fatigans is an almost tropicopolitan mosquito of great economic significance. Along with other species it is a carrier of *Wuchereria bancrofti* which produces elephantiasis. Both *C. fatigans* and *Aëdes aegypti* are able to transmit the virus of dengue from one human being to another. Several species of *Aëdes* are intermediary hosts of *Dirofilaria immitis* of the dog and several species of Culicidae transmit the plasmodium of avian malaria from one bird to another.

The literature on the Culicidae is now extremely large. Perhaps the best general work on the family is that by Howard, Dyar & Knab (1912) which deals with the species of North and Central America. The general biology of the group is discussed by Hackett (1937) and Bates (1949) and the behaviour of the adults by Muirhead-Thomson (1951). Boyd (1949) deals especially with the relation of mosquitoes to malaria. Amongst the more important regional taxonomic studies are those of Hopkins (1952) and Edwards (1941) (Ethiopian), Edwards (1921) (Palaearctic), Natvig (1948) (Scandinavian), Marshall (1938) (British), Matheson (1944) (N. American). Lane (1939) has catalogued the large and peculiar S. American fauna. The work of Russell *et al.* (1946) includes keys to the Anophelini of the world.

FAM. BLEPHAROCERIDAE.—*Elongate flies with long legs: eyes in both sexes often holoptic, and usually bisected into areas of different-sized ommatidia: ocelli present. Thorax with transverse suture: wings with a complex network of permanent folds. Mouth-parts in female adapted for lacerating. Larvae aquatic, onisciform, with ventral suckers.* A small family of very wide but discontinuous geographical range. It is confined to hilly or mountainous districts and is unrepresented in the British Isles. The adults frequent the borders of streams; they are weak fliers, and are less often met with than the larvae. The females are predacious (Pryor, 1948), preying upon small Diptera, and the males probably feed upon nectar. The wings possess a fine network, or 'secondary venation', of creases or folds in the membrane, which have not been obliterated after emergence from the pupa. The larvae inhabit swiftly running hill streams where they fix themselves by means of their ventral suckers to rocks and stones, usually in places where the current is swiftest. The head, thorax and first two abdominal segments are fused together, and the remaining segments are deeply incised laterally. A longitudinal row of median ventral suckers, usually six in number, is their most characteristic feature: to the outside of each sucker is a group of digitate processes which are regarded by Kellogg as being tracheal gills. The tracheal system is peripneustic: the spiracles are minute and situated ventrally, but in all probability are closed. The pupae are broad, and flattened beneath, adhering tenaciously to rocks, etc.: the respiratory horns are lamellate, and the legs extend almost to the apex of the abdomen. For information about the family the works of Mannheim (1935), of Tonnoir (1924; 1930) (larvae) and Edwards (1929) (adults) should be consulted.

FAM. DEUTEROPHLEBIIDAE.—*Antennae filiform, very elongate. Wings with a network of creases: ocelli, mouthparts and true venation absent.* This small family consists of a single genus, *Deuterophlebia*, which is perhaps allied to the Blepharoceridae and occurs in N. America, Japan and the mountains of C. Asia. Pennak (1945) has revised the group and summarized its biology. The larva has seven pairs of large segmental outgrowths bearing suckers and posteriorly what have been described as anal blood-gills.

FAM. THAUMALEIDAE.—*Antennae of 2 apparent segments terminated by a 10- or 11-segmented style-like appendage: palpi longer than antennae: eyes holoptic in both sexes. Larvae aquatic, amphipneustic, Chironomid-like.* A small family readily distinguishable from all other Nematocera by the structure of the antennae. The adults are small sluggish insects and in Britain *Thaumalea testacea* may be swept from grass and other herbage bordering hill-streams. The larva of this species has been described by Saunders (1923), and in general appearance it resembles that of a Chironomid. Prothoracic and anal pseudopods are present, together with paired dorsal anal blood-gills, and spiracles are evident on the first and penultimate segments. The pupa is almost entirely covered with small warts which even extend on to the short respiratory horns. Its anal segment is provided with a pair of slender upwardly directed processes and two elongate setae. For a revision of the family, see Lindner (1930).

FAM. CECIDOMYIDAE (Gall Midges).—*Minute delicate flies with long moniliform antennae adorned with conspicuous whorls of hair; ocelli present or absent. Wings with few longitudinal veins, for the most part unbranched, and with no obvious cross-veins. Coxae not elongate, tibiae devoid of spurs. Larvae peripneustic with a reduced head and usually a sternal spatula.* The Cecidomyidae include a large number of fragile and often very minute insects. The antennal characters, and the greatly simplified venation, enable these midges to be easily recognized. Among the best known species is the Hessian Fly (*Mayetiola destructor*) whose larvae are often destructive to wheat (Enock, 1891); from Europe it has been introduced into N. America and New Zealand. The Pear Midge (*Contarinia pyrivora*) is one of the most serious pests of that fruit in Europe; its larvae feed gregariously in the young fruitlets, which become deformed and subsequently decay.

A general monograph on the family is that of Kieffer (1900) while the plant galls are described and catalogued by Houard. A good deal of information is also given in the numerous reports of Felt, and most of the British galls are dealt with in the works of Connold and Swanton; for the Cecidomyids affecting cultivated plants, see Barnes (1946–49).

Larval Cecidomyidae exhibit great diversity of habits and may be classified as follows.

I. Zoophagous species of which very few are true parasites: Kieffer instances *Endaphis pervidus* which parasites *Drepanosiphon platanoidis*. A considerable number are predacious, preying mainly upon Homoptera, but others attack Acari; a few (species of *Lestodiplosis*) attack Dipterous larvae and pupae, including those of other Cecidomyidae.

II. Saprophagous species. Kieffer records species which live among the excrement of Tipulids and Lepidopterous larvae, and a few are found among decaying vegetable matter.

III. Phytophagous species which may be divided into *a.*—Those which live on or within various parts of plants without producing any gall formation. A number of species live on the spikelets of Gramineae, others in the flowers of Compositae, in fruit, or among fungi. *b.*—Gallicolous forms: a few live in galls formed by Coleoptera, Trypetidae and other Cecidomyidae. *c.*—Cecidogenous or true gall-making species. The vast majority of the family come under this category and all parts of the plant may be affected. Felt (1911) computed that 438 species, included in 44 genera, of American Cecidomyidae affected 177 plant genera comprised in 66 families. Of these 146 species formed bud-galls, 44 fruit-galls, 218 leaf-galls, 130 stem-galls, and 4 formed root-galls. The Compositae, Salicaceae and Gramineae are the most frequently selected both in America and Europe. One of the most generalized of true gall-makers is *Rhabdophaga* which is partial to *Salix*, producing simple deformities such as bud and subcuticular galls. *Dasyneura* also forms comparatively simple leaf- and bud-galls on various plants.

The larval structure is dealt with at length by Kieffer, and the larvae are usually rather short and somewhat narrowed at both extremities. They vary in colour, being frequently white, yellow, orange or bright red, and occasionally brown. The head is very small and incompletely differentiated; pigment spots are present but there are no eyes. Thirteen trunk segments are evident, the first being intercalated between the head and prothorax. There are nine pairs of spiracles situated on the prothorax and first 8 abdominal segments. According to Kieffer the larva of *Rhinomyia perplexa* is exceptional in possessing 10 pairs, the additional pair being situated on the anal segment. The most characteristic structure associated with Cecidomyid larvae is the sternal spatula or so-called 'breast bone' (Fig. 466), which is situated mid-ventrally on

the thorax. It is an elongate sclerite either toothed, pointed, or bilobed anteriorly: in some genera it is wanting. The function of this organ has been variously interpreted as an organ of perforation used for abrading plant tissues, as a locomotory organ, or for changing the position of the larva in its cocoon or case. Many larvae possess the power of leaping (*Contarinia*, etc.) and, according to Giard, in performing this act the anal crochets lock into the extremity of the spatula. The larva is thus curved into

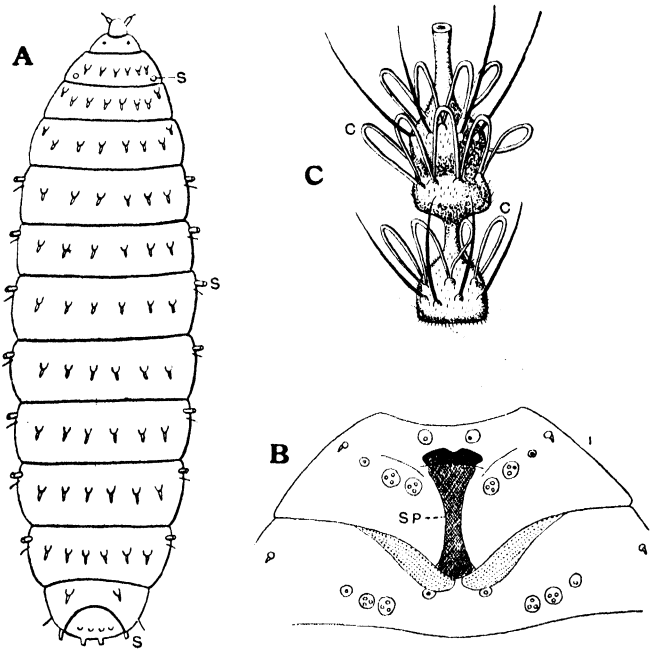


FIG. 466.—A, larva of *Contarinia pyrivora*, dorsal view; *s*, spiracles. B, ventral aspect of 1st thoracic segment (1) showing sternal spatula *SP*. C, antennal segment of *Xylodiplosis praecox* male showing circumfili *c*

Adapted from Kieffer, *Ann. Soc. ent. Fr.*, 1900.

a loop, perpendicular to the surface upon which it is resting. By means of a sudden release of the tension it may be projected a distance of several centimetres.

Two methods of pupation occur in Cecidomyidae. In the usual method the pupa is enclosed in a cocoon which may be either single or double: in *Mayetiola* and *Chortomyia* the outer layer is a puparium, formed by the persistent larval skin.

The adults usually bear *circumfili* on the antennae: they are best developed in the males and are curious looped filaments or tortuous threads. In *Contarinia* and its allies each loop is fused basally with its fellows, thus producing an apparent whorl around each segment (Fig. 593, C). Their function is obscure, but it is presumably sensory. For the occurrence of paedogenesis in this family, see p. 191.

FAM. ANISOPODIDAE (Rhyphidae).—*Discal cell present: eyes in male often holoptic, ocelli evident. Antennae 16-segmented, about as long as thorax. Larvae amphipneustic, saprophagous.* A small family of gnat-like flies represented in all zoogeographical regions. In the presence of a discal cell *Anisopus* (Fig. 36) differs from other Nematocera excepting the Tipulidae, but is separable from the latter on account of the absence of the V-shaped mesonotal suture and the presence of ocelli. The whitish larva of this genus is well known (Keilin & Tate, 1940) and lives in decaying vegetable matter and manure. It is about 10 mm. long, elongate-cylindrical, and devoid of pseudopods. The thoracic segments are longer than broad, and those of the abdomen are separated by intercalary rings, giving the appearance of an increased number of segments. Spiracles are present on the prothoracic and last abdominal segments. *Mycetobia* as far as adult characters go would be placed in the Mycetophilidae, but Edwards (1916) and Keilin showed its true affinities by a study of the larva which occurs in sap and in fungi growing on trees.

FAM. BIBIONIDAE.—*Antennae* 8 *to* 16*-segmented, usually shorter than the thorax, the segments usually bead-like and closely apposed* (Fig. 451). *Wings large, anterior veins usually more strongly marked than posterior* (Fig. 594). *Eyes in males usually holoptic or approximated, ocelli present. Larvae terrestrial, peripneustic.* This family is somewhat variable in adult structure and is split into five by Hendel; it seems better, however, to treat them together, at least until the metamorphoses of some of the aberrant types are known. Typical Bibionidae are robust flies, often pubescent, with shorter legs and wings than most other Nematocera. In the males the eyes often occupy nearly the whole of the head and the upper facets are much larger than the lower, the two series being sharply differentiated. Certain species exhibit colour dimorphism, the females often being reddish-brown, while the males are entirely black.

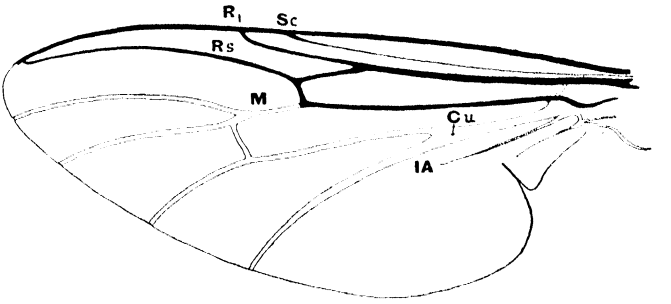


FIG. 467.—*Bibio marci*, venation

The species of the subfamily Bibioninae frequent meadows, grassy hillsides or decaying vegetation and often appear in great numbers. Their larvae feed gregariously at the roots of grasses, cereals, hops and in leaf mould. Those of *Bibio* (Morris, 1921–22) are often gregarious and, structurally, they are the most primitive of all Dipterous larvae. They are 12-segmented with a large exserted head, well-developed mouthparts and are devoid of pseudopods (Fig. 468). Each segment is provided with a band of short fleshy processes, the latter attaining their greatest length on the 11th and 12th segments: the first segment is transversely divided and carries two bands of these processes. Open spiracles are present on each segment except the 2nd and 11th, the

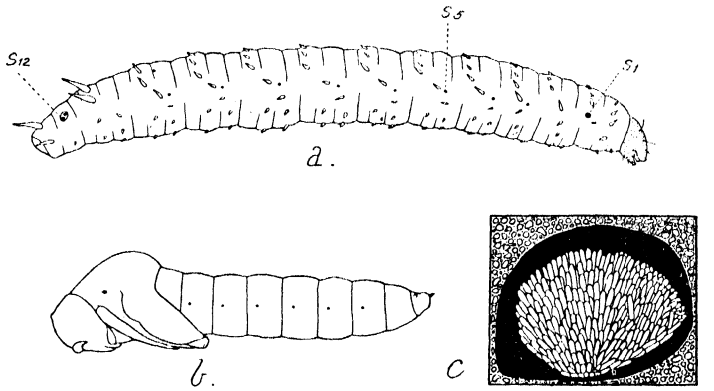


FIG. 468.—*Bibio marci*

a, larva: s_1, s_5, s_{12}, spiracles of their respective segments; *b*, pupa; *c*, egg-mass in subterranean chamber. *After* Morris, *Bull. entom. Res.*, 1921.

hindmost pair being considerably larger than its fellows. Pupation occurs in an earthen cell below ground.

The larvae of the Scatopsinae live in decaying organic matter and pupation takes place in the persistent larval skin. In *Scatopse* (Lyall, 1929), the larva is provided with longitudinal and transverse bands of hairs: nine pairs of spiracles are present on the 1st segment and on the 4th to 11th segments respectively, the hindmost pair being carried on stout cuticular pedicels. The 11th segment bears two posteriorly directed processes fringed with long hairs. For the British Bibionidae, see Edwards (1925a).

FAM. MYCETOPHILIDAE (Fungus Gnats).—*Small flies provided with ocelli, antennae long, usually lacking whorls of hair in the male; coxae elongate, tibiae spurred.*

Larvae smooth and vermiform with a small dark head, 8 pairs of spiracles, and living gregariously in fungi or decaying vegetable matter. The fungus gnats are delicate flies of a small or medium size, often bearing a resemblance to gnats or midges, and exceedingly numerous in individuals and species. Upwards of 2,000 species are known, and the geographical range of the family is very wide. In coloration fungus gnats are seldom striking—blacks, browns and yellowish hues predominating. The body is elongate and compressed, with the thorax more or less arched, and sometimes markedly so. The antennae (Fig. 451) are almost always long and filiform, and composed of 12–17 segments, 16 being a common number. The tibiae are slender and armed with apical spurs, and the tarsal claws are toothed or pectinate. Sexual dimorphism occurs in a few species of the *Sciarinae*. In *Sciara semialata*, for example, the male possesses greatly reduced wings while the female is normal. In *Pnyxia scabiei* the female is destitute of both halteres and wings, while the male exists in two forms—one with reduced and the other with normal wings.

The larvae of a number of species have been described and the valuable paper by Osten-Sacken (1862) should be consulted together with more recent work by Keilin (1919) and Madwar (1937). They are soft and whitish, with a small black or brown strongly sclerotized head, and 12 body segments. They are elongate and vermiform in shape, and generally sufficiently transparent to reveal much of their inner anatomy. The cuticle is smooth and devoid of hairs or setae; on the ventral surface there are often transverse swellings which, in many cases, are furnished with minute spines aiding in locomotion. The antennae are always very short and frequently almost absent; they are better developed in *Bolitophila* than in most other genera. Situated below the antennae an oval pellucid spot is often present (*Bolitophila*, *Mycetophila*, *Leia*, *Epidapus*, etc.) which is probably of the nature of an ocellus. The respiratory system is peripneustic with 8 pairs of spiracles. The latter are found on the prothoracic and first 7 abdominal segments, the prothoracic pair being the largest. Exceptional genera include *Ditomyia* and *Symmerus* with 9 pairs of spiracles (Keilin, 1919); *Platyura* is devoid of spiracles and provided with protrusible anal gills and *Speolepta* is propneustic.

The imagines are found in a variety of situations, most commonly in damp or dark places, where there is fungoid growth, or decaying vegetation. Cellars, sheds, manure heaps and damp secluded parts of woods furnish many species. One of the characteristic features of these flies is their power of leaping, the hind legs being adapted for the purpose; many species simulate death when disturbed. The popular name of fungus gnat is derived from the fact that the larvae feed upon fungi more often than any other substance. A number of species however are found in rotting wood and other decaying organic matter, including leaf-mould and manure. The larvae are markedly gregarious, and many species construct a loose slimy web on their pabulum. Some of these, such as *Platyura* (Mansbridge, 1933), are predatory, feeding on small insects and worms which are killed by oxalic acid, secreted on the web. Most larvae, however, feed on fungi or other vegetable matter, often burrowing in their food and lining the tunnels with a slimy secretion, as in *Exechia*; *Phronia* (Steenberg, 1943) lives in a case made of particles of excrement, shaped into the form of an *Ancylus*-shell.

Larvae of the Sciarinae (often treated as a separate family) have been found in decaying apples, pears, turnips, potatoes, etc., and sometimes attack seedlings. In certain species of *Sciara* they exhibit the curious habit of travelling in vast numbers, so closely together as to almost constitute a single mass. This phenomenon is not infrequent at certain seasons in woods in Germany, Sweden, Russia and also in N. America. The migratory columns are elongate in form, and have been termed 'snake worms' in the United States, on account of their snake-like movements and appearance, which are said to resemble a thin grey reptile. They progress as a single mass with the larvae several deep over each other, and the movement is stated to be at the rate of about an inch a minute. In Europe they have been termed the 'army worm', but in America this expression is more properly applied to certain Noctuid caterpillars. Lintner mentions the stream of larvae as often being 12–15 ft. long, 2–3 inches broad, and perhaps $\frac{1}{2}$ inch in thickness. In the United States one species has been reared and identified as *Sciara fraterna*; the common European 'army worm' is *Sciara militaris*. No satisfactory explanation has yet been advanced to account for the assemblage of these hordes of footless larvae.

Several species exhibit luminosity, which appears to have been first observed in the larvae and pupae of *Ceroplatus sessiodes* by Wahlberg in 1838. A particularly brilliant light was observed by Hudson in a New Zealand species (*Arachnocampa luminosa*), who remarks that the light emitted from a single larva kept in a caterpillar

cage may be seen streaming out of the ventilators at a distance of several feet. Wheeler & Williams (1915) describes it as being emitted from the distal portion of the Malpighian tubes. The pupa and female imago are also strongly luminous but, according to Norris (1894), the male does not exhibit this property.

Some Mycetophilids spin true cocoons for pupation while others construct a fragile case of earthy material: the pupa in *Leia* is simply suspended by means of loose threads. In *Epicypta* the larval skin is adapted to form a shell in which to pupate but the pupa itself is free. The eggs are laid singly or in small groups, occasionally in strings, on whatever substance serves as food for the larvae. Many species pass through several generations in the course of a year, and as a general rule larval and pupal life is of short duration although certain species hibernate as pupae. According to Johannsen the time occupied from the egg to the adult may not exceed two weeks in midsummer. Edible mushrooms are frequently attacked by larvae of *Sciara*, *Exechia* and *Mycetophila*. They completely riddle the plants and may ruin a whole mushroom bed. Not infrequently they are introduced into the mushroom cellars through the agency of the manure used in the beds. According to Hopkins there are forms of potato scab and rot which are not due to fungoid disease, but are the direct result of the attacks of species of *Sciara* and *Epidapus*. *Sciara tritici* damages roots and stems of young wheat plants, and Johannsen remarks that there is no lack of evidence that Sciarinae damage the roots of cucumbers, grass and potted plants.

The most important works on the family are those of Johannsen (1909) and, for Palaearctic species, those by Landrock (1926–27) and Lengersdorf (1928–30) in Lindner's *Die Fliegen*. Edwards (1925) describes most of the British species.

FAM. NYMPHOMYIDAE.—*Small flies with reduced venation, with long fringes to the wings, mouthparts atrophied, antennae with* 3 *stout segments and a short style, eyes meeting beneath head but separated above,* 2 *ocelli present. Larvae aquatic.* These extraordinary flies were discovered by Tokunaga in 1932 in a fast-flowing stream, in Japan. He has since published several studies of the only known species which seems to be a highly specialized Nematoceran, retaining, however, some archaic features (Tokunaga, 1935; 1936). The larva has not been described, but the pupa (Tokunaga, 1935a) shows some affinity to the Psychodidae (Hennig, 1950).

FAM. SIMULIIDAE.—*Small stoutly built flies with short legs and elongate mandibles. Wings broad, anterior veins thickened, the others faint. Antennae* 11*-segmented, scarcely longer than the head: ocelli wanting, the males holoptic. Larvae in running water attached to rocks by the anal extremity, spiracles closed.* A small family of world-wide distribution and including the familiar 'buffalo gnats' of America (Fig. 469). In the males the eyes have the upper facets markedly larger than the lower, and the 1st tarsal segment is usually much dilated. Both sexes possess elongated piercing mandibles which are broader in the female than in the male (cf. Nicholson, 1945). The females of certain species are active blood-suckers and in some countries are veritable scourges. *S. indicum*, the 'potu' fly, is a troublesome pest in parts of the Himalayas, and *S. columbaschense* is at times a great scourge of man and domestic animals, particularly in regions bordering on the Danube. It often appears in enormous swarms and the flies attack the orifices of the body entering the ears, nostrils, margins of the eyes, etc., in great numbers, and their punctures produce an inflammatory fever often resulting in death. *S. damnosum* bites man in C. Africa and carries the worm, *Onchocerca*, the cause of a filariasis. Certain other species are pests in many parts of N. America; *S. meridionale* causes the death of numerous turkeys and chickens in Virginia, and *S. pecuarum* is the common American buffalo gnat. In a few instances species of this genus have been observed to suck the blood of other insects.

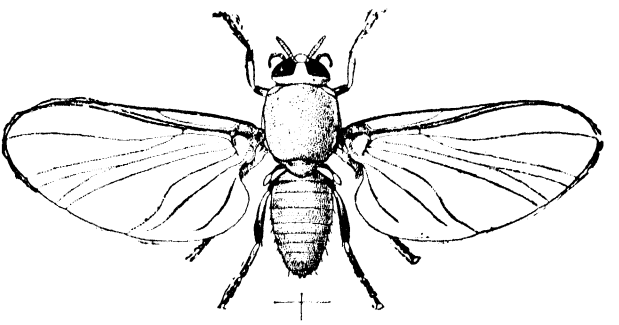


FIG. 469.—*Simulium venustum*, female. × 12. N. America

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Adult Simuliidae occur in the neighbourhood of streams and rivers; the eggs are

laid either on herbage or stones, above or beneath the surface of the water. Britten (1915) has observed the female of *S. maculatum* submerged to a depth of 1 foot during oviposition: the eggs are laid on vegetation and are coated with a gelatinous secretion.

The larvae are invariably aquatic and require swiftly flowing water for their environment, and for this reason they are often found congregated in the vicinity of rapids and waterfalls, etc. Information concerning the metamorphoses of the family is given by Johannsen (1903–05), Puri (1925) and Smart (1944). In the larvae the head is complete and is characterized by the large maxillae and the prominent mouth brushes. On the ventral aspect of the thoracic region there is a foot-like protuberance provided with hooklets: it functions as a kind of sucker and is formed by the fusion of a pair of pseudopods. On the anal segment there is a second sucker, armed with concentric series of stout hooklets and, associated with the anus, is a group of rectal gills which vary in number in different species. Nine pairs of minute spiracles are present from the mesothorax to the 7th abdominal segment; but respiration is performed by means of the rectal gills, which contain blood and are supplied with tracheoles (Taylor, 1902). The larvae fix themselves to their substratum by means of the anal sucker and, as a means of locomotion, they loop the body after the manner of Geometrid caterpillars, bringing the anal extremity forwards beside the anterior sucker. Before pupation the larva forms a pocket-like cocoon open above; the pupal respiratory organs are composed of long tube-like filaments, which protrude from the cocoon and obtain oxygen from the moving water. For the British species of *Simulium* and their larvae reference should be made to Smart (1944); the classification of the family as a whole is also discussed by Smart (1945).

FAM. CHIRONOMIDAE (Midges).—*Delicate gnat-like flies: antennae conspicuously plumose in the males, pilose in the female. Head small, often concealed by the thorax: ocelli absent. Mouthparts poorly developed. Fore legs elongate. Anterior wing-veins more strongly marked than posterior. Larvae apneustic: aquatic.* These insects bear a general resemblance to Culicidae but may be distinguished by the wings being unscaled. The adults occur in great numbers in the vicinity of lakes, ponds and streams: many appear on the wing just before sunset, and exhibit a characteristic gregarious habit of 'dancing' in the air in swarms. During these evolutions the number of females present does not appear to be large and, when pairing is accomplished, the mated couple leave the swarm. About 2,000 species have been described: in Britain nearly 400 species are listed but more await discovery. The antennae are 6- to 15-segmented and the mouthparts are poorly developed. In *Chironomus* no food is taken during adult life and the digestive canal is consequently shrunken and empty.

The eggs of Chironomidae are laid in a mass, enveloped by transparent mucilage secreted by the accessory gland of the female: these egg-masses or ribbons vary in shape and number, and arrangement of the eggs therein, in different species. The larvae usually inhabit slow streams and ponds, or even puddles or water troughs. A few species can live at great depths, having been obtained from the bottom of Lake Geneva and Lake Superior. Several species occur in the sea, both in shore pools and at a depth of 15–20 fathoms: vast numbers frequent the salt lakes adjoining the Suez Canal. A typical kind of Chironomid larva, such as that of *C. dorsalis*, has a well-developed head and 12 trunk segments, with a pair of pseudopods on the prothorax and last abdominal segment: in other forms pseudopods are present on the prothorax only or, more rarely, are absent. Two pairs of elongate blood-gills may be present on the 11th segment, and two pairs of papilla-like anal gills are placed around the anus. In *C. dorsalis* the tracheal system is greatly reduced and limited to the thorax, where there are two pairs of closed spiracles. A number of species are red, owing to the presence of haemoglobin dissolved in the blood-plasma, and are commonly known as 'blood-worms'. It was pointed out many years ago by Lankester that haemoglobin occurs among invertebrates when increased facilities for oxygenation are required, as by burrowing forms and those which lurk in the mud of stagnant pools. Surface-haunting Chironomid larvae are generally green. The larvae usually live in tubes either free, or attached to stones, etc., and composed of mud particles or of vegetable fragments, sticks, particles of green leaves, algae, etc. The pupae may be active (*Tanypus*), float at the surface of the water, or remain at the bottom of the water: in the latter case they rest in the old larval tube which is often provided with the addition of an operculum. The pupal respiratory organs either consist of a pair of much-branched filaments, or of simple tubes: they are rarely absent. The literature on Chironomid larvae is now very extensive, owing to the numerous investigations of limnologists. References may be made to the papers by Johannsen (1937) and Brundin (1947).

The Clunioninae include certain remarkable maritime genera whose larvae live among algae, and the adults are apterous. Among them are *Belgica* from Patagonia, *Halirytus*, Kerguelen I., and the European *Clunio*, the males of which are winged. For an account of marine Chironomids see Edwards (1926).

Parthenogenesis is known to occur in a few Chironomids and results in the production of females only. The first observations were made by Grimm on *Tanytarsus* in 1870 and have been confirmed by Zavrel. Both the pupae and newly-emerged imagines are parthenogenetic. *Corynoneura celeripes* and *Chironomus clavaticornis* also lay parthenogenetic eggs (Edwards, 1919). Paedogenesis has been recorded in the larva of *Tanytarsus dissimilis* by Johannsen in America (1910) but see p. 192. For the classification of the family see Edwards (1929a), Coe in Oldroyd *et al.* (1950) and Goetghebuer and Lenz in Lindner (1936–50).

FAM. CERATOPOGONIDAE (Biting Midges).—*Small or very small, gnat-like flies: antennae plumose in male, pilose in female. Head not concealed by the thorax: ocelli absent: mouthparts adapted for piercing: fore legs not elongate. Larvae without prothoracic pseudopods: aquatic or terrestrial.* The small flies of this family are all in some way predatory in the adult stage. They may suck vertebrate blood (*Culicoides*), or blood of large insects such as moths, caterpillars or dragonflies (*Forcipomyia*, etc.) or catch insects smaller than themselves (*Palpomyia*, etc.). More than 400 species are known, so far principally from the Holarctic region, though they are found in all the continents. The family falls into two groups—those with aquatic, vermiform larvae whose imagines are more or less bare-winged (*Culicoides*, *Bezzia*) and those with terrestrial larvae found in sap, under bark or in decaying organic matter. The latter include *Forcipomyia* and *Dasyhelea* whose imagines have hairy wings. The distinctions, however, are not absolute as some larvae of *Culicoides* are terrestrial and certain of those of *Forcipomyia* are aquatic. For the British species, see Edwards (1926a). Macfie (1940) has tabulated the world genera and de Meillon (1937) and Lee (1948) have dealt with S. African and Australian species, respectively. The larvae have been described by Saunders (1924–25), Johannsen & Thomsen (1937) and Kettle & Lawson (1952).

Suborder II. BRACHYCERA

The Brachycera include fourteen families whose antennal characters are so varied that the student will probably recognize many of its members more readily by means of the venation and the short porrect palpi. This applies particularly in the case of *Xylophagus*, *Rhachicerus* and *Coenomyia* where the 3rd antennal segment is annulated to such an extent as to resemble the flagellum of some Nematocera and, furthermore, the style is wanting. It is also noteworthy that the discal cell is absent in the Dolichopodidae and certain Empididae. For a discussion of the affinities of the Brachycera and their larvae the student is referred to the introductory pages of Verrall's work (1909). With the exception of the Stratiomyidae, the head in Brachycerous larvae is usually retractile within the thorax. The tracheal system is typically amphipneustic, and rarely peripneustic or metapneustic. If we except Stratiomyidae, the pupa is free and not enclosed in the larval skin: very rarely a cocoon is present (Dolichopodidae and *Drapetis*). The pupae may be recognized by their thorny appearance, spines being present on the antennal sheaths and other regions of the head and thorax. The abdominal segments are also usually provided with girdles of spines and the terminal somite is armed with pointed processes. The prothoracic respiratory organs are usually sessile.

Table of the families of Brachycera:

1. Arolium pad-like, nearly or quite as large as the two pulvilli 2
–. Arolium replaced by a hair-like empodium or absent (except in a few Dolichopodidae which are known by their wing-venation). 7
2. A number of veins running parallel with the hind margin of the wing. . NEMESTRINDAE (p. 626)
–. Veins not running parallel with hind margin of the wing 3

3. Vein C not entirely surrounding the wing . . STRATIOMYIDAE (p. 622)
–. Vein C entirely surrounding the wing 4

4. Squamae extremely large 5
–. Squamae small 6

5. 3rd antennal segment usually more or less annulated. Thorax not inflated. Mouthparts adapted for biting in the female . . . . TABANIDAE (p. 624)
–. 3rd antennal segment not annulated, often with an arista. Thorax inflated, head small. Mouthparts vestigial or proboscis elongate, but not adapted for biting ACROCERIDAE (p. 626)

6. 3rd antennal segment subcylindrical, annulated, without an arista . . XYLOPHAGIDAE (p. 622)
–. 3rd antennal segment short, not annulated, with a style or arista . . RHAGIONIDAE (p. 623)

7. Antennae terminating in a club. R_1 long. . . . . MYDAIDAE (p. 629)
–. Antennae not terminating in a club 8

8. Flies devoid of bristles. 3rd antennal segment without style or arista. No trace of C on hind margin of wing . . . . . SCENOPINIDAE (p. 628)
–. Flies nearly always with bristles, at least on the legs. 3rd antennal segment with style or arista 9

9. Cu_1 and 1A separate or meeting near the wing-margin. C extending to hind margin 10
–. Cu_1 and 1A meeting near base of wing (except a few Empididae), rarely junction difficult to see in forms with reduced venation. C not extending to hind margin 13

10. Veins M_3 and M_4 distinct, only meeting near the wing-margin. Proboscis short. Flies more or less densely hairy . . . . . THEREVIDAE (p. 627)
—. Veins M_3 and M_4 coincident 11

11. Vein M_1 terminating before apex of wing. Proboscis short or long but not adapted for piercing . . . . . APIOCERIDAE (p. 628)
—. Vein M_1 extending to apex of wing. Proboscis usually long or else stout and adapted for piercing 12

12. Often densely hairy or scaly flies. Proboscis usually long but not adapted for piercing. Vertex little depressed between the eyes . BOMBYLIIDAE (p. 629)
—. Bristly flies. Proboscis not elongate, stout, adapted for piercing. Vertex depressed between the eyes . . . . . ASILIDAE (p. 628)

13. Vein R_1 meeting C at or beyond middle of fore margin, cross-vein *r-m* not close to base. Colours not metallic . . . . . EMPIDIDAE (p. 630)
—. Vein R_1 meeting C at or before middle of fore margin, cross-vein *r-m* close to base. Colours often metallic . . . . . DOLICHOPODIDAE (p. 631)

FAM. XYLOPHAGIDAE.—*Bristleless flies with 3rd antennal segment annulated, squamae small, at least mid tibia with spurs, vein C encompassing the wing, arolium padlike.* The members of this somewhat heterogeneous primitive family are difficult to place in the system. The adult has a more or less elongate form and the larva has an almost complete head and lives in decaying wood (Verrall, 1909; Perris, 1870; Malloch, 1917). *Xylophagus* has two British species and *Coenomyia* occurs in southern Europe. The gigantic *Pantophthalmus* and its allies are found in S. America where the larva has been studied by Thorpe (1934). (See also, Rapp & Snow, 1945.)

FAM. STRATIOMYIDAE.—*Bristleless flies with the 3rd antennal segment annulated, squamae small, tibiae rarely with spurs; scutellum often conspicuously developed, sometimes with spines or projections, wing-veins crowded near costa and more strongly pigmented than those behind, C not encompassing the wing. Pulvilli and arolium pad-like.* The Stratiomyidae (Fig. 471) are small to rather large flies, more or less flattened and usually with white, yellow or green markings: in the Geosarginae, however, the prevailing colour is metallic. About 1,400 species are known and of these about 50 are British. They are not usually strong fliers and occur on umbelliferous and other flowers and herbage, especially in damp situations. The Solvinae are the most aberrant members both as regards their venation and in the presence of tibial spurs (also seen in some Beridinae); they are annectent between this family and the Xylophagidae.

The metamorphoses of a considerable number of Stratiomyidae are known: the eggs are laid on plants near the edge of water, or even on the surface of the water, also in dung and in the soil. The larvae are carnivorous or saprophagous, and either terrestrial or aquatic, the terrestrial larvae being largely scavengers: those of the Solvinae occur in rotting wood. Stratiomyid larvae exhibit considerable diversity of form: all have a peculiar thick leathery skin impregnated with calcareous matter. The head is small and exserted, and there are 11 trunk segments, none of which bear pseudopods (Fig. 470). Although often described as being peripneustic, it is doubtful whether they are functionally so: they appear to be physiologically metapneustic or in some cases amphipneustic. The lateral spiracles, with the exception of the prothoracic pair, are minute and difficult to detect. In *Stratiomyia* 9 pairs are present; they are situated on the 1st and 3rd thoracic segments, and on each of the first 7 abdominal segments. Although stated by Brauer to be peripneustic, Miall remarks that the lateral spiracles are closed. The terminal or posterior spiracles are always open and are situated in a horizontal fissure, fringed with hairs in the aquatic forms. The larvae of *Stratiomyia* and *Odontomyia* are greatly elongate and taper towards the anal extremity. In the former genus the last segment is much drawn out and tubular: these larvae live in water or mud, and hang from the surface film by means of the tail coronet of feathery hairs which is spread out in an asteriform manner. When the larva descends, the hairs are drawn inwards and enclose a large air bubble: as the latter becomes used up the larva returns to the surface.

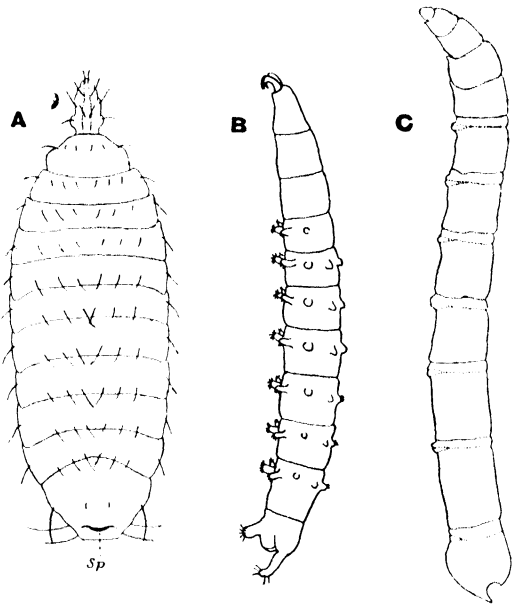


FIG. 470.—Larvae of Brachycera. A, *Microchrysa*; *Sp*, spiracles. B, *Tabanus*. C, *Rhagio*
A and C *after* Cameron, *J. econ. Biol.*, 8; B *after* King.

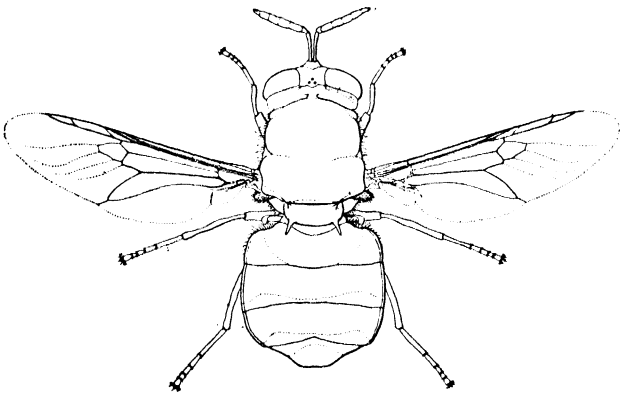


FIG. 471.—*Stratiomyia potamida*, female. × 4. Britain
After Verrall.

The larva of *Solva* resembles that of *Geosargus*, being broad with parallel sides, and the usual leathery skin is impregnated with calcareous matter. It is regarded as being amphipneustic with prothoracic and terminal spiracles: according to Lundbeck non-functional lateral abdominal spiracles are also present. Stratiomyid pupae differ from other Brachycera in being enclosed within the larval skin. Tables of the larval characters for each subfamily are given by Verrall (1909): further information will be found in the works of Lundbeck (1907) and Irwin-Smith (1921–23).

FAM. RHAGIONIDAE.—*Bristleless flies; with the 3rd antennal segment usually*

non-annulated with a terminal style (Fig. 451). *Some or all the tibiae spurred, squamae practically absent. Wing-veins well defined, not concentrated anteriorly. Pulvilli and arolium pad-like.* The Rhagionidae include rather elongate flies of sombre coloration, usually thinly pilose or almost bare (Fig. 472). Over 400 species have been described, of which about 19 are British. Normally they are predacious upon other insects, but it is recorded that the female of *Symphoromyia* in America and *Spaniopsis* in Tasmania are bloodsuckers (cf. Ross, 1940).

The metamorphoses of many Rhagionidae are known (Beling, 1875; 1882; Greene, 1926); the larvae (Fig. 470) are cylindrical, with a small exserted head succeeded by 11 trunk segments, which may or may not bear pseudopods. The abdominal segments often possess transverse denticulate, ventral swellings which aid in locomotion. The last segment is modified and marked by longitudinal folds or grooves, or provided with hairy processes. Rhagionid larvae are carnivorous, preying upon other insects or their larvae: according to Marchal the larva of *R. tringaria* lives upon small Oligochaetes. Their usual habitat is in the earth or in leaf mould: *Atherix*, however, is aquatic. The larva of *Atherix* has been described by Dufour, Brauer, and more recently by Malloch (1917): the head is minute and each abdominal segment bears a pair of pseudopods capped by spines. The sides of the body are fringed with numerous filamentous processes which have been regarded as gills, no spiracles having been detected. The anal segment carries a pair of prominent, hairy, backwardly directed processes. The females of *Atherix* deposit their eggs in masses on dry twigs, etc., overhanging water, into which the larvae fall upon hatching out. Many individuals lay their eggs on the same cluster, and afterwards die on the spot, often in numbers. As their dead bodies adhere together, large incrustrations are thus formed. In Oregon the Indians at one time collected these masses of eggs and flies for food (Aldrich). Females of *Vermileo* lay their eggs in sand, and the larvae construct conical pitfalls for the capture of their prey, after the manner of 'ant lions'. The 5th segment of the larva bears a ventral mobile pseudopod which assists in seizing and holding the prey. The 10th and 11th segments each carry a transverse row of long hooklets which serve as organs for boring and fixation (cf. Wheeler, 1930).

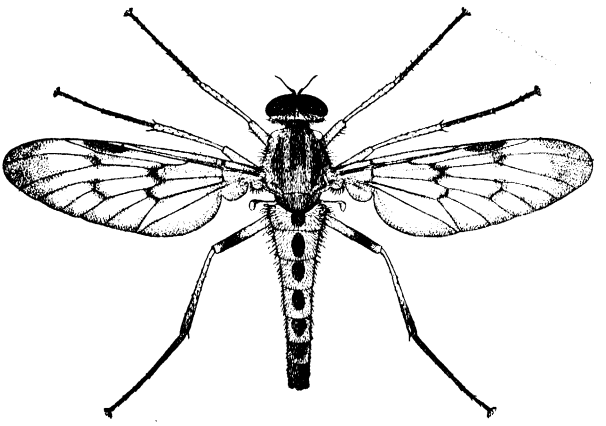


FIG. 472.—*Rhagio scolopacea*, male. × 3. Britain
After Verrall.

FAM. TABANIDAE (Horse Flies and Clegs).—*Bristleless flies of stout build with the 3rd antennal segment annulated but devoid of a style* (Fig. 451). *Eyes very large, laterally extended; proboscis projecting, adapted for piercing in the female* (Fig. 453). *Squamae large, pulvilli and arolium pad-like.* An extensive family of moderate to large sized flies (Fig. 473), including about 2,000 species, which are distributed over the whole world: 3 genera and 28 species are British. They are more or less flattened insects and, as a rule, mottled brown, tawny or grey in colour; *Chrysops*, however, has more conspicuous hues. During life the eyes are iridescent, exhibiting brilliant shades of green often marked with bands or spots of brown or dark purple. In British Tabanids the proboscis is always rather short, but almost every transition may be found among the various genera of the family culminating in species of *Pangonia*, where it may be more than twice the length of the body.

Horse flies are active on warm sunny days, and the females are well-known bloodsuckers, whereas the males mostly subsist upon honeydew and on the juices of flowers. In the absence of blood, the females will also imbibe these same substances (Hine). Many species are swift fliers, and those of *Tabanus* are particularly troublesome to horses and cattle, approaching their victims with a loud hum. The piercing action of the proboscis is often painful, but is seldom accompanied by inflammation. Experi-

mental evidence indicates that the disease of horses known as Surra is transmitted by the punctures of *T. striatus*, and other species, and that these flies play an important part in spreading the infection. According to Leiper *Chrysops dimidiata* is a vector of *Loa loa* which is responsible for the affection known as Calabar swellings among the natives of West Africa.

Pangonia may often be found hovering over flowers on the borders of forests; species have been observed to attack both man and cattle in various parts of the world. Their method of attack varies considerably in the experience of different observers. The labium is not adapted for piercing, the latter operation probably being performed by the other trophi, the proboscis only being used for sucking up the blood. In some species this is performed on the wing, in others it is stated to take place after the insect has alighted (Tetley, 1918). The species of *Haematopota* or 'clegs' are voracious blood-suckers and especially frequent damp meadows. They are notable for their quietness of approach, and often the pricking sensation of their punctures is the first intimation of their presence. *H. pluvialis* is the most abundant British Tabanid, and is particularly troublesome to man. According to Portchinsky, in parts of Russia, these flies are so numerous and offensive that agricultural operations have to be carried out at night. By covering the pools frequented by Tabanids with a thin layer of petroleum he succeeded in destroying large numbers of these troublesome insects, which were killed by the oil adhering to their bodies.

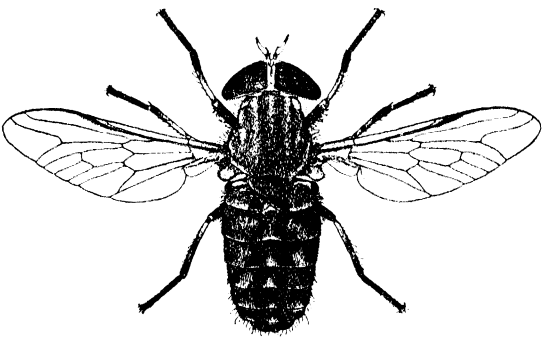


FIG. 473.—*Tabanus maculicornis*, female. × 3. Britain
After Verrall.

The eggs of Tabanidae are spindle-shaped and white, brown, or black; they are deposited in compact masses on the leaves and stems of plants, growing in water or marshy places. The larvae (Fig. 470) (Stammer, 1924) are 12-segmented with a relatively small retractile head, well-developed antennae and strong mouth-hooks. The trunk is cylindrical, tapering at both extremities, and usually longitudinally striated; there is a circle of prominent fleshy pseudopods around each of the first abdominal segments. They are metapneustic with the spiracles placed closely together in a vertical fissure at the anal end of the body. Near the hind extremity of the larva of *Tabanus* is a pyriform sac, narrowing posteriorly into a fine tube which opens at the surface between the last two segments. Within the sac is a series of capsules, each containing a pair of minute black pyriform bodies which are attached to the walls by means of delicate pedicels. The whole structure is known as *Graber's organ*, and can readily be seen through the integument of the living larva. It is well supplied by nerves and is presumably sensory in function. The larvae of *Tabanus* and *Chrysops* are closely alike but according to Malloch (1917) in *Chrysops* the thoracic segments are either smooth, or less markedly striated than the abdominal, and the apical antennal segment is much longer than the one preceding. In *Tabanus* the striation is uniformly well developed over the body, and the terminal antennal segment is shorter than the preceding one. The larva of *Goniops* differs from the usual Tabanid form in that the hindmost segments are stouter than those preceding thereby imparting to the body a pyriform or club-shaped appearance (McAtee, 1911). The larva of *Haematopota* resembles that of *Tabanus* but according to Perris (1870) and Lundbeck (1907) it is amphipneustic.

Tabanid larvae have been found in a variety of moist situations—in damp soil bordering ponds and streams, under stones in similar places, in mud, wet rotting logs, etc. They are carnivorous, devouring small earthworms, crustacea and insect larvae. The pupae are markedly elongate and cylindrical. They are characterized by the thoracic spiracles being connected subcutaneously with a large cavity on either side of the median line, near to the anterior margin of the thorax. Each abdominal segment carries 1–2 dorsal bands of closely contiguous setae and a weaker series ventrally. The terminal segment is armed with six stout pointed projections.

The literature on the family is considerable and for a general account, including

the British species, consult Verrall (1909), Lundbeck (1907), and the work of Edwards *et al.* (1939). Important studies of foreign species are those of Efflatoun (1930), Olsoufieff (1937) and Oldroyd (1952). For the morphology and biology vide Bromley (1926) on *Tabanus*, Cragg (1912) on *Haematopota*, the textbook of Patton & Cragg (1912) and Marchand (1920).

FAM. NEMESTRINIDAE.—*Rather large bristleless flies with many of the veins running parallel with the hind margin of the wing: Sc and R_1 very long. 3rd antennal segment simple with a terminal style, pulvilli and arolium pad-like but often minute.* A family of about 200 species (Fig. 474), none of which occur in the British Isles, but 57 are Palaearctic and 14 are European. They are for the most part inhabitants of hot and arid regions where there is a minimum of rainfall. They mainly frequent flowers, hovering over them while imbibing the nectar. The proboscis is very variable and often long, or very long; in *Nemestrina longirostris* it is about four times the whole length of the insect.

The larvae of this family have a very small retractile head and 12 trunk segments:

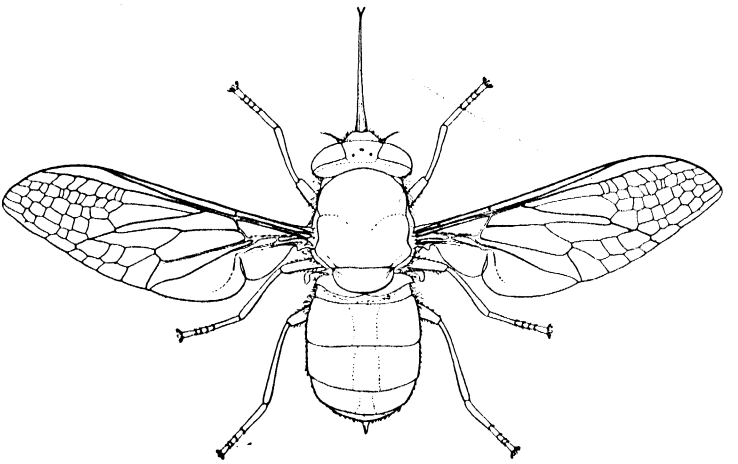


FIG. 474.—*Nemestrina perezi*, female. × 3·25
After Verrall.

the tracheal system is amphipneustic, with the posterior spiracles spaced apart in a transverse fissure. The life-history of *Hirmoneura* has been partially observed by Brauer (1883) and Handlirsch (1882). Its habits resemble to some extent those of the Bombyliidae and hypermetamorphosis also occurs. The young larva is slender and provided with a pair of pseudopods on the 6th and 12th segments, which are not present at a later stage. It appears that this species is parasitic upon *Amphimallon solstitialis*, and probably upon other Coleoptera. The eggs are deposited in clusters within the burrows of Coleoptera (other than *Amphimallon*) from whence the newly-hatched larvae issue in large numbers. They are stated to place themselves in an erect position by means of their terminal hooklets, and are blown away by the wind. Their subsequent history is unknown, but it is believed that they attach themselves to the body of the female *Amphimallon*, and are thus carried to the place in the earth where the latter lays her eggs.

FAM. ACROCERIDAE (Cyrtidae).—*Bristleless flies with the head very small and almost entirely composed of the eyes which are holoptic in both sexes. Thorax humped, squamae exceedingly large: abdomen greatly inflated and globular. Pulvilli and arolium pad-like.* A small family of medium-sized flies including about 200 species which are readily distinguishable from all other Brachycera. Although occurring in all parts of the world Acroceridae are local and uncommon: two genera, *Oncodes* and *Acrocera* (Fig. 475) are found in the southern portion of England (Verrall, 1909). (See also Sabrosky, 1948 for the N. American species.) So far as known, their larvae are parasitic upon spiders living in the egg-cocoons, or attached to the abdomen of their host. The eggs are black, and have been noted on dead twigs and on *Equisetum*: those of *Oncodes* are laid in masses (Maskell, 1888). The life-history of *Pterodontia* has been

partially followed by King (1916). The newly-hatched larva bears a striking resemblance to the triungulin of *Stylops*: it is strongly sclerotized, and armed dorsally and ventrally with segmental bands of powerful spines and pectinate scales. At the caudal extremity of the 8th abdominal segment is a sucker, which is flanked by a long anal seta on either side. In addition to a looping leech-like movement, the larva is able to leap by standing erect upon its sucker, with the caudal setae bent beneath the body: a sudden straightening of the setae lifts the larva 5 or 6 mm. in the air. The insect bores its way into the host by penetrating the articular membranes of the legs, and lives endoparasitically: according to King there are no spiracles. The older larvae in this family are short and stout, and apparently amphipneustic: König (1894) and Maskell state that the younger larvae, of presumably *Oncodes*, are metapneustic; they similarly possess leaping powers. According to Brauer (1869), the larva of *Astomella* lives within the abdomen of the spider, with its hind spiracles penetrating the lung-books of the latter. The pupae in this family are devoid of spines or bristles, and differ from those of other Diptera in the great size of the thorax, which exceeds the abdomen in length.

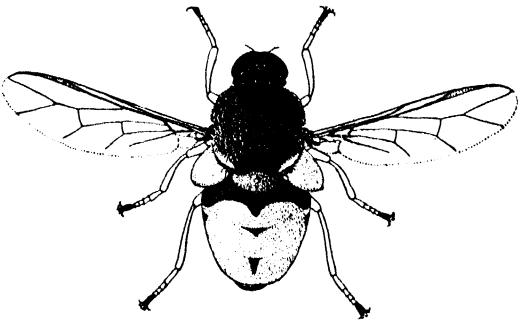


FIG. 475.—*Acrocera globulus*, male. × 7·5. Britain
After Verrall.

FAM. THEREVIDAE.—*More or less elongate densely pubescent flies with slender non-prehensile legs. 3rd antennal segment with an apical (sometimes jointed) style.* R_1 *usually long, cell* M_3 *present. Empodium absent, or represented by a weak bristle.* A small family including nearly 500 described species (Fig. 476) of which ten are British (Collin, 1948). They exhibit a resemblance to some Asilidae, but the weaker legs and the non-protuberant eyes enable them to be readily separated. In habits these flies are commonly stated to be predacious, but very few direct observations appear to have been made. The proboscis is rather prominent, and provided with fleshy labella, instead of the horny apex as in the Asilidae. The larvae (Fig. 477) of several species are known to be predacious upon those of other insects, including wireworms, etc. They live in the soil, among

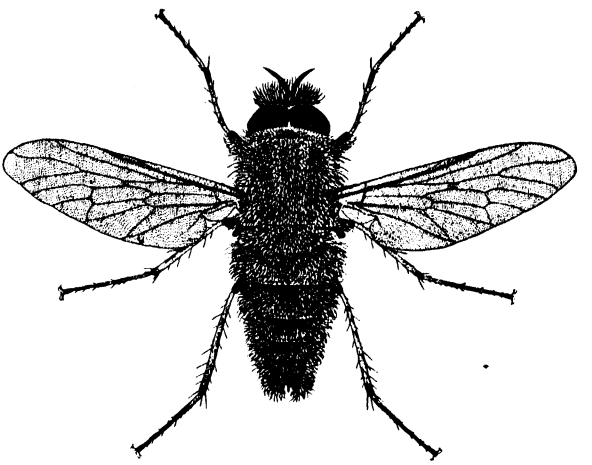


FIG. 476.—*Thereva nobilitata*, male. × 4. Britain
After Verrall.

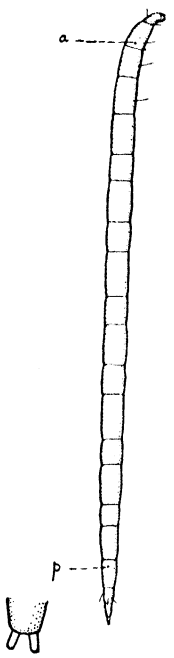


FIG. 477.—Larva of *Thereva* and anal segment more enlarged
a, anterior and *p*, posterior spiracles.

leaf-mould, in fungi, decaying wood, etc., and exhibit quick serpent-like movements. They are smooth and vermiform, bearing an extremely close resemblance to the larvae of *Scenopinus* (see below). The larva of *Thereva* (Malloch, 1915b) has a small though distinct head followed by 20 segment-like divisions. The labrum is hook-like, and the mandibles also exhibit a hooked form: small antennal papillae are present but no eyes. A pair of prominent lateroventral bristles are found on each thoracic segment, and three pairs of bristles on the 10th abdominal segment: the tracheal system is amphipneustic. At the anal extremity are two small styliform processes. The pupa has thorn-like, projecting antennae and a long curved spine at the base of each wing.

FAM. APIOCERIDAE.—*Rather large elongate bristly flies: antennae with or without a short style, palpi spatulate. Venation rather similar to Mydaidae, M_1 terminating before wing apex. Two pulvilli are present and the empodium is wanting or bristle-like.* A very small family comprising about 100 species, none of which is European but 70 are Australian (Paramonov, 1953). They are thickly pilose insects with a non-piercing proboscis. The larva of the Australian *Apiocera maritima* has been described by English (1947); it is very similar to the same stage in an Asilid.

FAM. SCENOPINIDAE. (Omphralidae).—*Narrow oblong flies devoid of true pubescence or bristles. First two antennal segments short, the third elongate and devoid of a style or arista. Vein M_{1+2} terminating before the apex of the wing. R_1 short. Pulvilli small. Empodium bristle-like.* This family includes rather small dark coloured flies and scarcely 50 species are known. The adults are occasionally found on windows, or about stables and outbuildings. The larva of *Scenopinus* (vide Perris, 1870) resembles that of *Thereva*. It is amphipneustic, white and vermiform, with serpent-like movements. The head is brown and well-developed, and is followed by 20 apparent segments. Most of the abdominal somites are subdivided by a strongly marked constriction, thus giving the appearance of an increased number of segments: the terminal segment bears two small styles. At one time it was believed that these larvae fed upon neglected carpets, horse-rugs, etc.: there is little doubt, however, that they are predacious upon the larvae of *Tinaea pellionella* and of other insects. Scenopinid larvae have also been found in *Polyporus*, in branches of trees, and other situations.

FAM. ASILIDAE (Robber Flies).—*Usually elongate bristly flies with a horny proboscis adapted for piercing, and the palpi never spatulate. Vein R_1 very long, M_1 terminating some distance beyond the apex of the wing. Legs powerful and prehensile: pulvilli large, empodium bristle-like.* The Asilidae are moderate to very large-sized flies (Fig. 478), always bristly, and in *Laphria* also densely hairy. They constitute the largest family of Brachycera, numbering at least 4,000 species: in the British Isles 27 species are recognized. The adults are predacious in habit, their powerful legs being adapted for grasping the prey. The proboscis is firm and horny, directed downwards or obliquely forward. A prominent tuft of hairs, forming a 'mouth-beard', and the protruberant eyes are characteristic of the family. The conspicuous male genitalia and the corneous ovipositor are also well marked features.

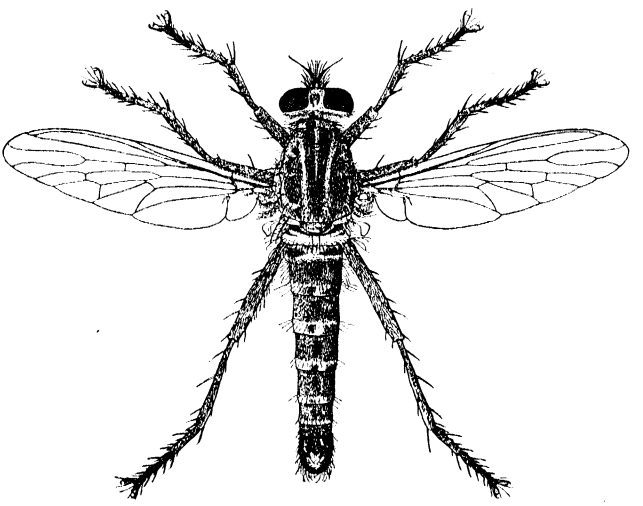


FIG. 478.—*Philonicus albiceps*, male. × 3. Britain
After Verrall.

The prey of Asilidae is extremely varied and information on the subject has been collected by Whitfield (1925), Hobby (1931) and others. It appears that the females are far more commonly found with prey than the males; it is remarkable as Poulton

adds, that the stings of Aculeates, the distasteful properties of the Danainae, Acraeinae, and of the odoriferous *Lagria*, the hard cuticle of Coleoptera, and the aggressive powers of the Odonata are alike insufficient protection against these voracious insects. Whether Asilids inject any poison into their victims or not has yet to be ascertained. It has been recorded that the captured insect collapses very rapidly after being perforated by the proboscis, which suggests that some toxic secretion may be present.

Asilid larvae live in soil, sand, wood, or in leaf-mould, and are either predacious or scavengers. They are cylindrical with a small, dark coloured, pointed head and are amphipneustic, the spiracles being situated on the prothoracic and penultimate segments. The mouthparts comprise a hook-shaped labrum, knife-like mandibles, and large broad maxillae with 2-segmented palpi. Small papilla-like antennae are present but no eyes. The anterior abdominal segments are provided either with ventral intersegmental areas, or circlets of pseudopods (*Laphria*) resembling those of Tabanid larvae. Ten or eleven segments are present, the higher number depending upon whether a short and indistinct segment-like swelling at the anal extremity is regarded as a true somite or not. The pupae are remarkably spined about the head: the abdominal segments have a dorsal girdle of spines, a ventral girdle of bristles, and the apex of the abdomen also bears spinous projections. The larva of *Laphria* has been found beneath bark and in the burrows of Longicorn larvae living in *Pinus*: it has been figured by Perris (1870) and later by Sharp (vide Verrall, 1909). For the metamorphoses of other genera vide Melin (1923) and Lundbeck.

FAM. MYDAIDAE.—*Very large flies devoid of bristles and obvious pubescence. Antennae terminating in a jointed and usually clubbed style. Venation complex;* R_1 *very long receiving several succeeding veins before its apex,* R_4, R_5 *and* M_{1+2} *bent forwards towards the apex of the wing. Pulvilli moderately large, no empodium.* A family of mostly exotic forms with a few moderate-sized species occurring in southern Europe. It includes the largest known Diptera, and the adults are stated to be predacious, but only very scanty observations are available. The larvae have been found in decaying wood and, in some cases, are known to be predacious upon Coleopterous larvae.

FAM. BOMBYLIIDAE (Bee Flies).—*Often densely pubescent with elongate slender legs, and often a long projecting proboscis. 3rd antennal segment simple, style small or vestigial, and not more than 2-segmented* (Fig. 451). *Cell* M_3 *absent. Pulvilli sometimes and an empodium always rudimentary.* Most of the flies of this family are moderate or rather large in size, often bearing bristles and dense pubescence (Fig. 479). The proboscis is usually very long and projecting forwards, but is sometimes short with broad labella. The wings are often darkly marbled and, when at rest, they remain half opened or outspread. Although only 12 species frequent Britain, considerably over 2,000 are known: cf. Hesse (1938) for the large S. African fauna.

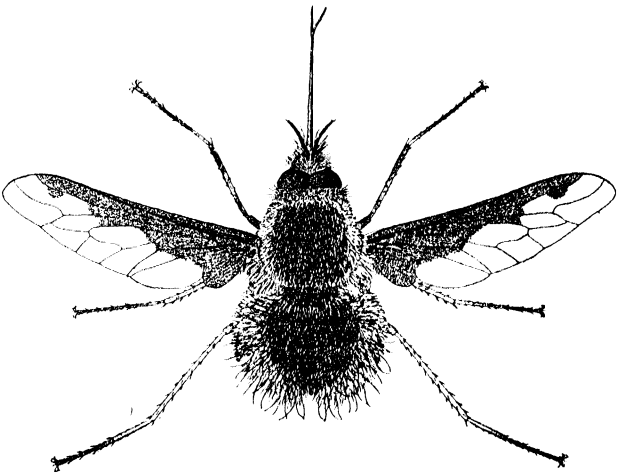


FIG. 479.—*Bombylius major*, male. × 3. Britain
After Verrall.

The larvae are parasites and when young, they are elongate and slender, with a very small head, and 12 trunk segments. They are stated to be metapneustic; each thoracic segment bears a pair of long setae, and a further pair is carried at the anal extremity. They undergo hypermetamorphosis and, when fully grown, are cylindrical or somewhat flattened, with a small retractile head and no eyes: the spiracles are found on the prothoracic and penultimate segments. The pupae are very characteristically spined on the head, with bands of hooklets across the dorsal side of the abdomen.

The larvae of *Argyramoeba* are parasites on those of solitary bees and fossorial wasps. The life-history of *A. trifasciata* has been observed by Fabre. The eggs are deposited on the ground, near the nest of the host (*Chalicodoma muraria*), and it appears that the young larva has to make its way into the cell of the bee. The pupa is armed with cephalic spines for the purpose of piercing the masonry enclosing its host. *Argyramoeba anthrax* (*sinuata*) has been bred from nests of *Anthophora*, *Chalicodoma* and *Osmia* and an account of its life-history is given by Verhoeff (1891).

Several species of *Anthrax* are parasitic upon Noctuid larvae or pupae, aculeate Hymenoptera, and also upon the eggs of Orthoptera. Other members of the genus are hyperparasites attacking Hymenopterous or Dipterous parasites of Lepidoptera.

The larvae of *Bombylius* are parasitic upon solitary bees (*Andrena*, *Halictus*, *Colletes*, etc.): those of *B. minor* have been studied by Nielsen (1903) who states that the young larva is very like that of *Argyramoeba* in form. At this stage it feeds upon the pollen stored in the cell of *Colletes*, but when it attains a length of 2 mm. it attacks its host larva: it subsequently moults, becoming maggot-like and amphipneustic. The life-history of *B. major* has been observed by Chapman (1878): the eggs were deposited on a sloping bank while the fly was on the wing, and descriptions of the larva and pupa agree in the main with those of *B. minor*.

Larvae of *Systoechus* live as parasites in the egg-cases of the locusts *Oedipoda* and *Stauronotus*: the larva and pupa of *S. oreas* are described and figured by Riley *et al.* (1880). According to Künckel d'Herculais (1905) the larva of *Systropus* parasitizes larvae of the Lepidopteron *Limacodes*. *Spogostylum* is parasitic upon *Xylocopa*, and other bees, and is also recorded from two genera of Coleoptera: for the life-history of *S. anale*, a parasite of Cicindelid larvae, vide Shelford (1913).

FAM. EMPIDIDAE.—*Bristly flies with a horny proboscis adapted for piercing; the style or arista (if present) almost always terminal. Cells M and 1st M_2 separate, cell Cu*

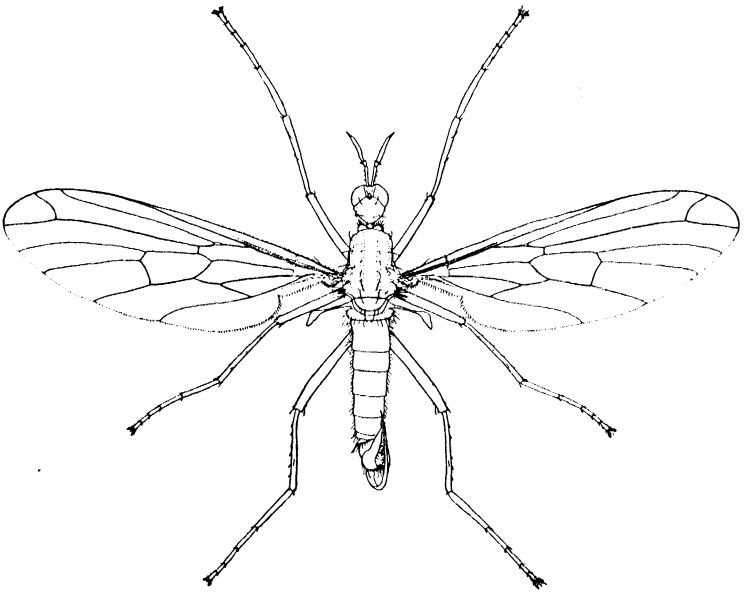


FIG. 480.—*Empis trigramma*, male. × 6. Britain
After Verrall.

generally short. Empodium linear—membranous, or setiform. A family of medium to very small sized flies of grey, yellowish, or dark coloration, very rarely metallic. About 2,600 species are known, and in Britain there are over 300 representatives. The proboscis is of variable length, and is generally rigid and downwardly projecting. The legs often display sexual characters, the male exhibiting special structural features such as thickened femora, tibiae or tarsi (Fig. 480). Empididae may be distinguished from the Asilidae by the absence of the face-beard and the much shorter cubital cell.

Their species are predacious upon smaller insects and, according to Poulton (1906), they prey most frequently upon Diptera; in this feature they are sharply contrasted with the Asilidae.

Species of *Empis*, *Hilara* and *Rhamphomyia* may often be observed 'dancing' or swarming in the air after the manner of Chironomids—a behaviour which is concerned with the meeting of the sexes. Either one or both sexes may perform these aerial evolutions and, in many species of the above genera, the males catch the prey, and kill but do not devour it. On meeting a female the latter receives the prey and feeds upon it during coitus: when copulation is accomplished the female drops the prey. The true significance of this remarkable habit is not understood (Hamm, 1909). An American species, *Empis aerobatica*, makes a curious frothy balloon, enclosing a small prey, which is probably transferred to the female during copulation; it is often released after the latter function is accomplished. Species of *Hilara* envelop their prey in a slight web before offering it to the female: the web is constructed by the male from a secretion of glands opening on the fore tarsi (Eltringham, 1928). *H. sartor* constructs a more extensive web than other species, and a whole literature has grown up around the subject of the origin and significance of this structure (Wheeler, 1924).

Larval Empididae are cylindrical, more or less spindle-shaped, with a very small retractile head and 11 trunk segments. They are amphipneustic, and most of the abdominal segments are provided with transverse ventral swellings, or more strongly developed pseudopods. The anal segment is somewhat rounded, and provided with a small terminal protuberance or spine, above which lie the posterior spiracles. Empidid larvae live in soil or among leaves and humus, in decaying wood, among moss, etc.: a few, such as *Hemerodromia*, are aquatic. Only scanty observations have been made with regard to their feeding habits but, in a few cases, they have been found to be carnivorous. The larvae of several genera are briefly described by Beling (1882; 1888); the metamorphosis of *Hemerodromia* is dealt with by Brocher (1909) and that of *Roederoides* by Needham & Betten (1901). Kieffer (1900a) has described the larva and pupa of *Empis meridionalis* and Brauer (1884) figures the larva of *Hilara lurida*.

FAM. DOLICHOPODIDAE.—*Small bristly usually metallic green or blue-green flies with a dorsal or terminal arista, and a short fleshy proboscis. Cells M and 1st M_2 confluent, cell Cu very short. Two pulvilli and a linear or narrowly lobiform empodium.* A large family comprising more than 2,000 species of which fully 250 are British (Fig. 481). The various species occur among grass and low herbage, generally in damp situations; several genera frequent the sea-shore. The work of Parent (1938) is useful for the W. European fauna.

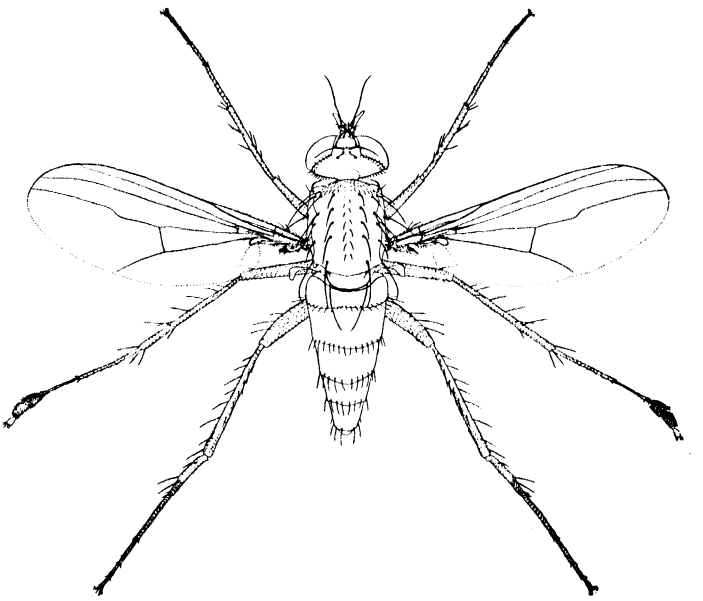


FIG. 481.—*Dolichopus popularis*, male. × 7·5. Britain
After Verrall.

The venation of the family is very similar to that of the Ephydridae, which certain species also resemble in their behaviour and habitat. The secondary sexual characters in the males attain a remarkable degree of development and may affect almost any of the outer parts of the body.

In adult life the Dolichopodidae are predacious upon minute soft-bodied insects, etc., which they envelop by means of the labella while extracting the juices. According to Becher (1882) some amount of mastication of the prey takes place on account of the mobility of the labrum during feeding. In America, according to Malloch, many species occur on flowers and undoubtedly feed upon nectar. It is likely that both habits are of frequent occurrence, though further observations are needed.

In *Melanderia* (Snodgrass, 1922) remarkable horny processes of the labella aid in grasping the prey. The adult mouthparts in general have been studied by Cregan (1941).

The larvae of this family have been found in a variety of situations and live beneath the ground, in rotten wood, among humus, etc., while others are aquatic. In *Aphrosylus* the larva lives among cast-up weed on the sea-shore, while those of several species of *Medeterus* prey upon the larvae and pupae of wood-boring Coleoptera. Most of the larvae of this family are probably carnivorous. They are elongate and cylindrical, 12-segmented, with a small retractile head, and most of the abdominal segments bear pseudopods armed with locomotory spinules. The last segment is obliquely truncated, often slightly swollen, and carries four short protuberances. The tracheal system is amphipneustic, and both pairs of spiracles are small; exceptions are met with in *Medeterus* (peripneustic) and *Argyra* (metapneustic).

The pupae are, as a rule, short and stout with a pair of elongate thoracic respiratory horns. Lundbeck states that larva of *Dolichopus* forms an earthen pupal cell, lining the interior thereof with a secretion forming a dense film-like layer. At one extremity the latter is wanting over a smaller area through which the pupal horns protrude. As the cocoon is apparently impenetrable to air Lundbeck thus explains the significance of the long pupal horns, so characteristic of the family. In other cases the cocoon is constructed of wood fragments, etc., and is lined by silken material. Although the metamorphoses of a number of species have been described the life-history has rarely been followed in any detail. Marchand (1918) has described the larva and pupa of *Argyra*, Perris (1870) those of *Medeterus*, and *Thrypticus* has been studied by Johannsen and Crosby (1913) and also by Lübben (1908).

Suborder III. CYCLORRHAPHA

The Cyclorrhapha are divided into three sections as given below:

Section A. ASCHIZA

Frontal suture absent: lunule often indistinct or absent: ptilinum absent. Cell Cu elongated (except in Phoridae) and extending more than half-way to wing-margin.

Section B. SCHIZOPHORA

Frontal suture and lunule distinct: ptilinum always present. Cell Cu short or vestigial (except in Conopidae).

Section C. PUPIPARA

Head closely united with thorax or folded back on same. Coxae widely separated. Usually flattened flies, with leathery or horny integument, adapted for ectoparasitic life on warm-blooded vertebrates. Ptilinum present or absent: wings often reduced or wanting. Viviparous; larvae extruded when about to pupate.

Section A

Table of the families of ASCHIZA:

1. Venation characteristically reduced, only C, R and M present as darkened veins near wing-base, other venation decolorized, no discal or cubital cell. Wingless forms common . . . . . PHORIDAE (p. 633)

–. Venation more complete 2

2. Discal and cubital cells very small and placed near wing-base, M_1 and M_2 long with a short common stalk. Sc runs into R_1 PHORIDAE subfamily Sciadocerinae (p. 634)
–. These cells larger (rarely absent), M_1 and M_2 coincident or shorter compared to their common stalk, or else Sc runs into C 3

3. Arista terminal. Hind tibiae and tarsi usually broadened, especially in the male. Cubital cell rather short . . . . . PLATYPEZIDAE (p. 634)
–. Arista dorsal, or M with 3 long branches 4

4. Wings narrow and pointed. M with 3 long branches. Cubital cell short. Arista sometimes subapical . . . . . LONCHOPTERIDAE (p. 633)
–. Wings broader and rounded at tip. M with 2 branches or M_2 short. Cubital cell long (or rarely absent) 5

5. Wings with a *vena spuria* between Rs and M, cell R_5 distally closed . . SYRPHIDAE (p. 635)
–. Wings without a *vena spuria*, cell R_5 open. Eyes very large. Female with a recurved, pointed ovipositor . . . . . PIPUNCULIDAE (p. 634)

FAM. LONCHOPTERIDAE.—*3rd antennal segment rounded or globular with a long terminal or subdorsal arista. Wings pointed at the apex and with no obvious cross-veins, Rs with its two branches closely approximated at the wing-apex. Empodium wanting.* This family includes a few small, slender, bristly flies, usually pale coloured, and often found along the borders of shady streams. The larvae of *Lonchoptera* have been found among leaves and other vegetable matter. According to de Meijere (1900) they are amphipneustic, much flattened and with long anterior and posterior setae. The head is vestigial and there are only 10 apparent trunk segments, of which the last appears to be of a composite nature, and bears a pair of widely separated spiracles (Fig. 482).

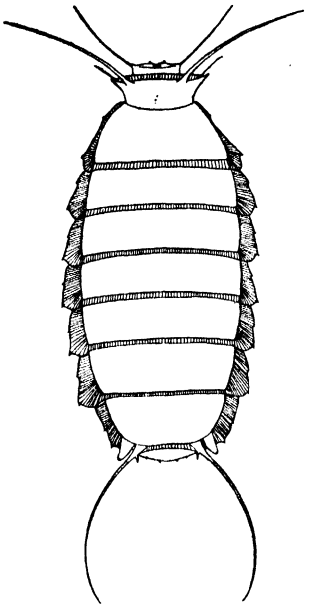


FIG. 482.—Larva of *Lonchoptera*; magnified. Britain

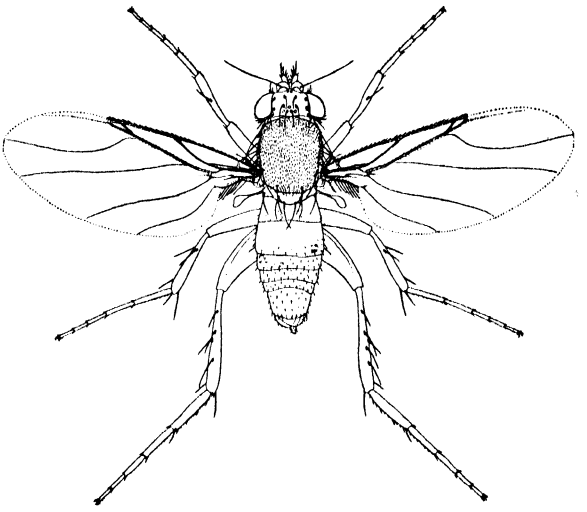


FIG. 483.—*Aneurina caliginosa* (= *Phora urbana*), male. × 10. Britain

After Verrall.

FAM. PHORIDAE.—*Antennae apparently consisting of one large segment, which conceals the others, and bearing a long apical or subdorsal arista. Wings often vestigial or absent. Anterior veins very heavily developed, and joining costa along the proximal half of the latter: remaining veins weak and abnormally distributed.* A family (Schmitz, 1929) of small or minute greyish-black or yellowish flies (Fig. 483): they are active runners and present a curious humped appearance. Their habits are varied but the adults are frequently met with among decaying vegetation, while others occur in the nests

of ants and termites. The wings exhibit a wide range of variation as regards degree of development, especially among the females; certain apterous and micropterous genera are only known from that sex. In *Ecitomyia* (female) for example, the wings are narrow and strap-like, and in *Puliciphora* (female) they are totally wanting.

The affinities of the Phoridae have been much discussed (Brues, 1907). They seem to be connected through the Sciadocerinae to the Platypezidae (Hendel, 1936–37). The larvae of Phoridae (Keilin, 1911) live in decaying vegetable matter and dead animals, especially *Helix* (Schmitz, 1917): others are mymecophilous and some are parasites. They resemble those of other Cyclorrhapha in their general morphology and consist of a reduced head, 3 thoracic and 8 abdominal segments. Furthermore, they agree with this suborder in being metapneustic in the 1st instar and amphipneustic subsequently. Each segment bears metamerically arranged bands of papillae. Pupation takes place in the larval skin, and the pupa carries a pair of elongate processes on the 2nd abdominal segment, which appear as the anterior respiratory horns on the puparium.

One of the most remarkable of all Phoridae is *Termitoxenia* (often placed in a separate family, Schmitz, 1938; 1939). It inhabits termite nests and has the wings reduced to minute vestiges; there are two types of individuals—stenogastric and physogastric. Wasmann (1900) claimed that it had lost the larval and pupal stages and that it was hermaphrodite, the same individual becoming successively male and female. It appears, however, from the observations of Mergelsberg (1935) and Wasmann (1940) that while most, perhaps all, the species have a normal metamorphosis, the adults are true hermaphrodites, an ovary and active sperm having been found even in a specimen extracted from the puparium. The method of reproduction is not known.

In *Puliciphora*, de Meijere (1913) has also found stenogastric and physogastric individuals, along with larval and pupal stages. On the other hand, according to Schmitz (1917), *Wandolleckia* is ametabolic, and has both types of individuals present: It is presumed to be a proterandric hermaphrodite. Further investigation of these remarkable genera is still needed. As Keilin (1919a) remarks, the only way to prove that proterandric hermaphroditism exists is the discovery of spermatogenesis in stenogastric forms. *Thaumatoxenia* is probably the most highly modified of all Phoridae (Trägårdh, 1908: Börner, 1908): originally regarded as belonging to the Hemiptera, further study has shown that it is a Phorid. The subfamily Sciadocerinae has been treated as a family but as Tonnoir has pointed out, the early stages (Fuller, 1934) are exactly like those of a Phorid. The adult shows some resemblance in its thorax to the Platypezidae, but in most respects is nearer the Phoridae. A few species are known in Australia and New Zealand and one in Patagonia.

FAM. PLATYPEZIDAE.—*Small thinly pilose flies with the hind tarsi remarkably dilated. 3rd antennal segment elongate and often pyriform, arista terminal. Cell R_5 open.* A small family including about 100 species of which more than a score are British (Verrall, 1901). They are usually to be met with dancing in the air in companies or running over herbage. Their most striking feature is afforded by the hind tarsi whose basal three or four segments are dilated, flattened, or ornamented in a curious manner, and very different in the male from the female.

An account of metamorphosis in *Callimyia* is given by de Meijere (1900a); Willard (1914) also figures the larva and pupa of *Platypeza agarici*. The larvae are broad and flattened with the sides bordered by long setae: in *Callimyia* the whole margin is deeply incised, each incision being strongly serrated. The trunk comprises 10 or 11 segments, the head and first segment being wholly ventral. The tracheal system is amphipneustic, with the anterior spiracles placed beneath the body; the posterior pair is inconspicuous and rather widely separated. So far as known the larvae live in Agaricini.

FAM. PIPUNCULIDAE.—*Thinly pilose or almost bare flies with a very large subhemispherical mobile head formed almost entirely of the eyes. Antennae with a usually long dorsal arista. Wings much longer than the abdomen, cell R_5 open; tibiae devoid of spurs. Ovipositor horny, exserted.* A very distinct family of small dark flies, the great majority of which pertain to the genus *Pipunculus*. They have a markedly hovering habit, and are usually to be taken on flowers, or by sweeping miscellaneous herbage. Their most striking feature is the great size and mobility of the head; the 3rd antennal segment is of peculiar shape, being sometimes prolonged into a curious beak-like process. For general information on the family the reader is referred to the works of Perkins (1905) and Verrall (1901); Hardy (1943) has reviewed the N. American species and Aczél (1943) has surveyed the literature.

The larvae are endoparasites of Homoptera. They are narrowed anteriorly, and capable of a good deal of extension and retraction: segmentation is obscure but apparently 10 or 11 somites are present. The anterior spiracles are small, and situated a short distance behind the mouth; the posterior pair is dark coloured, approximated, and placed some distance in front of the anal extremity. The puparium is provided with a pair of anterior spiracular tubercles, while the posterior spiracles are very much as in the larva. Dehiscence of the puparium usually occurs by the detachment of the dorsal plate through which the spiracular horns project. The head of the larval parasite is directed towards that of the host, and the fully grown parasite fills the greater part of the abdomen of the latter. In certain cases it has been found that 'castration parasitaire' results, and the abdomen of the female host is stated to undergo structural modification (Giard, 1889; Keilin & Thompson, 1915), but further research is greatly needed. When the Pipunculid larva quits its host, it usually escapes at the junction of the metathorax and abdomen, either above or below, the segments being ruptured at that point. It falls to the ground and buries itself beneath the soil or among rubbish, etc.

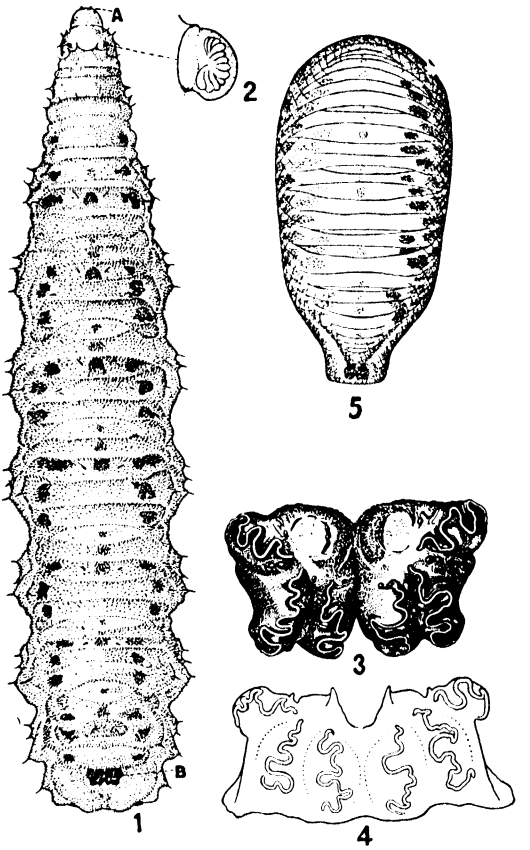


FIG. 484.—*Syrphus nitens*

1, larva × 7·5; A, antenna; B, posterior respiratory organ. 2, anterior spiracle more enlarged. 3, end view of posterior respiratory organ × 75. 4, posteroventral view of same × 75. 5, puparium, dorsal view × 7·5. Adapted from Metcalf, *Bull. 253 Maine agric. exp. Sta.*

FAM. SYRPHIDAE (Hover Flies).—*Moderate to large sized flies with brightly coloured markings, almost always bristleless. Arista, with few exceptions, dorsal. Certain of the veins forming a kind of secondary margin parallel with the outer wing-margin: cell R_5 closed; vena spuria present between R and M.* The Syrphidae are one of the largest and most sharply defined families of Diptera. They are usually very brightly coloured flies and may be striped, spotted or banded with yellow on a blue, black, or metallic ground-colour. The black and yellow coloration often imparts to them a superficial resemblance to wasps: other species are densely hairy and resemble bumble bees. Nearly all members of this family are attracted to flowers and may frequently be observed poised in the air, their wings vibrating with extreme rapidity, hence the name of 'hover flies'. The vena spuria (Fig. 485) is one of their most characteristic features and is rarely found in other Diptera. It is a vein-like thickening of the wing-membrane and may be distinguished from true veins in being fainter, and terminating without association with other veins.

The larval habits of Syrphidae are extremely varied. They may be: (*a*) *Phytophagous*, feeding externally upon plants (*Mesogramma polita*) or internally in bulbs (*Merodon equestris*, *Eumerus strigatus*), or within stems or in fungi (*Chilosia*). (*b*) *Carnivorous*, living predaciously upon aphids and the nymphs of other Homoptera (species of *Pipiza*, *Paragus*, *Melanostoma*, *Baccha*, *Syrphus*, etc.). (*c*) *Saprophagous*, living in decaying organic material, dung, liquid mud, or dirty water (species of *Eristalis*, *Helophilus*, *Sericomyia*, *Syritta*, *Tropidia*, etc.); in the sap and wet, rotting wood of diseased parts of trees (*Xylota*, *Mallota*, *Myiatropa*, *Myiolepta*, *Ceria*, etc.); or as scavengers in the nests of ants and termites (*Microdon*) or of Aculeate Hymenoptera

(*Volucella*). Verrall remarks that probably all the European species of *Volucella* are scavengers in the nests of large Aculeates, feeding upon diseased larvae or pupae, etc.: so far as known they are not predacious and the association is consequently friendly and not resented by the hosts. *Volucella bombylans* occurs in the nests of *Bombus* while the species *zonaria*, *pellucens* and *inanis* are found in the nests of social wasps.

Morphologically, Syrphid larvae (Fig. 484) may be recognized by the following characters. The head is greatly reduced and carries a pair of short fleshy, sensory processes. The cuticle is tough or leathery, and segmentation is obscure owing to the transverse corrugation of the body, but apparently 11 somites are present. The tracheal system is amphipneustic with the anterior spiracles on the 2nd apparent segment: the posterior pair is situated on two tubes of very variable length, which are fused together down the median line.

Three principal types of Syrphid larvae may be recognized. 1. The aphidivorous type with the ventral aspect flattened, the body much attenuated anteriorly, and the posterior respiratory tubes very short. The body is frequently marked with green or brown, and the general appearance is rather slug-like; all have a marked capacity for changing their shape (*Syrphus*, *Melanostoma*, etc.). 2. The short-tailed filth-inhabiting type with the body cylindrical and not attenuated anteriorly, and the respiratory tubes short. Three pairs of lateral fleshy protuberances are present on the 11th segment, and groups of branched plumose hairs are placed around the hind

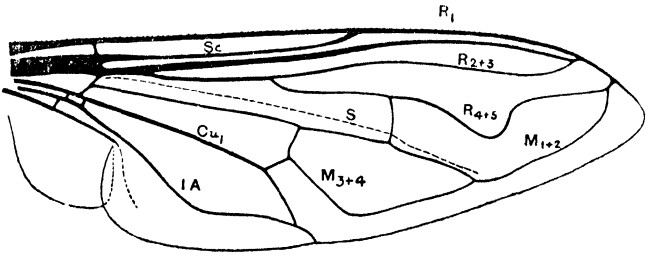


FIG. 485.—Venation of *Eristalis*
s, vena spuria.

spiracles (*Syritta*, *Tropidia*, etc.). 3. The rat-tailed type with the body terminating in a long flexible respiratory process which, in some species, is capable of being extended several times the length of the body (*Eristalis*, *Helophilus*, etc.).

In addition to the above three types there are several anomalous larvae. That of *Microdon* is broadly ovoid in outline and flattened ventrally, and is bordered by a row of marginal spines. The dorsal surface is convex and there is no evident segmentation or anterior spiracles. In general appearance it is slug-like and, when first described, it was regarded as a new genus of land Mollusca. This curious larva has been studied in detail by Cerfontaine (1907) and others. In the boring larva of *Merodon equestris* the body is cylindrical and much contracted, with rounded extremities: it comes nearest to type 2, but there are no fleshy protuberances on the 11th segment. In *Volucella bombylans* the larva is rather broad and fleshy, tapering anteriorly. The body is provided with numerous small lateral spinous outgrowths and larger terminal processes on the last segment (Künckel d'Herculais, 1875).

Prior to pupation Syrphid larvae come to rest in some suitable place on, or near, their habitat. In many species the caudal segments are cemented to a leaf, twig or other support with a secretion apparently derived from the hind gut; in other cases the larva buries itself in the soil or other medium. The puparium, as a rule, is considerably inflated dorsally and laterally: spiracles are present on the puparium in the region of the 4th or 5th larval segment and may be either sessile (*Melanostoma*) or elevated upon conspicuous horns (*Volucella*, *Eristalis*). Eclosion of the imago usually takes place by means of a dorsal rupture of the puparium. A good deal of information concerning the structure and biology of Syrphid larvae will be found in the writings of Metcalf (1916–17); Bhatia (1939) and Scott (1939) deal with the aphidiphagous larvae. The internal anatomy of both the larva and imago is dealt with by Künckel d'Herculais (1875) in his monograph on *Volucella*. The larva of *Eristalis* is described by Miall (1895) and its tracheal system has been studied in detail by Wahl (1899).

Economically, the predacious larvae of this family are notable in being important enemies of aphids, coccids and other Homoptera. The capacity of Syrphid larvae for the rapid destruction of aphids is remarkable and Metcalf states that a larva of *Syrphus nitens*, which had not been fasting previously, caught and destroyed 21 examples of the large aphid *Pterocomma flocculosa* in 20 minutes. The entire insect is never devoured, but only the soft and readily assimilated body-contents are sucked

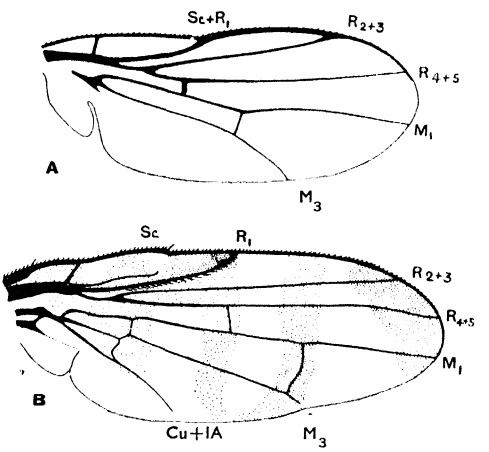


FIG. 486.—Venation of Acalyptratae. A, *Chlorops taeniopus*; B, *Trypeta tussilaginis*

out. Notwithstanding the great size of the family, and its varied larval habits, very few Syrphids are in any sense injurious to man. The 'Corn-feeding Syrphid Fly', *Mesogramma polita*, occurs in several states of N. America where its attacks are occasionally considered serious: the larvae feed upon the pollen grains and the saccharine cells in the axils of the leaves. Larvae of *Merodon* and *Eumerus* attack and destroy bulbs of *Narcissus*, *Amaryllis*, etc., and may occur separately or in association. They are well known pests in Europe and have been introduced, along with their host plants, into N. America and other parts. Larvae of a few species of the family, more particularly those of *Eristalis*, have been found as accidental parasites in the human body causing myiasis of the intestine.

Section B. SCHIZOPHORA

The classification of this group is a matter of great difficulty owing to the number of genera annectent between the families. The number of these recognized by some modern authors is very large and the key below only distinguishes the more important ones.

I. 2nd antennal segment above without a distinct external groove. Theca not developed at the base of the proboscis. Subcostal vein usually reduced. Squamae usually small or vestigial. Abdominal spiracles 2–5 usually in the pleural membrane . . . . . ACALYPTRATAE (p. 637)

II.—2nd antennal segment above with a distinct external groove. Theca developed at base of the proboscis. Subcostal vein complete. Squamae well developed. Abdominal spiracles normally in the sides of the tergites CALYPTRATAE (p. 645)

Group I. Acalyptratae

The following table (modified from Hendel, 1928 and 1937) is admittedly imperfect but it will probably serve to place the majority of genera in their family.

1. Wingless species. Tarsi broad and terminating in comb-like structures. Living in beehives . . . . . BRAULIDAE (p. 643)

–. Usually winged species; the tarsi quite different 2

2. Cell Cu_2 long and reaching or nearly reaching the wing-margin. Proboscis usually very long and often conspicuously jointed. Palpi reduced CONOPIDAE (p. 640)
–. Cu_2 short, not reaching wing-margin, or absent 3

3. Mouthparts vestigial and quite non-functional . GASTEROPHILIDAE (p. 645)
–. Mouthparts normally developed 4

4. Eyes swollen, vertex depressed between them. Hind tibia compressed and curved RHOPALOMERIDAE (p. 642)
–. Eyes, vertex and hind tibia not so modified 5

5. Costa complete 6
–. Costa more or less interrupted either at the end of Sc or of R_1 . . . 22

6. Sc vestigial, not reaching C 7
–. Sc complete, meeting C 8

7. R_1 reaching middle of wing, C ending at R_5, cell R_5 not distally narrowed PERISCELIDAE (p. 643)
–. R_1 ending well before middle of wing, C ending at M_1, cell R_5 distally narrowed ASTEIIDAE (p. 643)

8. Eyes on long stalks. Scutellum with two long spines . DIOPSIDAE (p. 642)
–. Eyes rarely on stalks. Scutellum then without long spines . . . 9

9. Vibrissae present 10
–. Vibrissae absent 11

10. Palpi reduced . . . . . SEPSIDAE (part) (p. 642)
—. Palpi normally developed . . . . NEOTTIOPHILIDAE (part) (p. 642)

11. Tibiae with preapical bristles. Ovipositor membranous 12
—. Tibiae without preapical bristles, or else the ovipositor is strongly sclerotized 17

12. Scutellum enlarged, covering the abdomen . . . CELYPHIDAE (p. 642)
—. Scutellum normal 13

13. Postvertical bristles convergent 14
—. Postvertical bristles divergent, parallel or absent 15

14. Vein IA reaches hind margin of wing as a fold. Legs bristly and sometimes with woolly hairs . . . . . COELOPIDAE (part) (p. 643)
—. Vein IA not reaching the margin. Legs not strongly bristly LAUXANIIDAE (p. 642)

15. Clypeus hidden 16
—. Clypeus well visible . . . . . DRYOMYZIDAE (p. 642)

16. No groove for the reception of the antennae. No peristomial bristles SCIOMYZIDAE (p. 642)
—. Antennae received into a groove and the peristomium bristly COELOPIDAE (part) (p. 643)

17. Legs long and stilt-like. Abdomen also elongate 18
—. Legs not specially long 19

18. Mid and hind tarsus as long or longer than their tibiae. Male holoptic TANYPEZIDAE (p. 642)
—. Tarsi shorter than their tibiae. Male dichoptic . MICROPEZIDAE (p. 642)

19. R_1 bare above, outer end of cell Cu_2 not pointed. Ovipositor membranous . 20
—. R_1 bristly above, or else the end of cell Cu_2 is pointed. Ovipositor more or less sclerotized . . . . . OTITIDAE (p. 640)

20. All femora with 2 ventral rows of strong bristles . MEGAMERINIDAE (p. 642)
—. Femora without strong ventral bristles, except sometimes beneath the front pair of male 21

21. Palpi rudimentary . . . . . SEPSIDAE (part) (p. 642)
—. Palpi normally developed . . . . . CHAMAEMYIIDAE (p. 642)

22. Costa more or less interrupted well before end of R_1, at point where Sc ends or would end if complete 23
—. Costa more or less interrupted at end of R_1; Sc, if complete, ending at the same point 40

23. Sc either complete or (Trypetidae) ending suddenly and sending a perpendicular fold to C 24
—. Sc vestigial or absent 35

24. Postvertical bristles convergent. Vibrissae present. Costa usually spiny HELOMYZIDAE (p. 643)
—. Postvertical bristles divergent, parallel, or absent 25

25. Stout, bristly, bumblebee-like flies . . . TACHINISCIDAE (p. 642)
—. Flies not of this type 26

26. Inner orbits completely sclerotized, almost always with inwardly directed anterior orbital bristles 27
—. Inner orbits not sclerotized in front, anterior orbital bristles absent . . 28

27. Legs stilt-like. Prothorax forming a neck . . PHYTALMIIDAE (p. 641)
—. Legs and prothorax normal . . . . . TRYPETIDAE (p. 641)

28. Vibrissae present 29
—. Vibrissae absent 34

29. Base of M_{3+4} absent so that there is only 1 intermedian cell AULACOGASTRIDAE (p. 643)
—. Base of M_{3+4} developed so that there are 2 intermedian cells . . . 30

30. Vertex sclerotized to near the antennae. Cross-veins *r-m* and *i-m* close together. CLUSIIDAE (p. 643)
—. Front part of vertex not well sclerotized 31

31. Male eyes approximated. Female with a sclerotized ovipositor LONCHAEIDAE (part) (p. 642)
—. Male eyes well separated. Female ovipositor membranous. 32

32. R_1 bristly above. IA reaching the wing-margin NEOTTIOPHILIDAE (part) (p. 642)
—. R_1 bare above. IA not reaching the margin 33

33. Antennae lying in deep grooves. Scutellum elongate THYREOPHORIDAE (part) p. 642)
—. Antennal grooves shallow. Scutellum normal . . . PIOPHILIDAE (p. 642)

34. Wings with a conspicuous pattern. Space between Sc and R_1 sclerotized, forming a pterostigma . . . . . RICHARDIIDAE (p. 641)
—. Space between Sc and R_1 not sclerotized . LONCHAEIDAE (part) (p. 642)

35. Vein IA and base of M_{3+4} not developed. Cell Cu_2 absent, only 1 intermedian cell . . . . . CHLOROPIDAE (part) (p. 644)
—. At least vein IA and cell Cu_2 developed 36

36. Posterior basitarsus short and broad. Vibrissae present SPHAEROCERIDAE (part) (p. 643)
—. Posterior basitarsus normal 37

37. True vibrissae absent; if some peristomial bristles are enlarged, there is only 1 posterior orbital bristle. Costa reaching M_1 38
—. Vibrissae present, or else costa not reaching M_1 39

38. Ocellar triangle small. Sternopleural and humeral bristles present OPOMYZIDAE (p. 643)
—. Ocellar triangle large. Sternopleural and humeral bristles absent PSILIDAE (p. 642)

39. Fore femur with a strong spine beneath. Postvertical bristles convergent ANTHOMYZIDAE (p. 643)
—. Fore femur without such spine. Postvertical bristles divergent AGROMYZIDAE (part) (p. 641)

40. Inwardly directed anterior orbital bristles present 41
—. No such bristles present 42

41. Vertex without interfrontal bristles. Foremost posterior orbital bristle directed more or less obliquely backwards . . AGROMYZIDAE (part) (p. 641)
—. Vertex with interfrontal bristles. Foremost posterior orbital bristle directed forwards and usually outwards . . . MILICHIIDAE (part) (p. 645)

42. Hind basitarsus short and broad . . . SPHAEROCERIDAE (part) (p. 643)
—. Hind basitarsus normal 43

43. Sc entirely absent. Ocellar triangle very large . CHLOROPIDAE (part) (p. 644)
—. Sc at least partially developed 44

44. Costa interrupted at end of humeral vein as well as at end of R_1 . . . 45
—. Costa interrupted only at end of R_1 48

45. Sc complete to costa . . . . THYREOPHORIDAE (part) (p. 642)
—. Sc more or less strongly reduced 46

46. Convergent postvertical bristles absent . . . . EPHYDRIDAE (p. 644)
—. Convergent postvertical bristles developed 47

47. Cell Cu_2 and vein 1A absent . . . MILICHIIDAE (part) (p. 645)
—. Cell Cu_2 and vein 1A present . . . DROSOPHILIDAE (part) (p. 643)

48. Postvertical bristles divergent. Vein Sc reduced AGROMYZIDAE (part) (p. 641)
—. Postvertical bristles convergent, or else Sc is complete 49

49. Vibrissae and sternopleural bristles absent. Ocellar triangle large . . CANACIDAE (p. 644)
—. Vibrissae present, even if small 50

50. Scutum with anterior dorsocentral bristles. Posterior orbital bristles directed outwards. . . . . TETHINIDAE (p. 644)
—. Scutum with posterior dorsocentral bristles only. One posterior orbital bristle directed forwards . . . . . DROSOPHILIDAE (part) (p. 643)

FAM. CONOPIDAE.—A family of more or less elongate, moderate-sized flies, thinly pilose or almost bare, and frequently bearing a striking resemblance to solitary wasps or other Hymenoptera. Most species visit flowers; they are slow fliers and less than 20 kinds occur in the British Isles. The larvae are endoparasites of adult bees and wasps or of Orthoptera (de Meijere, 1904; 1912a). The species of *Conops* parasitize *Bombus*, *Odynerus*, *Sphex*, *Vespa*, etc.: *Physocephala* parasitizes *Apis*, *Xylocopa* and *Bombus*, while *Myopa* is known to attack *Andrena*, *Bombus* and *Vespa* (Séguy, 1928).

The eggs of the Conopidae are elongate oval with a group of hooks, filaments, or other outgrowths at the micropylar end. In certain cases the eggs are stated to be deposited on the bodies of the hosts during flight. The larvae are generally found in the region of the anterior abdominal segments of the host, and are attached by their hinder extremity to a large trachea or air-sac: the exact relation between the Conopid larva and the tracheal system of the host is in need of further investigation. The mouthparts are greatly reduced and the larvae are mainly haemophagous. In general shape the larvae are ovoid or pyriform with considerable powers of changing their form. Their most conspicuous features are the large convex plates of the posterior spiracles. The latter are complex structures, and distributed over the surface of each spiracle is a series of small sieve-like areas.

FAM. OTITIDAE.—A large family many of whose members have mottled wings and consequently resemble Trypetidae. Unlike the latter family, Sc meets the costa at an acute angle and is not abruptly elbowed distally. In the male there are 5 evident abdominal segments and an elongate rolled up aedeagus: in the female there are 6 abdominal segments with a flattened corneous ovipositor. The flies are commonly met with wherever there is abundant vegetation, and nearly twenty species are British. According to Banks (1912) the larvae are usually more slender than those of the Muscidae; the anterior spiracles have about 10 lobes and the posterior pair are borne on two slight processes, each spiracle being provided with three short slits. The larva of *Platystoma lugubre* (= *umbrarum*) is described by Perris (1855) and that of *Euxesta nitidiventris* by Brues (1902). The latter species lives beneath the bark of dead trees and is 11-segmented with the head nearly as long as the first two thoracic segments. The larva of *E. notata* attacks oranges, apples, onions, cotton bolls, etc., and has also been found in human excrement.

The Otitidae are today often split up into about six families. The most distinct of

these groups is the Pyrgotidae in which the adults usually lack ocelli. The larvae of these is parasitic in Scarabaeid beetles such as *Phyllophaga* and *Popillia*. The adult female is nocturnal and lays her egg through the soft cuticle of the abdominal tergites when the beetle is in flight (Clausen, 1940). Two other small exotic families are somewhat closely allied to the Otitidae. The **Richardiidae** with about a hundred mostly neotropical species, and the **Phytalmiidae** which are mostly African; in neither group is anything known of the early stages.

FAM. TRYPETIDAE.—The 'fruit-flies' form an easily recognizable and natural family of almost cosmopolitan distribution. About 1,200 species are known of which 72 are British. The wings as a rule are conspicuously marbled and a horny, flattened ovipositor is very characteristic: in *Toxotrypana* it exceeds the rest of the insect in length. The standard systematic work on the family is that of Loew (1862); more recent papers are those of Bezzi (1913), Hendel in Lindner (1927), and Munro (1947), while Collin (1947) should be consulted for British genera.

The larvae are phytophagous and those of several species are well known (Phillips, 1946). When fully grown they are rounded or barrel-shaped: a pair of rounded anal tubercles are present, and the posterior spiracles each contain three simple slits. The prothoracic pair are many-lobed, from about 14 to 38 processes being present. The larvae may be grouped under four headings with reference to their habits. (1) Living in fruits, preferably of the fleshy type: *Dacus*, *Ceratitis*, etc. (2) Living in the flower heads of Compositae: *Tephritis*, some *Urophora*. (3) Leaf- or stem-miners, *Philophylla*, *Euribia*, etc. (4) Gall formers on various parts of plants, some *Urophora*. *Ceratitis capitata* is the well-known Mediterranean fruit-fly (Quaintance, 1912) whose larva attacks almost all commercial and other succulent fruits, and becomes extremely injurious wherever established. The eggs are deposited inside the fruit, and the whole life-cycle occupies about 30 to 40 days, pupation taking place in the ground. This species occurs throughout the tropics and warmer regions, including the Mediterranean countries of Europe. *Philophylla* (= *Acidia*) *heraclei* (vide Smith & Gardner, 1922) is the celery fly whose larvae cause considerable damage by mining the leaves of that plant and the parsnip: it also affects certain wild Umbelliferae. The life-history of *Urophora solstitialis* (correctly *jaceana*) is described by Wadsworth (1914) and that of *Dacus cucurbitae* by Back & Pemberton. Observations on the anatomy of the larva and imago of *Dacus tsuneonis* are given by Miyake (1919).

FAM. AGROMYZIDAE.—A family of ill-defined limits whose members are small to minute flies. The larvae are usually leaf-miners. Their range of food-plants varies greatly; thus many species of *Phytomyza* are confined to one or a few allied species of plant while *P. atricornis* and *Liriomyza pusilla* utilize species of many natural orders. *Melanagromyza aeneiventris* tunnels into the stems and roots of many Compositae, while *A. pruinosa* mines the cambium of birch and hazel. *Odinia* which is often placed in a separate family is associated with the flowing sap of trees, in which it breeds. The majority of species of the family pass through several generations in the year—five or more in the case of *Liriomyza pusilla*. The larvae are cylindrical, tapering somewhat anteriorly, and more or less truncated posteriorly. The mouthparts are conspicuous on account of their dark colour and strong sclerotization: on the ventral surface of the anal segment is a small sucker-like organ. The posterior spiracles are situated at the apices of backwardly projecting processes of variable length, usually contiguous and porrect. The puparia are broadly fusiform with the segments well defined: both the anterior and posterior spiracles are prominent and projecting. Pupation either occurs in the larval mine or in the soil. For information on the metamorphoses of various species reference should be made to the papers of Hendel in Lindner (1934–36) and Frick (1952); Phillips (1914) for *Agromyza parvicornis*; Malloch (1915) for *A. pruni*; Webster & Parks (1913) for *L. pusilla*; Miall & Taylor (1907) and Smulyan (1914) for *Phytomyza*; and Barnes (1933) for the cambium miner *Dizygomyza*. The most remarkable life-cycle occurs in *Cryptochaetum*, whose larvae are endoparasites of coccids. In *C. iceryae*, which parasitizes *Icerya*, there are four larval instars (vide Thorpe, 1941). The 1st-instar larva is an embryo-like sac devoid of tracheae and mouthparts, with the digestive canal closed: caudally it bears a pair of finger-like processes. In the successive instars the caudal processes increase in length and become filamentous until, in the last stage, they are much longer than the whole body: these organs appear to be mainly respiratory in function. A characteristic feature of the larvae of this family is the presence of sphaeroidal concretions of calcium carbonate in the Malpighian tubes and these products appear to be only wanting in *Cryptochaetum* which is carnivorous in habit; but the affinities of this genus are very doubtful.

The family **Tachiniscidae** includes two monotypic genera, one S. African, the other S. American. They are of about the size of bumblebees, but nothing is known of their biology.

FAM. LONCHAEIDAE.—This family is somewhat heterogeneous. In the genus *Lonchaea* the male eyes are more or less approximated and the colours are dark. The larvae are scavengers in rotting vegetation or dung, or feed on living plants, or live under bark and attack the larvae of bark-beetles. Some of the phytophagous species make galls on grasses and *L. aristella* does much damage to figs in the Mediterranean region. The larva of *Lonchaea* has been described by Cameron (1913) and Silvestri (1917a). The genus *Palloptera* includes flies of a paler colour, with widely separated eyes and with the lunules hidden. The larvae develop in the flowers and stems of various plants.

FAM. TANYPEZIDAE, MICROPEZIDAE, NERIIDAE.—These flies all agree in having long, stilt-like legs. Only the second family has more than a few species; the Micropezidae are abundant (ca. 200 species) in the neotropics, and 8 species are British (Collin, 1945). The adult flies are often associated with decayed wood and a few larvae have been bred from this habitat (Berg, 1947).

FAM. SEPSIDAE.—Small flies, of somewhat ant-like build, with the habit of waving their wings which often have a dark spot towards the tip. In many species the fore femora and sometimes tibiae are toothed or otherwise modified, especially in the male. The larvae are saprophagous and have been found in dung; the adult flies are often extremely abundant on the larval food or on flowers.

FAM. PIOPHILIDAE.—Another group of small flies with larvae of saprophagous habit. *Piophila casei* is the well-known 'Cheese Skipper' whose larvae may do much damage to cheese and other fatty foods. In the last larval instar it is capable of jumping by attaching its anal end to the substratum, bending itself into a circle with its mouth-parts engaged near the anus, and then suddenly releasing its hold (Wille, 1922). The non-domestic species mostly seem to breed in carrion; the metamorphoses of the group are reviewed by Hennig in Lindner (1943).

The **Thyreophoridae** is a very small family of flies, very rare in the adult stage, and associated with old, dried-out carcases.

FAM. DIOPSIDAE.—These extraordinary flies are chiefly found in Africa (Shillito, 1940). While the long stalk which supports the eye is characteristic, it re-occurs in other families (Otitidae, Drosophilidae, etc.). The early stages are saprophagous or phytophagous (Hennig, 1952) and the adults are sometimes extremely abundant by streams in E. Africa.

FAM. PSILIDAE.—About 100 flies with a mainly Holarctic distribution are included (cf. Collin, 1944). The larvae are phytophagous and *Psila rosae* is the well-known carrot fly whose larvae cause much damage by eating into the tap root of the carrot and other roots (Körting, 1940); see also several papers by Petherbridge, Wright and others, mostly in *Ann. appl. Biol.*, 1942–47.

The **Megamerinidae** include a few rare flies of a habitus similar to the Psilidae; the larva has been found under bark and is perhaps predacious (Hennig, 1952).

FAM. RHOPALOMERIDAE.—This includes a few peculiar S. American flies which associate with the sap exuding from trees. They are usually found on the coast or along rivers (Curran).

FAM. SCIOMYZIDAE.—These flies are mostly found in damp situations and many of the larvae are aquatic. Those of *Sepedon* and *Tetanocera* are described by Needham & Betten (1901). While they are mostly phytophagous, others, such as those of *Salticella*, feed (possibly as parasites) on water-snails.

The family **Dryomyzidae** includes a few species associated with excrement or decaying fungi. *Helcomyza* (= *Actora*) breeds on the sea-shore and all stages can withstand immersion (Joseph, 1880). The **Neottiophilidae** includes two species of which *Neottiophilum praeustum*, though rarely seen in the adult stage, is common as a larva in the mud-lined nests of thrushes and blackbirds. It sucks the blood of the young nestlings, sometimes with fatal results.

FAM. LAUXANIIDAE (Sapromyzidae).—As many as 1,200 species (47 British) of this family are known. The larvae are mostly scavengers, feeding on dead leaves; they have numerous transverse rows of tooth-like projections. That of *Lauxania aenea* attacks the leaves of clover (Marchal, 1897a).

The **Celyphidae** is a small family of flies, mostly oriental in distribution, known by the greatly enlarged scutellum which covers the wings when at rest. Metamorphoses unknown.

FAM. CHAMAEMYIIDAE (Ochthiphilidae).—These minute, grey, some-

times black-spotted flies appear to be predatory on coccids and aphids in their early stages. This habit is well-known in the genus *Leucopis* and in *Chamaemyia* of which the larva is said to inhabit galls the same habit may be suspected.

The **Braulidae** of which the adults superficially resemble Pupipara are probably allied to the preceding family (Imms, 1942). The adults of *Braula coeca* (Fig. 487) are usually found clinging to queen or worker honeybees, especially the former. The eggs are laid on the walls or beneath the cappings of honey cells, Skaife (1921) having first shown that the genus is oviparous. The larvae make tunnels in the wax, boring from one cell to another but seem to do little damage. The pupa is unique amongst the Cyclorrhapha in that it is enclosed in the unmodified last larval cuticle which does not become brown or barrel-shaped. The affinities of the family have been much disputed; the adult characters seem to be largely due to adaptive convergence, but the larva shows some resemblance to that of *Leucopis*.

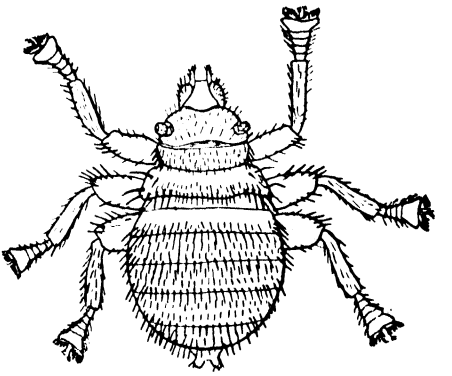


FIG. 487.—*Braula coeca*. × 24
After Carpenter.

FAM. COELOPIDAE.—The Kelp flies are found on the seashore where they breed in decaying seaweed, sometimes in immense numbers.

FAM. HELOMYZIDAE.—The flies of this family, in which there are about 250 species (63 British), are of small or moderate size and often of yellowish colour. The larvae are scavengers in fungi, excrement, etc.; a number of species has been bred from nests of birds and mammals and some occur in caves.

FAM. CLUSIIDAE (Heteroneuridae).—A small family in which the adult stage is not very often seen; the early stages are spent in decaying vegetable matter, especially rotten wood. The larva of *Clusiodes albimana* has been described by Perris.

The **Anthomyzidae** and **Opomyzidae** both include a few species of small flies whose early stages are spent in the stems or leaves of grasses (cf. Hennig, 1952). The British species have been tabulated by Collin (1944a; 1945a) and the early stages of *Opomyza* and *Geomyza* have been described by Thomas (1933; 1934; 1938).

FAM. DROSOPHILIDAE.—The flies pertaining to this family usually have a somewhat swollen appearance, with light red eyes, and are commonly taken by sweeping herbage. Others are prevalent about flowing sap, decaying fruit, cider presses, wine vats, vinegar factories, etc., where they are attracted by certain by-products of fermentation. A few (*Scaptomyza*) are leaf-miners and others, e.g. *Acletoxenus* which feeds on Aleyrodids, have predatory larvae. The eggs of *Drosophila* are often spindle-shaped, bearing elongate processes at one extremity: as the eggs are frequently submerged in fluid media, with the filaments at the surface, it has been suggested that the latter are concerned with respiration. The larva is 11-segmented with each segment surrounded by a girdle of minute hook-like spines (*D. funebris*), or the body may be uniformly invested with these structures (*D. fenestrarum*). Three pairs of conical lateral outgrowths are borne on the anal segment, together with a longer median retractile process, carrying the posterior spiracles. The pupae are fusiform with the anterior dorsal surface flattened to form an ovoid plate which is forced upwards to allow of the eclosion of the imago. Arising from this plate is a pair of stalked, digitate or plumose spiracular processes. Traces of the anal processes of the larvae are also evident upon the puparium. Details of the early stages are given by Sturtevant (1921) and Mayer (1935).

Associated with the Drosophilidae are six small groups to which many authors give the status of families. The more distinct of these are the **Asteiidae, Periscelidae,** and **Aulacogastridae.** The flies of the first-named family have a characteristic venation and are found in shady places, often on windows. The larva of one species has been found in water collected in sheathing leaf-bases (F. X. Williams). The adults of the Periscelidae are attracted to fermenting sap in which it is thought that the larvae live; the single species of *Aulacogaster* has similar habits (Robinson, 1953).

FAM. SPHAEROCERIDAE (Borboridae).—In these small, usually black-bodied, flies, the individual species often have a very wide distribution. They mostly

breed in decaying plant materials or excrement. Some species of *Ceroptera* hang on to the backs of *Scarabaeus* and other dung-beetles and probably lay their eggs in the burrows. There are a number of short-winged or apterous species, such as *Anatalanta* of Kerguelen Is. and a series of genera found in the tree-heath zone of the E. African mountains. The British species were tabulated by Richards (1930) and a number of puparia were figured by Goddard (1938).

FAM. EPHYDRIDAE.—The flies of this family are black or darkly coloured, inhabiting marshy places, damp meadows, etc. The family is closely related to the Drosophilidae and clear distinctions are sometimes difficult to recognize. Jones (1906) has described the life-history of *Ephydra millbrae* which is aquatic. The eggs are partially clothed with hairs and are attached to floating vegetation, etc. The amphipneustic larvae are densely covered with short pubescence, with the anterior spiracles 7-branched, and a pair of respiratory tubes emerge from a terminal anal siphon. Eight pairs of conspicuous pseudopods, armed with hooks, are present on the abdomen. The puparium is provided with an elongate siphon whose apex rests at the surface of the water. Larvae of *Notiphila* occur in the stems of water plants, while those of *Hydrellia modesta* are found in the leaves of *Potamogeton* and are metapneustic throughout life (Keilin, 1915). The pupa of *Notiphila* (Varley, 1937) obtains oxygen from the roots of water-plants which are pierced by the posterior spiracular processes. Other larvae occur in salt or alkaline waters, particularly those of *Ephydra hians* and *E. californica* which often appear in such vast numbers as to have been used by the N. American and Mexican Indians as food. A few species are parasitic, e.g. *Trimerina* on eggs of spiders. An account of the anatomy of the larva of *E. riparia* is given by Trägårdh (1903) and the metamorphosis of *Teichomyza fusca* by Vogler (1900) (cf. also Johannsen, 1935; Hennig, 1943a). The larva of *Psilopa petrolei* (Thorpe, 1930) is a veritable biological curiosity since it has long been known to live in pools of crude petroleum in California. Morphologically it differs little from many other Ephydrids and its adaptation to its mode of life appears to be physiological. The food of this larva consists of insects trapped in the oil and possibly of metabolites of the bacteria which occur in that medium.

The **Canacidae** are found in salt marshes and the early stages are not very different from those of Ephydrids. The **Tethinidae** are also found on the sea-coast but usually in drier places; the metamorphoses are unknown.

FAM. CHLOROPIDAE.—Small, bare, often light-coloured flies, plentiful among miscellaneous herbage about roadsides, meadows, etc. Although closely allied to the Ephydridae they may usually be separated therefrom by the absence of anterior orbital bristles, the small oral fossa, and the bare arista. The larvae are essentially phytophagous, although those of a few species are predacious. The larva of *Oscinella frit* (Balachowsky & Mesnil, 1935–36) is very narrow in proportion to its length. The anterior spiracles are 6-lobed, and the posterior pair open at the apices of short tubular projections at the hind extremity of the body: each spiracle has three circular openings separated by sclerotized ridges. In *Oscinosoma* the larva is less elongate and more musciform with ambulatory swellings on the abdominal segments: the spiracles closely resemble those of *Oscinella* (vide Silvestri, 1917). The larva of *Chloropisca glabra* is predacious on aphides and its life-history has been followed by Parker (1918), and the anatomy of the larva of *Platycephala* by Wandolleck (1899). The 'frit-fly' *Oscinella frit* (Fig. 488) is a pest of cereals in Europe. The flies of the first generation oviposit in May on the leaves or stems of spring oats and various grasses. The larvae migrate to the shoots causing the death of the central leaves. Flies of the second generation oviposit during July on the ears of oats, and the larvae feed on the spikelets and young grain. Oviposition in the third generation occurs during September on winter cereals and various grasses. Winter is passed in the larval condition at the bases of the shoots which they ultimately destroy. The 'gout fly' *Chlorops taeniopus* lays its eggs during

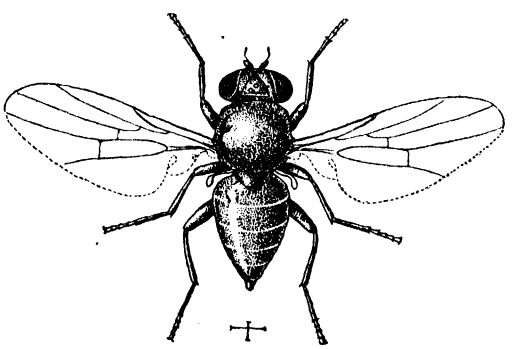


FIG. 488.—*Oscinella frit*

Reproduced by permission of the Ministry of Agriculture.

June on the leaves of spring barley or occasionally on couch grass. The larvae migrate into the shoots which become thickened and the leaves are distorted. If the barley ear is about to be formed the larva eats a groove down one side of it and the internode. The ear fails to grow away from the ensheathing leaf. The flies of the second generation oviposit from the middle of August until the middle of October mainly on couch grass, but sometimes on self-sown or winter cereals. The shoots become greatly thickened, the leaves distorted, and no ear is formed (Frew, 1923). Certain species of *Siphunculina* and *Hippelates* probably transmit conjunctivitis and other eye diseases in the Orient, California, etc. Such flies have spinous pseudotracheae which appear to make incisions in the conjunctiva and so aid the entry of pathogenic organisms carried on their bodies (Graham-Smith, 1930a).

FAM. MILICHIIDAE.—Small flies which seem to be fundamentally saprophagous but in several genera have developed peculiar habits. In *Desmometopa* the adults are often seen sucking the prey of larger predators (Reduviids, spiders); others, such as *Phyllomyza*, live with ants. *Leptometopa latipes* has been bred from excrement, but the early stages are little known. *Meoneura* (found on carrion or in birds' nests) and *Carnus* are sometimes placed in a family, **Carnidae.** *Carnus hemapterus* is exclusively found in birds' nests and the wings break off by the time the adults are mature; the flies feed on the blood of the hosts (Eichler, in Hennig, 1952) but the larval habits are not known.

FAM. GASTEROPHILIDAE.—The structure of the adult flies is to some extent intermediate between the Acalyptratae and the Calyptratae; many authors treat them as forming no more than a subdivision of the Oestridae. The larval stages are found in the alimentary canal of mammals—*Gasterophilus* (Equidae), *Gyrostigma* (Rhinoceros), *Cobboldia* (Elephants).

The horse bot-flies lay their eggs on the hair. In *G. intestinalis* they are found on various regions, preferably the fore legs. The young larvae hatch upon the application of moisture and friction supplied by the licking of the horse; they are ingested, and attach themselves to the walls of the stomach. *G. nasalis* oviposits on the hairs beneath the jaws, and to some extent on the shoulders, etc. The larvae attach themselves to the pharynx, stomach and duodenum. *G. haemorrhoidalis* lays its eggs singly on the hairs around the lips: the larvae attach themselves to the stomach-wall, eventually migrating to the rectum, where they become re-attached. Before leaving the host they again become attached close to the vent and protrude therefrom. In all three species the larvae are ultimately voided through the anus and pupate in the ground.

The most complete account of the metamorphoses and habits of *Gasterophilus* is that of Dinulescu (1932).

Group II. **Calyptratae**

Authors are still not agreed on how to arrange in families this, the largest section of the Diptera. It seems that eventually, by bringing in larval characters (Roback, 1951; Hennig, 1952), a more satisfactory system will be evolved.

Table of the families:

1. Oral fossa very small. Mouthparts small or very small, usually functionless. Bristles reduced or absent and more or less replaced by woolly hairs, in particular on the hypopleura . . . . . OESTRIDAE (p. 645)
–. Oral fossa and mouthparts normal, or, if somewhat reduced, hypopleuron with bristles 2

2. Pteropleural and hypopleural bristles present 3
–. Pteropleural bristles absent; hypopleural bristles present only in the genus *Eginia* MUSCIDAE (p. 649)

3. Postscutellum (= mesopostnotum) well developed and convex. 2nd abdominal sternite with its edges overlapped by the tergite . . CALLIPHORIDAE (p. 646)
–. Postscutellum little developed and not convex. 2nd abdominal sternite with its sides visible, usually lying above those of its tergite . TACHINIDAE (p. 648)

FAM. OESTRIDAE (Warble or Bot Flies).—A comparatively small family of stoutly built more or less pilose flies, often bee-like in appearance. The antennae are

short and partially sunken in facial grooves and the venation almost always is of the Tachinid type. There are no sternopleural setae while the hypopleural setae are represented by a group of hairs. The ovipositor is extensile and often long but not adapted for piercing: the eggs are laid on the body hairs of the hosts and are provided with special clasping flanges. The larvae are endoparasites of mammals but, with few exceptions, the life-histories are imperfectly known owing to difficulties attending observations of the cycle in the living animal. While the Oestridae are usually regarded as a separate family, they have definite affinities with the Tachinidae with which they are associated by some authorities.

Oestridae are more frequently met with as larvae than as adults, and a number of species have been described from the larval phase only: only six species occur in Britain. Parasitization of the mammalian hosts occurs in the nasal and pharyngeal cavities, and beneath the skin. As a rule each species parasitizes a single species of host, and each genus or group of allied species attacks allied hosts. The larvae, when fully grown, are broadly cylindrical or somewhat barrel-shaped, narrowing relatively little at the extremities, and never tapering anteriorly in a manner comparable with other cyclorrhaphous larvae. Twelve segments are present with the first two much reduced and annular. The body-wall is very tough with lateral swellings and groups of spinules. As a rule Oestrid larvae are amphipneustic, the anterior spiracle lying in a deep pit. Carpenter & Pollard (1918) have detected the presence of 6 pairs of vestigial lateral abdominal spiracles in *Hypoderma* and *Oedemagena*. Mouth-hooks are present in all 1st-stage Oestrid larvae but subsequently they may become reduced or vestigial.

The larvae feed upon the serous and other exudations into the tissues of their hosts, which fluids are usually either altered or increased owing to irritation induced by the presence of the parasites. When mature the larvae leave their hosts and pupate in the ground or among surface litter.

Hypoderma includes the well known 'warble flies', *H. bovis* and *H. lineatum*. The adults are active from May to August and the eggs are mostly laid on the hairs of the flanks, legs, and feet of cattle. According to Hadwen *H. lineatum* lays 1–14 eggs on a single hair, usually between the point of the hock and the ischium, and on the inside of the legs. *H. bovis* lays its eggs singly on the hairs, chiefly about the legs. In both species they hatch in 4 to 5 days, and the larvae bore their way beneath the skin, and migrate for several months through the body, until they reach the wall of the gullet. Here they are found from late summer until winter: from December onwards they commence to arrive beneath the skin of the back. Later, the skin is pierced and the posterior spiracles then communicate with the exterior. From February until May or later the fully grown larvae are found in the swellings or 'warbles' on either side of the spine of the host-animal. Ultimately each larva works its way out and falls to the ground where it pupates. The pupal instar lasts about 5 to 6 weeks. Squeezing out the larvae is the best remedy at present available as no efficient preventive methods have been devised (Min. Agric., 1926). The injuries caused by the perforation of the hide, and the deterioration of the flesh, and reduction in the milk occasioned by the presence of these larvae, entail great losses to the trades concerned. Further research is needed to ascertain the course followed by the young larvae during their migration from the skin to the gullet. Not infrequently they are found in the spinal canal having apparently deviated from their normal path after leaving the gullet. Most of what is known of their biology is contained in the papers of Hadwen (1912; 1916), Carpenter and his co-workers (1908 onwards), Cameron (1932) and Eichler (1941).

The Sheep Nostril Fly (*Oestrus ovis*) is usually larviparous depositing its larvae in the nostrils of sheep. The young larvae migrate into the frontal sinuses of the head where they attach themselves to the mucous membrane. When mature they release their hold and leave the animal. The presence of these parasites causes nasal discharge in the sheep and often obstruction of the air passages. The Human Warble-fly (*Dermatobia hominis*) is widely distributed in N. and S. America. The females seize mosquitoes, particularly *Psorophora*, and attach the eggs to these vectors (Bates, 1943): more rarely Muscidae are utilized for this purpose. When the mosquito, or other carrying insect, settles on man the warmth evidently induces eclosion of the larvae which bore their way beneath the skin and cause warble-like swellings. In addition to man most kinds of domestic animals function as hosts.

FAM. CALLIPHORIDAE.—This family includes a very large number of species whose larvae may be saprophagous, or flesh-feeders or parasites of various Arthropods, the parasitic habit being less developed in this family than in the Tachinidae.

The British species are dealt with in the works cited under the Tachinidae and the works of Hall (1948) and Senior-White *et al.* (1940) may be consulted for N. American and Oriental species.

The Sarcophaginae are characterized by the arista being plumose up to, or slightly beyond, the middle and bare distally: macrochaetae are usually only present on the distal part of the abdomen, the disc being rarely bristly, and the eyes are but little approximated in the male. The subfamily includes comparatively few genera but numerous species, often very much alike. For the most part they are uniformly coloured flies, with a grey longitudinally striped thorax, and marbled abdomen. The larvae (Thompson, 1921) are of the Muscid type and taper anteriorly with the posterior extremity rounded. Transverse bands of denticles differentiate the segments, and the posterior spiracles are situated in a deep stigmal pit bearing, as a rule, three straight subparallel slits. The larvae occur in decaying animal or vegetable matter or are parasites of insects and other animals (Aldrich, 1915). Their hosts include Orthoptera, Lepidopterous larvae, adult Coleoptera, scorpions, earthworms, etc.; snails are also not infrequently utilized as hosts. According to Pantel (1910) the parasitic larvae lie free within the body of their insect hosts, and do not acquire any organic connexion with the latter as in Tachinids. Species of *Sarcophaga* (or flesh flies) are larviparous, with large eggs, and the uterus is greatly enlarged to form an incubatory pouch: on an average a female will deposit 40–80 larvae in their 1st instar. Although mainly living in decaying flesh the habits of this genus are extremely varied. Several species parasitize grasshoppers (Kelly, 1914), their larvae boring beneath the body-wall of the host soon after deposition. Others have been found beneath the skin of tortoises, in the stomachs of frogs, in snails (Keilin, 1919a) or causing nasal myiasis in man: *S. haematodes*, however, is coprophagous. Fabre observed that the carrion fly *S. carnaria* will deposit its larvae from a height of 26 inches, and that the ordinary wire meat cover affords imperfect protection, since the larvae can fall through the mesh unless the latter is very fine. *Wohlfartia magnifica* is abundant in Russia, causing great suffering to domestic animals owing to even the smallest wound becoming infected with its larvae: in man it often causes myiasis of the ear, nose, eyes, etc. In *Theria muscaria*, a parasite of snails, the larviparous method of reproduction reaches a high degree of specialization: the female produces a single enormous egg which gives rise to a correspondingly large-sized larva (Keilin, 1916). The species of *Miltogramma*, *Metopia* and their allies live, as larvae, in the nests of solitary bees and wasps which burrow in the ground. The female fly lays the eggs in the nests of the bees, or on the prey of the wasps, and the resulting larvae devour the food of their hosts.

The Calliphorinae are very often metallic green or blue flies and are distinguished by the weak development of the macrochaetae, which are usually absent from the dorsal surface of the abdomen: the arista is markedly plumose, usually for nearly its whole length. Many of the species are of importance in medical and veterinary science and in the typical genus *Calliphora*, which includes the well-known 'blue bottles' or 'blow flies', the larvae occur in carrion, flesh, etc. *Lucilia* includes the 'green bottle flies'. The almost cosmopolitan *L. caesar* breeds in carrion and excrement while *L. sericata*, the 'sheep maggot fly', lays its eggs on the wool of sheep: its larvae bore into the flesh, causing death when present in large numbers. In Australia the sheep blow-fly problem of cutaneous myiasis is one of great importance. The species *Lucilia cuprina* is of primary significance in this connexion and passes its larval development on the living sheep. *L. sericata* and species of *Calliphora* may also play a part in initiating the attack. They are followed by secondary flies, including *Chrysomyia rufifacies*, and other forms, which take advantage of the diseased conditions thus set up. Tertiary flies may also participate during the end-stages of the attack on the sheep. There is thus involved a complex biological association of larvae which entails great losses among the flocks (Tillyard & Seddon, 1933). Among other Calliphorinae producing myiasis is *Auchmeromyia luteola*, whose larva is the Congo 'floor maggot', frequenting the floors of native huts, and is an ectoparasite sucking human blood (Roubaud, 1913). *Protocalliphora azurea* is an ectoparasite in the nests of swallows, larks, sparrows and other birds: its larvae suck the blood of nestlings, attaching themselves to the skin by means of a suctional disc on the 1st segment (Coutant, 1915; Roubaud, 1915). The larvae of *Callitroga macellaria*, the 'screw-worm fly' of N. and S. America, and of *Cordylobia anthropophaga*, the 'tumbu fly' of Africa, cause cutaneous myiasis in man and other mammals.

The 'cluster fly' *Pollenia rudis* is a parasite of earthworms of the genus *Allolobophora* (Keilin, 1915). The eggs are laid in the earth in September, and the young larva probably makes its way through the genital aperture into the vesicula seminalis

of its host, where it remains during the winter. At the beginning of May it awakens and enters the body-cavity, if it has not already done so earlier. For a period of one to four days it migrates forwards and, during the last part of the journey, its spiracular extremity is directed towards the prostomium of the worm. Arriving at the latter region, it wears through the body-wall by means of the denticles around the anal segment, and the spiracles are thus placed in communication with the exterior. Six to ten days after perforating the prostomium the larva moults and, growing considerably, eats its way into the pharynx of the worm. After a further period of nine days it passes into the 3rd instar, and gradually eats its way backwards until only the hinder segments of the host remain: pupation subsequently takes place, and the imago appears in 35 to 45 days. A very similar host relationship occurs in the genus *Onesia* (Fuller, 1933).

The Rhinophorinae include a small number of species which are mostly parasitic on terrestrial Isopoda (Thompson, 1934).

FAM. TACHINIDAE.—This is a very large assemblage of flies whose classification presents great difficulty; Mesnil (1939, and in Lindner, 1944–52) is in the process of publishing a new system. The British species have been tabulated by Wainwright (1928; 1932) and Day (1948). The larvae are uniformly parasites of other insects, or rarely of other arthropods. They are conspicuously bristly flies, thinly or not at all pilose and with the abdomen usually clothed with marginal, lateral and discal setae: the arista is most often bare (Fig. 489). Their habits are very much alike and they are mostly found among vegetation, particularly on flowers. Biologically they are of great interest and importance and Pantel (1910) has divided the species into a number of groups according to their manner of placing the eggs. Briefly, it may be said that many species have ovoid eggs, flattened below, and cement them to the skin of the host; the resulting larvae speedily bore their way internally (*Gymnosoma*, *Thrixion*, *Winthemia*, *Eutachina*, etc.). Others are virtually viviparous since the larvae hatch immediately and are deposited on the bodies of the future hosts (*Exorista*, *Voria*, *Plagia*, etc.). Numerous species lay abundant small darkly coloured eggs on plants: these eggs are swallowed with the food and hatch within the bodies of the hosts (*Sturmia*, *Rhacodineura*, *Zenillia*, *Gonia* (= *Salmacia*), etc.). A considerable number of Tachinids lay their eggs in situations frequented by the hosts: these hatch almost immediately into migratory and often armoured larvae which bore their way into the first suitable host (*Digonochaeta*, *Echinomyia*, *Dexia*, *Prosena*, etc.). There are again others which pierce the host with a special spine-like apparatus and deposit their eggs, or larvae, internally (*Ocyptera*, *Alophora*, *Compsilura*).

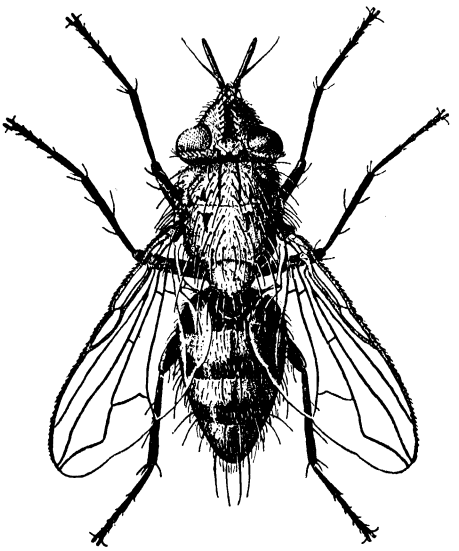


FIG. 489.—*Centeter cinerea*, female
From *Bull.* 1429 *U.S. Dept. of Agric.*

Tachinids select as their hosts larval and adult Coleoptera, Orthoptera and Hemiptera, but most often parasitize Lepidopterous larvae and to a lesser degree those of Hymenoptera: in a few instances they are known to select larval Diptera. Their larvae are usually broadly cylindrical, tapering but little towards the anterior extremity and with rather indistinct segmentation. The anterior spiracles are small but the posterior pair is conspicuous and often darkly coloured owing to sclerotization. Most of what is known of the biology of the family is due to the researches of Pantel (1898–1910), Nielsen (1909), Thompson (1923 onwards), Baer (1920) and Clausen (1940).

Within their hosts the larval life of Tachinids presents many variations but, in some stage of existence, they respire free air either by means of a perforation in the body-wall of their host, or by means of a secondary connexion with the tracheal system of the latter. In either case, the larva is enclosed in a sheath ('gaîne de fixation'

of Pantel, funnel or siphon of other observers) which may be either primary or secondary.

(1) The PRIMARY SHEATH: this is always cutaneous in origin, and is formed as an ingrowth from the lips of the original perforation by means of which the larva enters the host. This perforation persists as an air-hole ('soupirail' of Pantel) and the larva hangs, head downwards, with its spiracles respiring free air through the aperture. The sheath consists of an inner sclerotized layer and an outer layer of hypodermis; it grows around and closely embraces the parasite and maintains the latter in position. The sheath may be complicated by the adherence of the degenerating surrounding tissues which are often soldered together by the profuse secretion of the hypodermis. In this manner muscle fibres, fat-body and tracheae, along with dead phagocytes may become involved, the whole forming a dense, compact sheath surrounding the parasite. This type of sheath occurs in *Echinomyia fera*, *Winthemia 4-pustulata*, etc.

(2) The SECONDARY SHEATH: this may be either cutaneous or tracheal in origin according to the position of the air-hole. In species in which this type of sheath obtains, the parasite lives for a while free in the body-cavity of its host as in *Thrixion* or within some particular organ (nervous system, muscles, etc.) as in *Plagia trepida* and *Sturmia sericariae* (vide more especially Pantel, 1909; Sasaki, 1886). Sooner or later, owing to the respiratory needs of increasing growth, it seeks communication with the air. By means of the anal extremity the larva gradually bores its way either through the integument, or into a tracheal trunk, and thus forms a secondary air-hole. Whichever situation is chosen, a sheath grows round the larva either by means of an ingrowth of the integument (*Thrixion*) or as an outgrowth from the wall of a trachea or of an air-sac (*Blepharidea*, *Bucentes*, *Gymnosoma*). In either case the parasite becomes enclosed as in the primary sheath. Whichever way it is formed, the sheath is a pathological reaction of the host against irritation and microbic infection induced by the presence of the parasite. In *Compsilura* and *Sturmia* the parasite acquires a direct connexion with a spiracle of the host, and the sheath under these circumstances is little more than a collar-like rim around the caudal end of the parasite.

The mode of life of the parasite within its host varies not only among different Tachinids, but also during the life of an individual species. Thus in *Thrixion*, for example, the larva devours only the blood and fat-body and forsakes the host while the latter is alive. Furthermore, it does not void excretory matter until it leaves its host. In similar cases, in which the first diet of the larva consists of the blood plasma of the host, the surrounding sheath is closed, absorption taking place according to Pantel by means of 'physiological filtration'; at a later stage the buccal armature pierces the sheath and the larva then commences to devour the fat-body. The greater number of Tachinids rupture the surrounding sheath in the 3rd instar and, becoming free in the body-cavity of the host, they commence to devour the vital organs of the latter. In certain other Tachinids a still more complex mode of life is followed: thus in *Sturmia sericariae* (Sasaki, 1886), which parasitizes the silkworm, the eggs are deposited on mulberry leaves and are swallowed along with the leaf-tissue by the host. The eggs hatch in the gut of the latter, and the young larvae bore their way through the wall of the digestive canal, and penetrate into the ganglia of the nervous system. At a later stage they forsake the latter, and acquire connexions with the spiracles of their host. Other species similarly live an intra-organic life within the nervous system, muscles, etc., of the hosts, during part of their existence (Pantel, 1909; 1910). Such species have remarkably small eggs adapted for being swallowed by their host. Pupation in Tachinids takes place as a rule in the soil: in some species, however, such as *Carcellia gnava*, which is a parasite of *Malacosoma neustria*, the pupal stage occurs within the pupa of the host.

FAM. MUSCIDAE.—This large family includes the Anthomyidae and Cordyluridae of many authors. The latter group, although in some ways distinct, shows many connexions in the adult stage with the Coenosiinae and the larvae also are of a Muscid type. Most of the species of Muscidae are small to rather large flies, many of which bear a general resemblance to the house-fly. Although the family includes the haematophagous genera *Stomoxys*, *Glossina*, *Lyperosia* and *Haematobia*, in which both sexes suck the blood of man and other mammals by means of piercing mouthparts, the vast majority of its members are innocuous in this respect. The larvae (Fig. 448) show great diversity of habit: some are plant-feeders and are serious pests of agriculture and very many inhabit decaying organic matter, more especially of vegetable origin. Of these latter the majority are saprophagous, while the rest are carnivorous preying upon other Dipterous larvae, small Oligochaeta, etc., which inhabit the same medium.

Musca domestica may be taken as a typical representative of the family. It is, as

a rule, most abundant during the hottest months of the year and in Europe and N. America attains its greatest numbers from July to September. According to Roubaud, the insect usually does not hibernate but continues reproduction during winter in warm rooms and stables, but further research is much needed with particular reference to various climatic conditions. The eggs are cylindrical-oval, 1 mm. long, with two curved rib-like thickenings along the dorsal side: they are laid in masses of 100–150 and the usual number deposited by a single fly in a life of about 2½ months is probably 600–1,000. Dunn (1922), however, states that in Panama a single female may deposit 2,387 eggs during 31 days after emergence. The chief breeding places are accumulations of horse manure or stable refuse, but human and other excrement is often selected, and also most kinds of fermenting animal and vegetable substances, particularly the contents of ash bins, etc. At a temperature of 25–35° C. the larvae hatch in 8–12 hours. The first instar larva is 2 mm. long, metapneustic, and each posterior spiracle opens by a pair of small, oblique, slit-like apertures. This stadium lasts 24–36 hours under favourable conditions. The second instar larva is amphipneustic with larger posterior spiracles and, at a temperature of 25–35° C., the stadium lasts about 24 hours. The third instar is also amphipneustic and measures about 12 mm. long when fully grown. The anterior spiracles have 6–8 processes, and each posterior spiracle is a D-shaped ring surrounding three sinuous slits. Incubated at 35° C. this stadium lasts 3–4 days, and the pupal stadium averages 4–5 days. The developmental cycle, from the egg to the eclosion of the imago, varies in different parts of the world with the temperature and other factors. According to Herms it varies from an average of 44·8 days at 16° C., to an average of 10·4 days at 30° C. Roubaud states that, in a heap of actively fermenting manure in warm weather, the life-cycle may only require six days. The house-fly has an important bearing upon the welfare of man as a carrier of the germs of summer diarrhoea, typhoid and possibly other diseases: there is also evidence pointing to the probability of its acting as a carrier of the eggs of certain species of intestinal worms. Preventive and remedial measures are numerous, and of these the most important is the elimination of the larval breeding places, or the rendering of the latter fly-proof or unsuitable for the insect. The destruction of adult flies must also form part of any system of eradication: this may be brought about by the use of fly traps baited with attractive chemotropic substances, by means of adhesive fly-papers, or by spraying walls with DDT. The literature on this species has assumed extensive proportions: a general account of the insect and its relation to man is given by Hewitt (1914) and West (1951). Observations on its breeding habits are given by Newstead (1908) and Roubaud (1922), while the relation of the insect to medical science and sanitation is dealt with by Graham-Smith (1913). Additional observations on this insect and other common flies will be found in papers by the latter author (1916 and 1919).

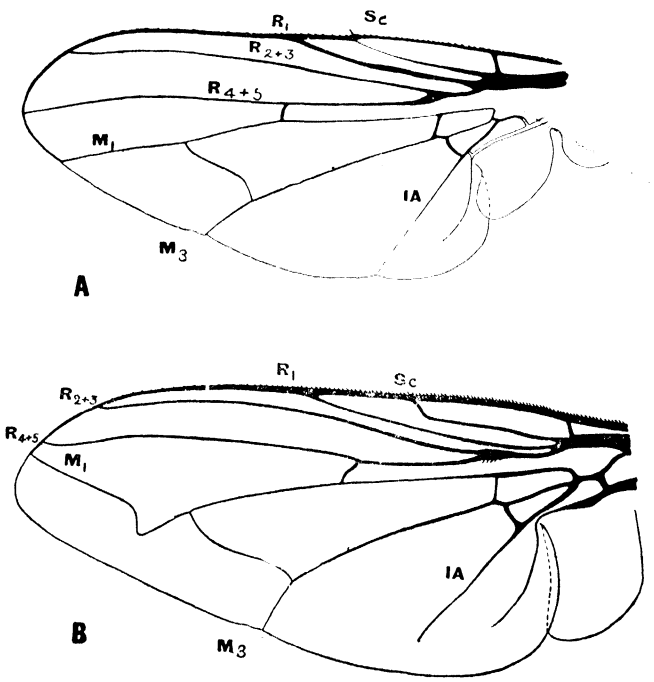


FIG. 490.—Venation of A, *Hylemyia strigosa* and B, *Calliphora erythrocephala*

The biting house-fly *Stomoxys calcitrans* breeds principally in horse manure and stable refuse, but the larva may also be found in grass mowings, sewage beds, etc. The life-history has been studied by Newstead (1906), Bishopp (1913), Mitzmain (1913) and others. The duration of the life-cycle depends upon temperature, humidity and the nature of the food supply, while the minimum period for complete development is 23–32 days. According to Newstead two important conditions are necessary for development—an absence of light and an abundance of moisture. The ova are laid in batches of 60–70 and about 600 is the greatest number deposited by one female (during 65 days). At an average day temperature of 72° F., and 65° F. by night, the larvae hatch out in 2–3 days. When fully grown they measure 11–12 mm. long, and differ from the larvae of the house-fly in that the hind spiracles are rounded and smaller, with the three apertures on each plate only slightly curved instead of being sinuous. In England, during August, the larval period lasts 2 to 3 weeks and 9 to 13 days are spent as a pupa: in the tropics the pupal stage may only last 4 days.

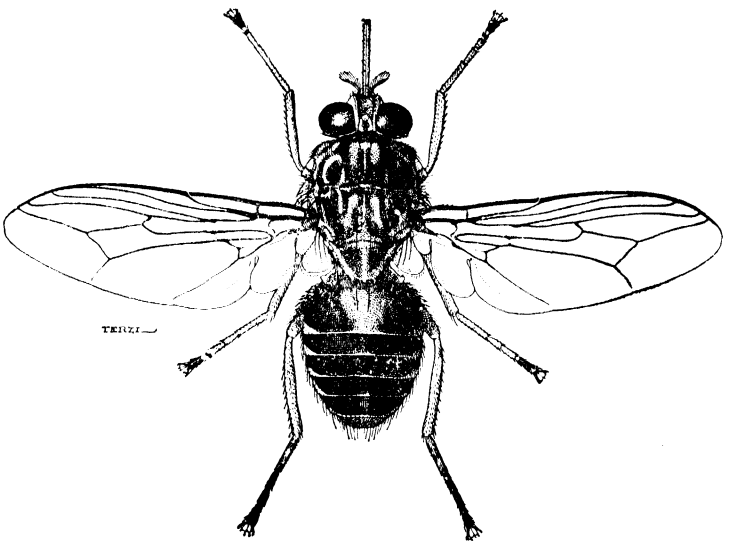


FIG. 491.—*Glossina palpalis*, female. × 5

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The species of *Glossina* or Tsetse flies (Austen, 1911; Austen & Hegh, 1922; Swynnerton, 1936) are now well known to be the carriers of the pathogenic agents of certain virulent diseases in Africa. Thus *Glossina palpalis* (Fig. 491) transmits *Trypanosoma gambiense*, the causal agent of sleeping sickness, from man to man by means of its piercing mouthparts. In a similar manner *G. morsitans* transmits *Trypanosoma rhodesiense* which is responsible for the more local or Rhodesian form of that disease. *Glossina morsitans* is also the chief carrier of the trypanosomes which cause the disease known as nagana among domestic animals. Although widely distributed through tropical and sub-tropical Africa, species of *Glossina* do not occur continuously throughout that area, but are largely restricted to patches of forest and bush where there is warmth, damp and shade, such tracts being known as 'fly belts'. The larvae in this genus are nourished within the uterus of the parent and, when mature, are deposited singly and at intervals in a shady situation on the ground. When newly born, the larva is yellowish-white, with a black posterior extremity bearing a pair of polypneustic spiracular lobes. It speedily burrows or otherwise conceals itself and pupates, the imago appearing about a month later.

Among the phytophagous members of the family those of agricultural importance are discussed by Smith (1948). For instance, the larva of *Erioischia brassicae* is extremely destructive to vegetables of the Brassica tribe and also affects wild Cruciferae. It destroys the roots of those plants and the eggs are deposited around the stem near the soil-level. *Hylemyia coarctata* is the Wheat Bulb Fly, which is a serious pest in

many parts of Europe: it is exceptional in laying its eggs on bare soil and not necessarily in proximity to its host plant. The larva of *Pegomyia* are leaf-miners and those of *P. hyoscyami* are destructive to beet and mangolds.

The carnivorous forms have been studied in detail by Keilin (1917) and are more especially enemies of saprophagous larvae of other Diptera. They include species of *Limnophora* (= *Melanochelia*), *Graphomyia*, *Phaonia*, *Mydaea*, *Hydrotaea* and other genera. Perhaps the most remarkable of the carnivorous larvae are those of *Passeromyia* which are blood-sucking parasites of birds (Rodhain & Bequaert, 1916). The larvae of certain species of *Mydaea* are also subcutaneous avian parasites (Nielsen, 1911). Mention needs also to be made of the larvae of *Fannia* which live in excrementous and other decaying organic matter. They are unusual in being broad and somewhat flattened with paired segmental outgrowths of the body-wall (vide Hewitt, 1912).

The Cordylurinae are mostly phytophagous and include leaf- and stem-borers, such as *Cordylura* and *Norellia*. *Hydromyza* feeds on water plants in the larval stage (Welch, 1914). A few larvae seem to be predacious and others are saprophagous, such as the well-known dung-fly, *Scatophaga stercoraria*, whose life-history has been described by Cotterell (1920). The adults are probably all predatory on small insects (Hobby, 1931a). *Mormotomyia*, a form with reduced wings which lives on bat-guano in caves in Kenya, has in the past been placed in a monotypic family, but its larva shows clear affinities with the Cordylurinae (van Emden, 1950).

The best work to consult for information as to British species of Muscidae is that of Karl (1928).

Section C. PUPIPARA

A remarkable group of Diptera whose structure has been greatly modified in accordance with an ectoparasitic life. The winged forms do not fly any considerable distance, and all species are adepts at clinging to their hosts and working their way among the hairs or feathers. The claws are highly developed, and toothed or spined for the purpose. The abdomen is indistinctly segmented and, like the rest of the body, tough and leathery. All species are blood-sucking ectoparasites of mammals and birds, but do not utilize man as a normal host. The larvae are retained within the uterus of the parents, where they are nourished by the secretion of the greatly developed accessory glands. When fully mature they are deposited on the ground, or in the abodes of their hosts, and almost immediately change to pupae. A list of the Palaearctic species arranged according to their hosts is given by Bezzi (in Becker, 1905). For the structure of the proboscis see Jobling (1926–28), and for the general biology and morphology of the family consult Massonat (1909) and Falcoz (1926). The phylogeny and distribution is discussed by Speiser (1908) who has also monographed the world's genera. The group owes its existence more especially to the similarity in reproduction and parasitic habits exhibited by the adults. There is no doubt that they are to be regarded as degraded members of the Schizophora, but opinions are divided whether they fall nearer to the Acalyptrates or to the Calyptrates (Hennig, 1941).

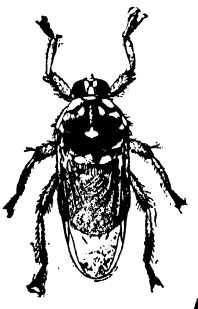


FIG. 492.—*Hippobosca rufipes*. × 2. S. Africa

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FAM. HIPPOBOSCIDAE.—*Head sunk into an emargination of the thorax. Palpi neither leaf-like nor forwardly projecting, forming a sheath to the proboscis. Eyes round or oval, ocelli present or absent. Antennae inserted into a depression, 1-segmented, with or without a terminal bristle or long hairs. Legs short and stout, claws strong and often toothed. Wings present or absent.* These insects (Fig. 492) are dorsoventrally flattened and of a tough leathery consistency, both features being correlated with an ectoparasitic life. The family includes such well-known insects as the 'forest fly' *Hippobosca equina* which affects horses and cattle, and the sheep 'tick' or 'ked' *Melophagus ovinus*.

Among other British species *Ornithomyia avicularia* is a parasite of many wild birds and *Lipoptena cervi* is found on deer. All these species have a very extensive geographical range and *O. avicularia* has been carried by birds almost all over the world. The degree of development of the wings differs greatly in various members of the family. In *Hippobosca* and *Ornithomyia* they are fully formed: in *Allobosca* they are vestigial while in *Melophagus* (Fig. 493) wings and halteres are absent. Both sexes of *Lipoptena cervi* are winged but upon discovering a host the females soon cast their wings near the bases: wingless males similarly occur. The palpi in this family are rigid organs projecting forwardly downwards and forming a partial sheath to the proboscis. The latter is curved and slender, protrusible, and hidden from view when retracted. Both sexes are equally active bloodsuckers, but their punctures are seldom painful. The females produce at intervals single larvae which are whitish, or pale yellow, with a black cap at the posterior end which involves the spiracles. They are immobile with little or no traces of segmentation, and very soon transform into puparia. For the genera of the family consult Bequaert (1940) and an account of the structure and biology of the members of the family is given by Bequaert (1953): the British species are discussed and figured by Edwards *et al.* (1939).

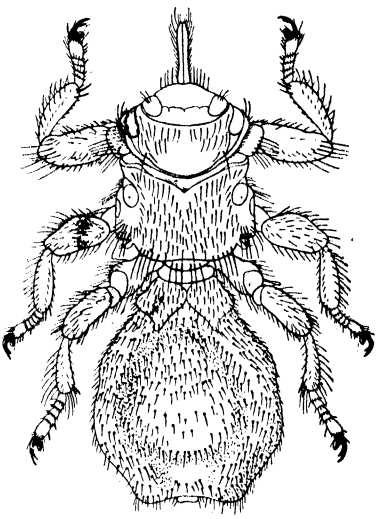


FIG. 493.—*Melophagus ovinus*, magnified

FAM. NYCTERIBIIDAE.—*Head folded back at rest in a groove on dorsum of thorax, eyes and ocelli when present vestigial; antennae 2-segmented, terminated by bristles inserted on tubercles. A fan-shaped comb of bristles (ctenidium) inserted in a hollow at the anterior end of the thorax; legs elongate, wings absent.* A very small family of highly modified and completely apterous insects (Fig. 494) parasitic upon bats. They are

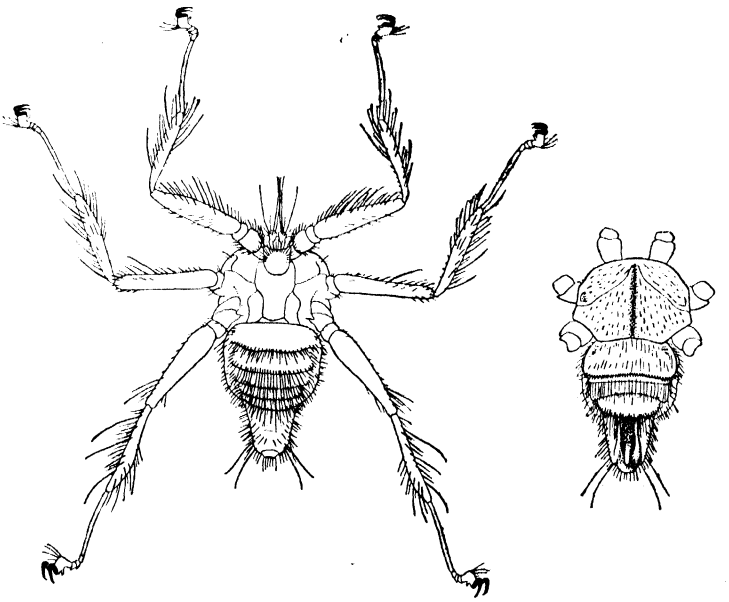


FIG. 494.—*Penicillidia jenynsi*, Formosa; dorsal view of male with ventral view of thorax and abdomen on right. Enlarged

more particularly characteristic of the Old World, the countries bordering on the Indian Ocean being especially rich in species; only *Nycteribia* is British. In view of their hosts' power of distribution it is not surprising that certain species have a very wide geographical range. Frequently, a single species of Nycteribiid may utilize several species of host which may be of different genera or, more rarely, of different families. Conversely a species of bat may support several species of Nycteribiids: thus, at least 9 species of the latter have been recorded from *Miniopterus schreibersi* in various countries. Information on the general structure and classification of the family is given by Speiser (1900): the papers of Kolenati (1862) and Scott (1917) should also be consulted and that of Ryberg (1939) for their biology. Rodhain & Bequaert (1916a) have published a detailed account of the behaviour of *Cyclopodia greefi*. The larvae are deposited in a less advanced stage of development than those of certain Hippoboscidae and the spiracles are posterodorsal in position. The puparia were found adhering to the perches and parts of the cages in which the hosts were confined. According to Müggenberg (1892) a ptilinum is wanting in this family.

FAM. STREBLIDAE.—*Head not flexed on dorsum or thorax; eyes when present small, no ocelli; antennae in pits, 2-segmented. Palpi leaf-like, projecting in front of the head but not sheathing the proboscis. Hind coxae enlarged, claws not distinctly toothed. Wings well-developed, vestigial or absent.* A small family widely distributed throughout the tropics and warm regions of the world. In habits they are almost exclusively parasitic upon bats, and most of what is known concerning the family is included in a paper by Speiser (1900). *Ascodipteron* (Queensland, E. Indies) is one of the most remarkable of Pupipara and is unique on account of the degeneration undergone by the female. Both sexes are winged but exhibit marked differences in the structure of the proboscis: in the female the labellar teeth are very large and blade-like, on the other hand, in the male, the teeth are exceedingly small. On reaching its host (*Miniopterus*) the female makes a way beneath the skin near the base of the ear, and casts both legs and wings. In this situation she develops into a greatly enlarged, flask-shaped sac, with the hinder extremity communicating with the exterior (Muir, 1912). Typical genera of the family include *Nycterobosca* which extends into Europe, *Raymondia* and *Strebla* (see Jobling, 1936; 1938; 1939; 1949; 1951). Very little is known concerning their biology but Speiser states that they are larviparous.

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Order 26. **SIPHONAPTERA (Aphaniptera:** Fleas)

Small, apterous, laterally compressed insects whose adults are ectoparasites of warm-blooded animals. Eyes absent, 2 ocelli usually present: antennae short and stout, reposing in grooves: mouthparts modified for piercing and sucking, maxillary and labial palpi present. Thoracic segments free: coxae very large, tarsi 5-segmented. Larvae elongate, eruciform and apodous. Pupae exarate, enclosed in cocoons.

The Siphonaptera, or fleas, may be readily distinguished from other apterous parasitic insects since they are strongly compressed laterally instead of being dorsoventrally flattened. They constitute a very sharply defined order of insects without close connexion with any other group. Traces of mesothoracic wings are found in some pupae (Sharif, 1935) and some resemblances can be seen to the Diptera and Mecoptera (Potter, 1938). In their metamorphoses they possess certain features in common with the Diptera Nematocera.

Fleas are blood-sucking ectoparasites of mammals and birds. They are negatively phototactic and respond to warmth: when a host dies the fleas leave as soon as the body cools and seek fresh hosts which are not always of the same species. Many kinds are apparently confined to one species of animal while others infest a range of hosts. The relation between different species of fleas and their hosts, however, is not a very close one, and in the absence of the elective species of the latter, many will feed readily on the blood of other animals. Their chief method of progression is walking but they can also progress by leaping. According to Mitzmain the maximum vertical height attained by the leap of *Pulex irritans* is $7\frac{3}{4}$ inches, while the horizontal range may extend to 13 inches.

About 1,000 species of the order have been described of which 51 are known to occur in the British Isles (*vide* Rothschild, 1915). During the present century the work of the Indian Plague Commission, and of many independent observers, has resulted in a great increase of knowledge relating to these insects. Many species have proved capable of transmitting bubonic plague (Brumpt, 1949). In India the species mostly implicated is the rat flea, *Xenopsylla cheopis* (Fig. 495). The rat is particularly susceptible to this disease, and the flea itself becomes infected with the plague bacillus by feeding upon an infected animal. When the latter dies, the fleas desert the body, and many find their way to man, particularly when the human population lives under crowded conditions in rat-infested quarters. It is impossible here to detail the evidence as to the manner in which the rat flea transmits the disease to man as the problem is a complicated one. It may be pointed out, however, that while feeding, the contents of the gut of the flea, which contain the pathogenic bacteria, are voided from time to time. This excretory matter may be introduced beneath the skin by scratching. Bacot and Martin have demonstrated that plague-infested fleas also convey the disease by a method

comparable to inoculation. When placed on a host they suck vigorously but owing to the fact that, in a certain number of the insects, the digestive canal is blocked by a dense mass of rapidly multiplying plague bacteria, the blood that is imbibed fails to enter the stomach and is regurgitated into the puncture. Since this blood is now contaminated with bacteria derived from the previous host, the disease is thus transmitted to the new host. This seems to be the common method of transmission. Rats are not the only animals attacked by plague, squirrels and other rodents being also liable to the disease; consequently fleas of any species, which attack both ground rodents and man, in lands where plague is prevalent, are to be regarded as possible agents in the transmission of the malady.

One of the most familiar of these insects is the cosmopolitan human flea *Pulex irritans*. Although man used to be its favourite host it is found now mainly on pig-farms. The extensive genus *Xenopsylla* includes the plague flea *par excellence* (*X. cheopis*) which has been previously alluded to: it is almost tropicopolitan and is a scarce vagrant in the British Isles. *Ctenocephalides* (Fig. 496) includes the dog and cat fleas (*C. canis* and *C. felis*) both of which occur on dogs and cats. The rabbit flea (*Spilopsyllus cuniculi*) commonly affects the ears of rabbits, and sometimes becomes transferred to cats while the latter are hunting those animals. The genus *Ceratophyllus* includes a number of species affecting birds: *C. gallinae* is frequent in hen-houses and in the nests of many wild birds. *Leptopsylla segnis* is harboured by the mouse and species of *Nycteridopsylla* and *Ischnopsyllus* are essentially bat parasites. In addition to the foregoing species, which occur in Great Britain, mention needs to be made of the well-known 'jigger' or 'chigoe' (*Tunga penetrans*) of the tropics whose females remain attached to the skin in one position for the greater part of their existence. The modifications of external structure associated with this habit are so marked that the abdomen becomes distended to the size of a small pea, the insect bearing a close resemblance to a tick. It has a large number of hosts and its attacks are usually confined to the feet: in man it particularly affects the toes. Instead of remaining at the surface of its host, the fertilized female burrows into the flesh, until it may become completely embedded, though most of the eggs reach the exterior before hatching.

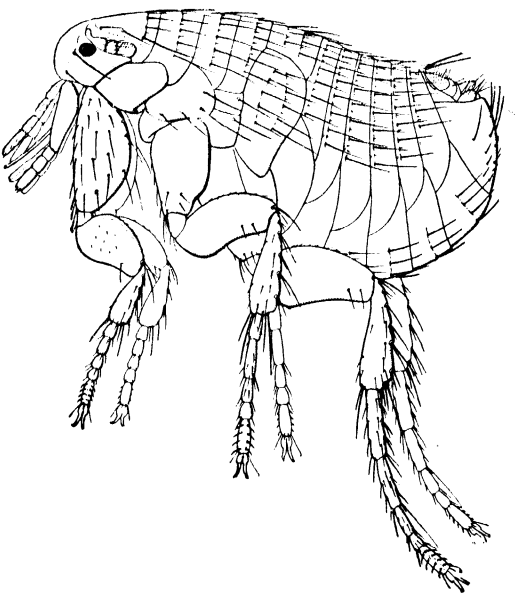


FIG. 495.—*Xenopsylla cheopis*, male. × 20

After Waterston. Reproduced by permission of the Trustees of the British Museum.

External Anatomy.—The body in the Siphonaptera (Snodgrass, 1946) is strongly compressed, and well sclerotized, with the evident advantage of enabling these insects readily to work their way among the hair or feathers of

the host. There is usually a prominent armature of spines and bristles which are sharply inclined backwards, thus aiding forward progression, and the claws of the feet are strong in conformity with the necessity for grasping. The *head* is very closely attached to the thorax with a small cervical sclerite at each side. Situated on the middle line of the frons there is, in many species, a tubercle which has been thought to help in opening the cocoon but this is very doubtful. The two *ocelli* (cf. p. 98) are laterally displaced, and may be deeply pigmented but, in a number of species, they are vestigial or absent. The latero-ventral border of the head often carries a row of powerful spines forming the *genal comb* which is present on either side: these organs are frequently referred to as ctenidia and are well seen, for example, in *Ctenocephalides*. The *antennae* are lodged in antennal grooves and are short and stout with three evident segments. The terminal portion is pectinated and exhibits a number of annular divisions, which vary in completeness of development in different genera, and sometimes in different sexes. A strong inter-antennal groove often connects the two sockets. The *mouthparts* (Fig. 497) are adapted for piercing and sucking, and the most important organs are the *laciniae* of the maxilla. These structures are rather broad blades which are serrated along the distal two-thirds of their length. Proximally, the inner surfaces of the laciniae are in contact with the short hypopharynx and, where the latter organ terminates, they are closely opposed to the epipharynx above. Each lacinia is distally grooved along its inner aspect from the point where the hypopharynx ceases, and they form together a channel through which the saliva is ejected. Basally, the lacinia articulates with the maxillary lobe (stipes) by means of a small rod-like sclerite which imparts to it considerable freedom of movement. The *labrum* is small and hidden beneath the clypeus but the *epipharynx* is a long slender organ which is ventrally grooved, and closely approximated to the laciniae, the combined organs thus forming an afferent channel through which blood is sucked up. The *hypopharynx* is a small sclerite which is concave ventrally and incurved at the margins: within the area thus defined the salivary pump and its operating muscles are lodged. Anteriorly, the hypopharynx is prolonged into a small process, which is

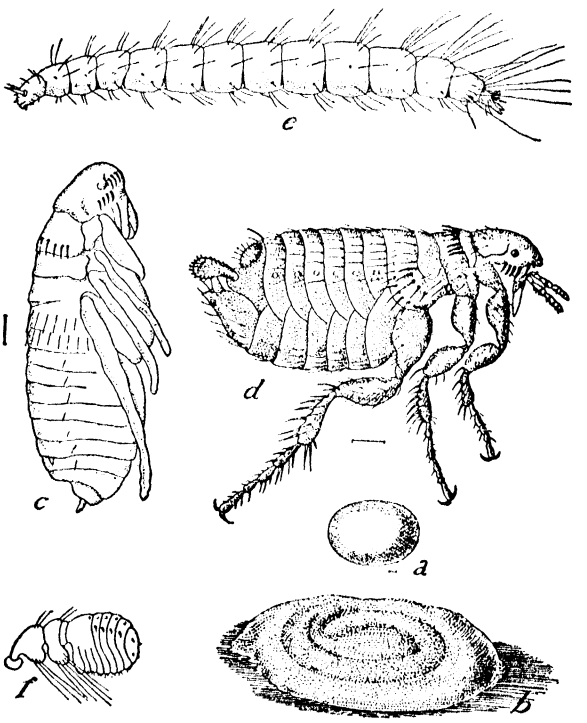


FIG. 496.—*Ctenocephalides canis*

a, egg; *b*, larva in cocoon; *c*, pupa; *d*, imago; *f*, antenna of imago; *e*, *Ceratophyllus fasciatus*, larva. From Bishopp, *U.S. Dept. Agric. ent. Bull.* 248 (all except *e*, *after* Howard).

perforated by the salivary duct, and extends for a short distance between the epipharynx and the mandibles. The *maxillary lobes* are mainly derived from the stipes: each consists of a single lobe, on either side of the mouth, and a 4-segmented palpus: they are not cutting organs and apparently do not enter the puncture made by the laciniae. The labium is formed of a *postmentum* more or less fused to the head and an articulated *prementum* which carries distally a pair of labial palpi: these usually have 5 segments but may have 1 or 3. The stylets are held in the grooved prementum by the appressed palpi. In feeding, the laciniae rock on the sclerite articulating with the stipes, so that they have an up and down movement like a pneumatic drill; the epipharynx penetrates with them in a passive manner. The muscles of the salivary pump inject saliva into the perforation thus formed and the cibarial and pharyngeal pumps draw up the blood.

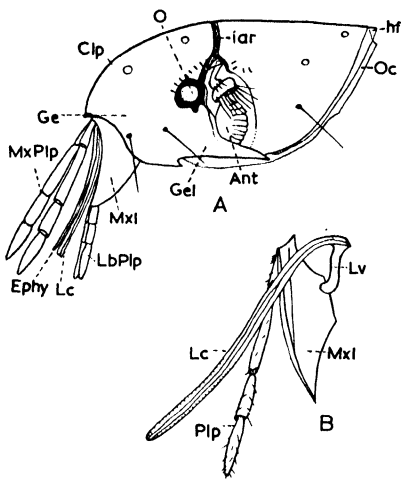


FIG. 497.—A. Head of *Pulex irritans*, female. B. Right maxilla of *Anomiopsyllus* sp. (Both redrawn from Snodgrass, 1946)

Ant, antenna; *Clp*, clypeus; *Ephy*, epipharynx; *Gel*, subantennal lobe of gena; *hf*, head flange; *iar*, interantennal ridge; *LbPlp*, labial palpus; *Lc*, lacinia or maxillary stylet; *Lv*, lever of lacinia; *MxI*, palpus-bearing lobe of maxilla; *MxPlp*, maxillary palpus; *O*, ocellus; *Oc*, occiput; *Plp*, palpus.

The *thorax* is composed of three quite distinct segments which admit of a certain amount of movement. In many species the hind margin of the pronotum carries a row of stout spines forming the *pronotal comb*. The terga are simple, broad, arched plates and the metathorax is characterized by its greatly developed epimera which overlie the base of the abdomen. The legs are adapted for clinging and leaping with large flattened coxae, short stout femora and elongate 5-segmented tarsi (Jacobson, 1940).

The *abdomen* is composed of 10 segments, the first of which has the sternum wanting, and the last three segments are modified for sexual purposes. The 9th segment in the male is reduced in the tergal region. The 9th sternum is V-shaped, one branch of the V projecting beyond the large 8th sternum. To it are articulated a pair of two-segmented claspers. The *aedeagus* which projects between the claspers has an extremely complex structure. The 10th segment consists of a dorsal sensory plate or *sensilium* (= pygidium) and a more posterior *proctiger*, provided with dorsal and ventral plates. In the female the terminal segments are less modified than in the male. The 8th segment is large but the 9th is almost obliterated. The 10th bears a sensilium, as in the male and the proctiger consists of a small dorsal plate bearing a conical setiferous process known as the *stylet* and the corresponding sternum is represented by a small ventral plate.

Internal Anatomy.—The mouth is surrounded by the ring-like base of the epipharynx and forms the definitive opening into the alimentary canal. The pharynx is an elongate chamber with strongly sclerotized dorsal and ventral walls. It is followed by a long oesophagus of very small calibre, which leads into a somewhat conical organ termed the proventriculus. The inner walls of the latter are beset with a series of long backwardly directed sclerotized rods. It has been claimed that the function of this arrangement is to break

up the ingested corpuscles by a rhythmic movement of the spines. The stomach, when fully distended, occupies a large part of the abdominal cavity, and, near its junction with the hind intestine, are found the insertions of the four Malpighian tubes. Near the termination of the hind intestine there are six rectal papillae resembling those found among Diptera. The *salivary glands* consist of a pair of ovoid sacs on either side: their ducts eventually combine to form a common canal which enters the salivary pump beneath the hypopharynx. The *nervous system* is exceptionally primitive in that the ventral nerve cord consists of three thoracic and seven abdominal ganglia in the female and one more abdominal ganglion in the male (Minchin, 1915): these centres are very much approximated owing to the great reduction in length of the intervening connectives. The *male reproductive organs* consist of a pair of fusiform testes whose contents pass down extremely fine vasa deferentia: the latter unite to form a single passage opening into a small vesicula seminalis. The ejaculatory duct is associated with a copulatory organ of complex structure. The *female reproductive organs* are composed of a pair of ovaries, each formed of from four to eight panoistic ovarioles. Attached to the vagina are one or two sclerotized spermathecae whose shape and size differ among various species. The *respiratory system* is well developed and communicates with the exterior by ten pairs of spiracles: two pairs of the latter are located on the thorax, the remainder being abdominal in position. In a few sedentary species some of the spiracles may lose their function.

Biology and Metamorphosis (Fig. 496).—The eggs of these insects are ovoid and white or cream in colour: unlike those of many ectoparasites they are not glued to the hair or feathers of the host. When deposited on the body of the latter they readily fall off and are normally found in the haunts or sleeping-places of the animal parasitized. In houses fleas breed in the cracks of floors, under matting or beneath carpets and almost always in uncleanly dwellings. Rat fleas often breed in granaries, barns, etc., particularly in those where there is an accumulation of floor litter. The dried excrement, feathers, straw, etc., which accumulate in chicken houses also afford a favourable environment. The incubation period varies on an average from three to ten days, according to temperature, and the young larva ruptures the chorion by the aid of a hatching-spine on the dorsal side of the head. The larvae (Bacot & Ridewood, 1914; Sikes, 1930; Sharif, 1937a) are active, whitish, vermiform objects usually measuring about 4 mm. in length when fully grown. They are non-parasitic and feed upon particles of organic matter found in the host's lair, or among the dust and dirt which collects on the ground in the vicinity. In some species, however, blood which has passed through the body of adult fleas appears to be a necessary part of their nutriment. Larval Siphonaptera possess a well-developed head but are devoid of both eyes and legs: in their general characters they resemble the larvae of certain Nematocera. The antennae are single-segmented but rather prominent, the mandibles are very definitely toothed and the maxillae assume a curious brush-like form with small 2-segmented palpi: each labial palp is composed of a short basal segment surmounted by stout setae. The trunk consists of three thoracic and ten abdominal somites, each of which is armed with a band of outstanding bristles, while the 10th bears a pair of anal struts. Spiracles are present on the pro- and metathorax and first eight abdominal segments. After undergoing two ecdyses, the larva spins a cocoon which is concealed by the fine particles of debris adherent to its outer surface. The adults remain quiescent for a variable period before emerging from the

cocoons, and they often issue in large numbers in response to slight mechanical stimuli. The vibrations set up by persons walking about a disused room, for example, have been explained as being the cause of the emergence of an abundance of fleas within a very short time. When newly emerged, the adults can remain alive for a considerable period without food, but they take the first opportunity of reaching their particular host. As a general rule the female needs to imbibe the blood of the normal host before becoming capable of laying fertile eggs.

The period occupied by the complete developmental cycle varies in different species and in different countries. Thus *Pulex irritans* in Europe requires from 4 to 6 weeks, while *Xenopsylla cheopis* in India passes through a complete generation in about 3 weeks: on the Pacific coast the life-cycle of the latter species occupies, according to Mitzmain, 9 to 11 weeks.

Classification.—The latest classification (Rothschild & Hopkins, 1953) recognizes seventeen families. The table given below is modified from theirs; five families which include not more than one or two genera each are omitted. Families which contain British species are marked with an asterisk.

1. Outer internal ridge of mid coxa absent. Hind tibia without an apical tooth on outside. Sensilium with 8 or 14 pits on each side. (**Superfam. PULICOIDEA**) 2
–. Outer internal ridge of mid coxa usually present. Hind tibia usually with pointed external apical tooth. Sensilium with 14, or more often 16 or more, pits on each side. (**Superfam. CERATOPHYLLOIDEA**) 3

2. Hind coxa internally without strong bristles. Sensilium with 8 pits on each side . . . . . TUNGIDAE
–. Hind coxa internally with strong bristles. Sensilium with 14 pits on each side. PULICIDAE*

3. The outer of the 2 apical dorsal bristles of fore femur somewhat shorter than the inner. (Holarctic) . . . . . VERMIPSYLLIDAE
–. The outer bristle almost always the longer, or else there are no functional abdominal spiracles 4

4. Lower half of frons with a more or less trapeziform tubercle sunk in a groove; a conspicuous tentorial arch in front of ocellus; no combs of long spines; both sexes with a single long antepygidial bristle; female with anal stylet and one spermatheca (Neotropical and Nearctic) . . . RHOPALOPSYLLIDAE
–. Not all these characters present 5

5. Hind coxa with a row of strong bristles; last segment of all tarsi with 4 pairs of lateral bristles; sensilium in both sexes with 14 pits a side. (Ethiopian) HYPSOPHTHALMIDAE
–. Not all these characters present 6

6. Occiput with a subdorsal internal tubercle on each side. Head with 1 or 2 combs. (Australian and Neotropical) . . . . . STEPHANOCIRCIDAE
–. Occiput without a conspicuous internal tubercle or with a small central one 7

7. A short rod-like link plate present between basal abdominal sternum and metepimeron; furca of metasternum not forming a long, sharply pointed process. (Australian, Oriental, Ethiopian) . . . . . PYGIOPSYLLIDAE
–. This link plate absent or else the furca forms a long, sharp, pointed process. 8

8. Metanotum not margined with small spines . . . HYSTRICHOPSYLLIDAE*
–. Metanotum with small marginal spines 9

9. Interantennal suture strongly developed. 10
–. Interantennal suture very weak or absent 11

10. Head with a vertical comb of few or many spines behind or below the ocellus; rarely without a comb. (All regions except Neotropical) LEPTOPSYLLIDAE*
—. Head with 2 (very rarely 3) broad spines immediately behind the oral angle. (On bats) . . . . . ISCHNOPSYLLIDAE*

11. No genal comb; no arch of tentorium visible in front of ocellus which is usually well developed; no interantennal suture . . . CERATOPHYLLIDAE*

—. Genal comb present or absent; arch of tentorium visible in front of ocellus which is often reduced or vestigial; interantennal suture often indicated. (Holarctic) AMPHIPSYLLIDAE

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Order 27. **HYMENOPTERA** (Ants, Bees, Wasps, Ichneumon Flies, etc.)

Insects with 2 pairs of membranous wings, often with the venation greatly reduced; the hind wings smaller than the fore pair and interlocked with the latter by means of hooklets. Mouthparts primarily adapted for biting and often for lapping or sucking also. The abdomen usually basally constricted and its first segment fused with the metathorax; an ovipositor always present and modified for sawing, piercing or stinging. Metamorphosis complete; larva generally apodous with a more or less well-developed head, more rarely eruciform with locomotory appendages; tracheal system usually holopneustic or peripneustic throughout life, or at least in the final instar. Pupae exarate and a cocoon generally present.

This order is one of enormous extent comprising probably about 100,000 described species and many thousands of forms still await discovery. If the Hymenoptera be judged by their behaviour, they must be regarded as including the highest members of their class. Structurally the majority of their species have attained an advanced degree of specialization which is only surpassed by the Diptera. In certain species of the order the individuals have acquired the habit of living together in great societies, as in the case of the ants, wasps of the family Vespidae and bees of the family Apidae. A large proportion of the members of these societies have undergone structural changes, in some cases slight, in others more pronounced, so that they constitute a separate caste or type of individual known as the worker. These worker forms are imperfect females whose power of reproduction is either in abeyance or usually limited to the laying of male-producing eggs. Their functions include those of nest-building, feeding and tending the brood and the defence of the colony. The normal reproduction of the species in the social Hymenoptera is either performed, as in certain wasps, by many of the female members of a colony or more usually by a single individual of large size known as the queen. The sole function of the males is that of impregnating the females, an act which often comparatively few succeed in consummating.

Indications of what, in the higher Hymenoptera, constitutes social behaviour are found among solitary wasps and bees (Wheeler, 1928). Most solitary bees and wasps practise 'mass provisioning'—i.e. they store their cells with sufficient food to satisfy their developing offspring and close them down before the eggs hatch. There are, however, species which feed their larvae from time to time ('progressive provisioning'), thus becoming acquainted with their offspring. Among tropical Vespidae of the subfamilies Ropalidiinae and Polybiinae colonies are perennial and contain numerous fecundated females; their larvae are reared by progressive provisioning. Workers are often hardly differentiated and sometimes numerically weak. Such colonies, when fully developed, emit swarms consisting of fecundated females, usually accompanied by workers. This pleometrotic state is possibly more primitive

than what obtains among the Vespidae of temperate zones, whose colonies are haplometrotic, i.e. dominated by a single fecundated female or queen: such colonies are seasonal only and the worker caste is usually clearly differentiated. Among the social bees the most primitive are the species of *Halictus* (p. 737) and the Bombini. Humble bees construct no true comb but the larvae are reared in waxen pockets. They are at first fed by mass provisioning but in some species the older larvae are fed periodically. In temperate regions their colonies are haplometrotic and last only for a season. Among the Meliponini and Apini the colonies are perennial, haplometrotic and give off swarms. *Melipona* and *Trigona* practise mass provisioning and close their cells; apart from *Halictus*, they are the only social Hymenoptera where there is no contact between parent and larva; in many cases the three castes are all reared in identical cells on a similar diet. In *Apis* the cells are open throughout larval development: the castes are reared in differentiated cells, at least in *A. mellifera*, and queen-producing larvae are fed on a specialized diet. Among ants the castes exhibit their maximum differentiation: the larvae are reared in clusters, there being no cells, and there is a more intimate acquaintance between the workers and the brood than in other social Hymenoptera.

Wheeler attributed great importance to the phenomenon of *trophallaxis*, or the mutual exchange of food between imagines and their larvae. Ant larvae seem to produce a secretion highly acceptable to their nurses. In some species it is saliva, in others an exudation of the integument, while in the Pseudomyrminae it is a product of special papillae known as exudatoria. It appears that avidity for these larval secretions helps to sustain the bond between ants and their brood and it further accounts for the relations which ants have acquired with alien insects and other arthropods (Wheeler, 1923). Trophallaxis also occurs in the Vespidae but in them its function is less certain; it may be merely the disposal of excess water produced by the larvae (Brian, 1952). Among bees the phenomenon seems to be wanting.

Hymenoptera are also remarkable on account of the highly evolved condition which parasitism has reached in the order, and it has been independently acquired among species belonging to very diverse superfamilies. The Symphyta are essentially phytophagous, nevertheless *Orussus* is parasitic in its larval stage, but its habits have been very little studied. Among the Apocrita, about one half the known species of Cynipoidea are parasites, and this same habit occurs in the whole of the Ichneumonoidea and Proctotrupoidea, and in almost all the Chalcidoidea. Associated with parasitism is the phenomenon of polyembryony (vide p. 192) which is known to occur in a few of the Chalcidoidea and Proctotrupoidea. Among the aculeate families true parasitism is much rarer and, in the majority of cases of this kind, their larvae devour the provisions accumulated by the host for its own progeny. This involves the destruction of the latter but it is not parasitism in the strict sense. For a general discussion of parasitism in its different phases, and the more important literature thereon, reference should be made to papers by Wheeler (1919) and Clausen (1940).

The effects of Hymenopterous parasites upon their hosts vary in different cases. Certain of the Chalcid parasites of coccids are bivoltine. One generation attacks the young hosts who fail to reach maturity and succumb to the parasitism. The following generation of parasites attacks the older hosts and, in this case, the females of the latter are usually able to lay some or even all their ova prior to being overcome by the parasites. Wheeler has shown

that the ectoparasite *Orasema* produces abortion, or malformation, of certain parts in the ants which it attacks, and none of the latter become imagines. Certain of the Dryinidae are known to parasitize nymphal Homoptera and may modify or otherwise inhibit the development of the secondary sexual characters of their hosts. Lists of parasites and their hosts are given in the catalogues of Dalla Torre (1892–1902) and of Thompson (1943–51). Such lists have to be used with caution owing to the difficulties of identification.

Parthenogenesis (vide also p. 190) is more frequent among Hymenoptera than in any other order of the animal kingdom, and this method of reproduction is prevalent in a number of widely separated families. In many it is not an occasional phenomenon, but plays an important part in the continuity of the species, and may also be accompanied by an alternation of generations. The best known instance of parthenogenesis is found in the honey bee, in which unfertilized eggs, whether laid by the queens or by fertile workers, produce males and the same applies to *Vespa*. Among ants parthenogenesis has been less thoroughly investigated, and it has been claimed that the unfertilized eggs similarly only give rise to males, but Reichenbach, Donisthorpe and others have shown that the workers are capable of laying unfertilized eggs which develop into other workers. In the Cynipidae both sexes may be produced parthenogenetically and the generations, which arise in this way, alternate with those produced by the sexual method. In other species heterogony is absent, and females are produced parthenogenetically generation after generation; in some cases males are absent and in others rare. Among the Tenthredinidae parthenogenesis is also prevalent; in certain species only males arise from the unfertilized eggs, in others only females, or both males and females may be produced. In some Chalcidoidea parthenogenesis is the usual method of reproduction as in *Aphelinus mytilaspidis* and *Harmolita grandis*, in which examples males are very rare. Many other parasitic Hymenoptera are capable of both sexual and parthenogenetic reproduction and, in these cases, the latter process generally gives rise to males.

General Structure of the Imago

The general structure of the Hymenoptera has been well investigated in comparatively few types. The work of Snodgrass (1925) on the anatomy of the honey bee will serve as an introduction to the general morphology of the order. For the Formicoidea the numerous papers by Janet should be consulted. Other useful papers are: Ichneumonoidea, *Doryctes* (Seurat, 1899), *Microbracon* (Soliman, 1941); Chalcidoidea, *Euchalcidia* (Hanna, 1935), *Blastophaga* and *Philotrypesis* (Grandi, 1929 and 1930), *Monodontomerus* (Bucker, 1948); Vespoidea, *Vespula* (Duncan, 1939); Apoidea, Michener (1944).

A. EXTERNAL ANATOMY

The Head is free from the thorax and often extremely mobile. It varies considerably in form and, as a rule, the long axis is the longitudinal one. The cranial capsule is very completely consolidated but both clypeus and labrum are usually distinct; an epipharynx is well developed and trilobed in the higher forms, the median lobe being pointed and projecting. Acuteness of vision is a characteristic of the order and the compound eyes are therefore almost always large; in the male they are sometimes strongly convergent or holoptic. In certain species of ants belonging to the genera *Dorylus* and *Eciton* the eyes have atrophied, and in other species of the latter genus, they are reduced to a single facet on either side. Three *ocelli* are commonly present

but, in some cases, they are aborted, as in the Bembicinae and in the workers of many of the ants. The *antennae* are extremely variable in character in the Symphyta and among the parasitic families of the Apocrita. As a rule, they are longer in the males than in the females, and frequently exhibit pronounced sexual dimorphism. The latter feature attains its greatest development among the Protoctrupoidea and Chalcidoidea, where these organs in the male may be either filiform, clavate, pectinate, branched or verticillate. The number of segments present is singularly inconstant in the lower superfamilies: thus among the Ichneumonidae, for example, it may be as low as 14, or as high as 70. In the sawfly *Arge* there are only three segments, and four are present in some of the ants. In the Sphecoidea, Vespoidea and Apoidea the number for the most part is fixed, there being usually 13 segments in the males and 12 in the females.

The Mouthparts exhibit a wide range of differentiation from the generalized biting, orthopterous type found among the Symphyta to the highly modified sucking type of *Apis*, *Euglossa* and other bees. Mandibles are universally present throughout the order but, except in the predacious members of the Tenthredinidae, their principal function is industrial rather than trophic. They are used to enable the imagines to cut their way through the walls of their cocoons in the case of the parasitic superfamilies, while among the Sphecoidea, Vespoidea and Apoidea their principal functions are the gathering of material and nest-building. If the mouthparts of *Nematus*, or other typical sawfly (Fig. 498), be examined it will be observed that well-developed dentate mandibles are present; the complete number of parts are evident in the maxillae, and their palpi are 6-segmented. In the labium both prementum and submentum are developed, the labial palpi are 4-segmented, and the ligula appears deeply cleft into three nearly equal lobes—a median glossa and lateral paraglossae. Among the Apocrita this same type of mouthparts is retained in the parasitic group, but it has undergone a variable amount of specialization. The labial and maxillary palpi usually exhibit a reduction in the number of their segments, particularly in the Chalcidoidea. The maxillae are frequently single-lobed, and the ligula is commonly formed by the broadened glossa, the paraglossae being either vestigial or absent. In the higher superfamilies, the glossa becomes increasingly prominent, in conformity with the habit of feeding upon and collecting nectar. This organ becomes progressively lengthened, the associated mouthparts become attentuated accordingly, and the result of these modifications is the formation of a proboscis. The latter organ is an adaptation which is necessary in order to extract the juices from the deeply seated nectaries of many flowers.

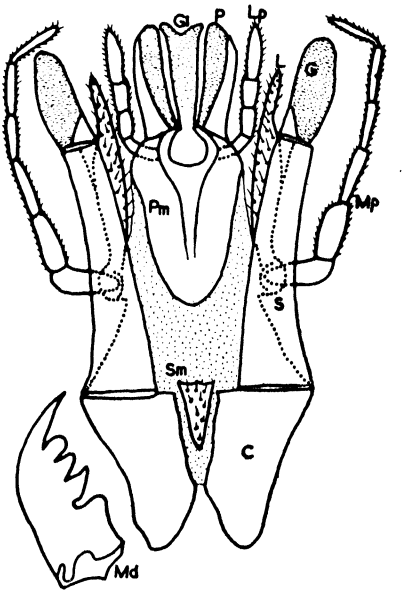


FIG. 498.—Mouthparts of *Tenthredo* (Symphyta), ventral view

C, cardo; *G*, galea; *Gl*, glossa; *L*, lacinia; *Lp*, labial palp; *Md*, left mandible (dorsal view); *Mp*, maxillary palp; *P*, paraglossa; *Pm*, prementum; *S*, stipes; *Sm*, submentum.

It is possible to trace the evolution of the proboscis in different genera of the Apoidea, from the simple condition found in the Colletidae, up to the highly specialized apparatus seen in *Apis*, *Euglossa*, etc. In the Colletidae the glossa is extremely short and broad with a bifid extremity; the labial palpi are non-sheathing and 4-segmented, and the maxillary palpi are 6-segmented. In *Andrena* the glossa, although still short, is acuminate, while in *Panurgus* and *Nomada* it is appreciably lengthened, as are also the labial palpi and the maxillary lobes. In *Melecta* the first two segments of the labial palpi ensheath the greatly drawn out glossa, and the maxillary palpi are reduced to small 4-segmented organs. In *Psithyrus* and *Bombus* the glossa is still further elongated, and the maxillary palpi are represented by inconspicuous 2-segmented organs, while in *Apis* they have undergone further degeneration and are in the form of minute papillae. In *Anthophora* the glossa is longer than in any other British bees, but the two pairs of palpi are not specialized to a correspondingly high degree. In the tropical *Euglossa* the maxillary palpi are single segmented, the labial palpi 2-segmented and the glossa attains a length exceeding that of the whole insect.

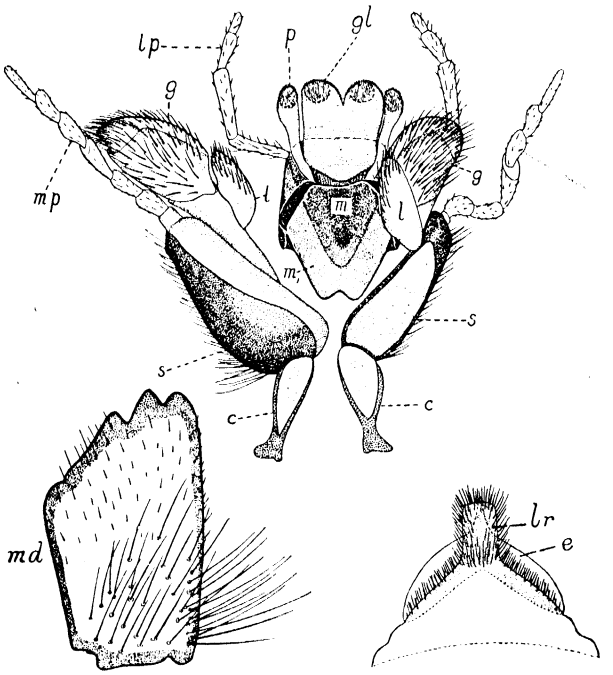


FIG. 499.—Mouthparts of *Vespula germanica* (worker), one maxilla is shown extended and the other in its natural position

c, cardo; *e*, epipharynx; *g*, galea; *gl*, glossa; *l*, lacinia; *lp*, labial palp; *lr*, labrum; *m*, m_1 prementum; *md*, mandible; *mp*, maxillary palp; *p*, paraglossa; *s*, stipes.

In Figs. 498, 499 and 500 the mouthparts of a saw-fly, *Vespula* and *Apis* are represented. In the case of the first mentioned type the essentially biting nature of their component parts is evident. In *Vespula* these organs are adapted both for biting (and mastication) and licking. The maxillae are comparatively little modified; the cardines and stipites are well developed, and the palpi are 6-segmented. The laciniae are reduced to small scales, while the galeae assume the form of broad membranous lobes. The labium is composed of a large shield-shaped prementum, the ligula is represented by the curious elongated paraglossae and a wide bilobed glossa, while the palpi are slender 4-segmented organs. In *Apis* the mouthparts are highly modified to form a proboscis and the glossa has become a sucking organ. The chief basal plate of the maxilla is the stipes and at its proximal end it is articulated with the stalk-like cardo, and near its apex on the outer border is a minute peg-like maxillary palp. Articulating with the distal extremity of the stipes is a large

blade-like lobe or galea; a reduced lacinia is present though often overlooked. In the labium, the large strongly sclerotized plate is the prementum, and the latter articulates with a small triangular sclerite or mentum. The base of the latter is supported by a flexible transverse band, the submentum (lorum of some authors), whose extremities are attached to the distal ends of the cardines. The labial palpi are conspicuous 4-segmented organs, each being carried by a basal palpiger. The elongate central organ of the proboscis is the glossa, and at the base of the latter are two small concealed lobes or paraglossae. The glossa is invested with long hairs and at its apex is a small spoon-shaped lobe—the *flabellum* or bouton. The side walls of the glossa are inclined downwards and inwards, until they almost meet along the mid-ventral line, and thereby form the boundaries of a central cavity. Embedded in the roof of the latter is a longitudinal rod which is grooved along its entire length, and this groove is converted into an imperfect tube by means of two rows of hairs which converge from its margins. The dorsal rod is flexible and becomes continuous basally with the ventral supporting plate of the ligula. The lining of the cavity of the glossa and its rod can be evaginated through the cleft, a process which admits of the cleansing of the parts in question. In transverse sections, the space between the outer and inner walls of the glossa is seen to contain blood and is in communication with the head cavity. The complete extension of the organ is due to blood pressure. Its retraction is partly due to the release of that pressure, and partly to the contraction of muscles inserted into the base of the dorsal rod. The latter, when drawn backwards, shortens the glossa which, as Snodgrass remarks, become bushy just as does a squirrel's tail if one attempts to pull out the bone at the base. When at rest, the mouthparts are folded down beneath the head against the stipites and mentum. During feeding they are straightened out with the two modified proximal segments of the labial palpi closely applied to the glossa, and partly embraced by the ensheathing laciniae. The glossa is very active while food is being imbibed: not only is the whole ligula alternately retracted into and protruded from the base of the mentum, but the glossa itself alters its length in the manner just described. The liquid food ascends by means of capillary action in the central channel of the glossa, and the effect of the shortening of the latter organ is to squeeze the nectar backwards, until it enters the space between the paraglossae, and so on into the mouth. Its passage onwards is probably ensured by means of a sucking action exerted by the pharynx. For a detailed investigation of the structure and mode of action

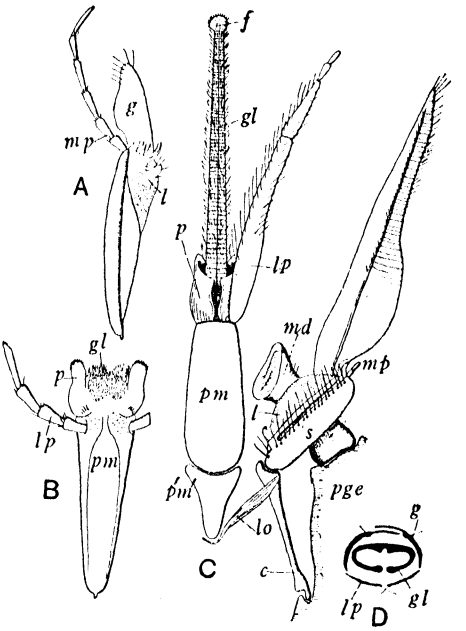


FIG. 500.—Mouthparts of bees

A, *Prosopis*, right maxilla and B, labium (ventral). *Apis*. C, mouthparts (ventral): D, cross-section of same when feeding; *f*, flabellum; *lo*, submentum; *pge*, postgena; *pm*, prementum; *p'm'*, mentum. Other lettering as in Fig. 498.

of the proboscis, and its musculature, reference should be made to the memoirs by Snodgrass (1925; 1942): the anatomy of this organ in different genera of bees is described by Saunders (1890) and Demoll (1908).

The Thorax of Hymenoptera (Fig. 501) is principally characterized by the fusion of the first abdominal segment with the metathorax, and its complete incorporation in the latter region. The transferred abdominal segment is termed the *propodeum* which was first described by Latreille as the 'median segment'. Among the Symphyta the latter is still evidently part of the abdomen and has undergone but little specialization. In the Apocrita it has become transferred to the thorax and fused up with the metapostnotum and metapleura. Its existence in all cases, however, may be ascertained by the

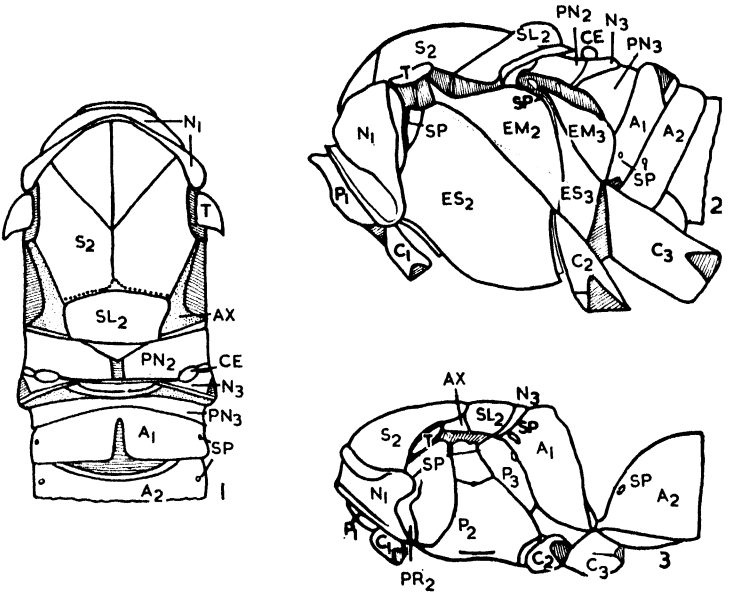


FIG. 501.—1. *Tenthredo*, Dorsal aspect of thorax. 2. The same, lateral aspect. 3. *Prosopis*, lateral aspect

A, abdominal segment; *AX*, axilla; *C*, coxa; *CE*, cenchri; *EM*, epimeron; *ES*, episternum; *N*, notum; *P*, pleuron; *PN*, postnotum; *PR*, prepectus; *S*, scutum; *SL*, scutellum; *SP*, spiracle; *T*, tegula.
Numerical suffixes indicate thoracic or abdominal segments.

fact that it bears the first pair of abdominal spiracles. The study of the thorax in the order, as a whole, indicates that a progressive series of modifications has taken place in the higher forms (Snodgrass, 1910). The *pronotum* is separated from the pleuron and attached to the front of the mesothorax. The propleuron and cervical sclerite of each side unite to form what may be conveniently called the *propleuron*; the sternum is sunk beneath the pleura and is only visible without dissection in some lower forms. The *mesonotum* is divided by a transverse suture into an anterior plate or *scutoprescutum* and a posterior one or *scutellum*. Areas at the sides of the scutellum known as the *axillae* belong however to the scutum. In some Parasitica (Fig. 502) longitudinal sutures demarcate *parapsides* (cf. Tulloch, 1929) at the sides of the scutum. A somewhat similar pair of sutures nearer the mid-line, the *notaulices*, are also sometimes present. Tegulae are present throughout the order. The *mesopostnotum* and its phragma are invaginated and concealed within the thorax; the phragma is often extensive, and may extend backwards

into the base of the abdomen, as in *Aphelinus* and some Mymarids. The *metanotum* is usually reduced to a single plate carrying the hind wings, while the *metapostnotum*, in all the higher members of the order, is indistinguishably merged into the front margin of the propodeum.

The Wings.—No insects have deviated so far from the primitive venational type as the Hymenoptera, and even the most generalized members of the order are highly specialized as regards the wing-veins. Great difficulties confront any attempt to determine their homologies and, as Comstock has pointed out, the courses of the tracheae do not afford a reliable clue in this respect. An examination of the young pupae of the honey bee reveals the fact that the venation is already foreshadowed before the tracheae develop, and that the latter are formed after the vein cavities are laid down. We have, therefore, to depend very largely upon comparative studies within the order and also with members of related orders. A dominant feature is the extensive fusion of the principal veins and the tendency of their branches to assume a transverse course. The venation is so difficult to interpret that a number of schemes has been proposed: two only

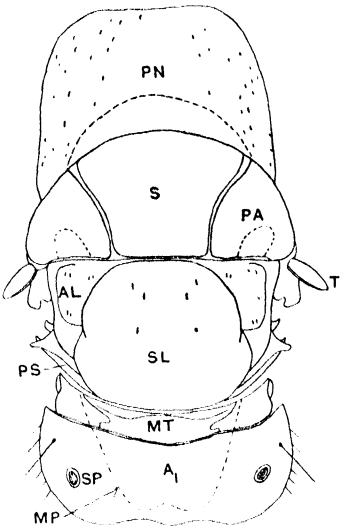


FIG. 502.—Dorsal aspect of the thorax of a Chalcid (*Philotrypesis caricae*)

AL, axilla; *MP*, mesophragma; *MT* metanotum; *PA*, parapsides; *PN*, pronotum; *PS*, postscutellum of mesothorax. Other lettering as in Fig. 501. *After* Grandi, *Boll. Lab. Zool. Portici*, 14, 1921.

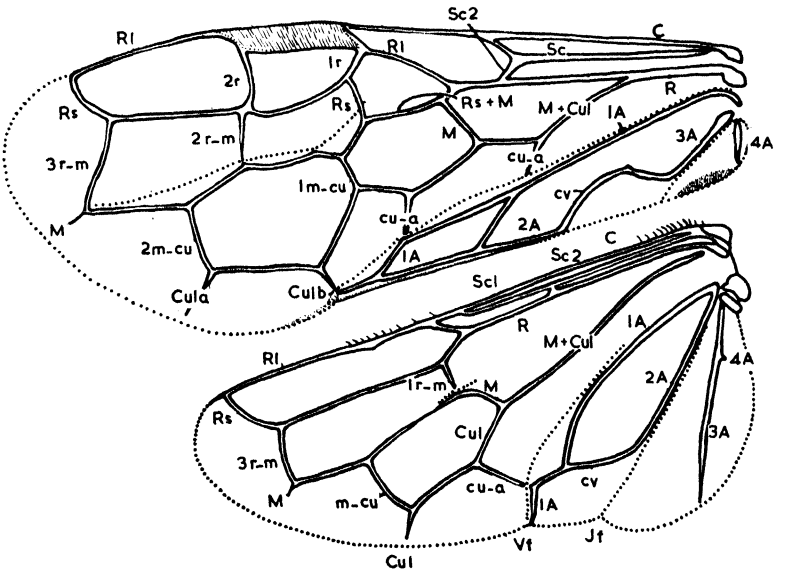


FIG. 503.—Left wings of *Pamphilius* (Symphyta), with the veins lettered

cv, anal cross-vein; *vf*, vannal fold; *jf*, jugal fold.

are referred to here. That of Ross (1936), based on a comparison with such forms as *Sialis*, has recently been accepted by a number of morphologists.

It is illustrated in Figs. 503, 504. An alternative terminology (that largely used by Cresson: Figs. 505, 506) is one of a number of more or less similar schemes, differing in detail according to the family, but widely used in the systematic literature. The term *cubital* (better *submarginal*) cells of Fig. 506 can be conveniently used in conjunction with Ross's terminology. Specialization by reduction and fusion is evident throughout the Apocrita and attains its maximum development among certain of the Evaniidae and the Chalcidoidea, where there is a solitary compound vein, running near the costa of the fore wing, and the hind wing is veinless; in

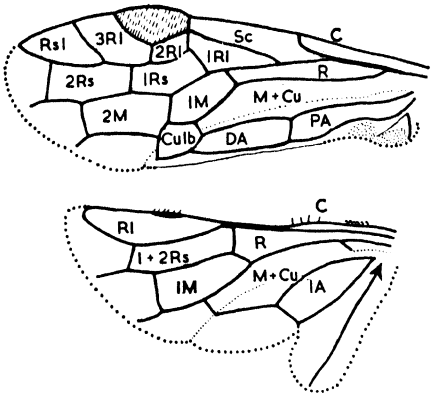


FIG. 504.—Left wings of *Xyela* (Symphyta) with the cells lettered

DA, *PA*, distal and proximal anal.

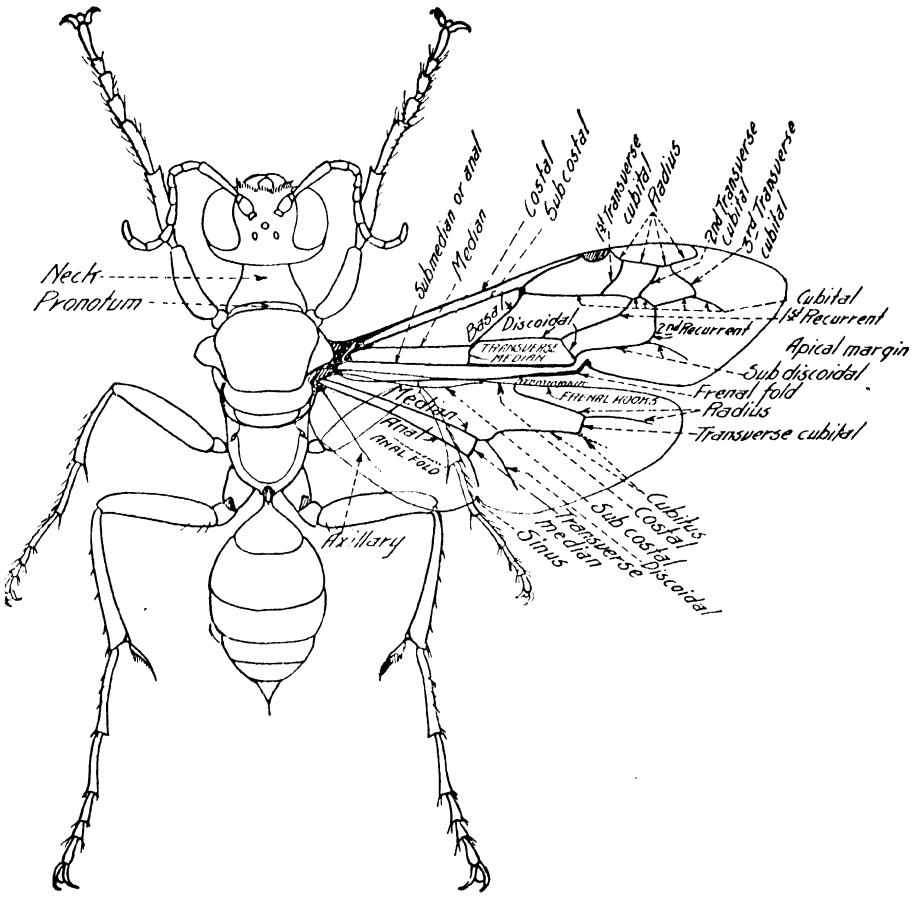


FIG. 505.—*Chlorion* (*Ammobia*). Typical Sphecoid, with the older nomenclature of the wing-veins

After Rohwer, *Bull. 22, Connecticut geol. and nat. Hist. Survey.*

the Platygasteridae both pairs of wings may be devoid of veins. In the Chalcids, the proximal part of the vein is the *submarginal*; more distally it runs along the front margin as the *marginal vein* and gives off a short *stigmal* vein. Throughout the order the wings of each side are held together by a row of hooks or *hamuli* along the costal margin of the hind pair: these hooks catch on a fold along the posterior margin of the fore wing, so that the wings of a side become interlocked. Among the Chalcids the hamuli are reduced to a localized group of two or three hooks and, in the Mymaridae, the latter may be totally wanting. Apterous forms are a common feature in the order, and are the rule among the workers of all species of ants, and occasionally also among the males of these insects and of many Agaonidae. Wingless females are present in the Mutillidae, Thynninae and Myrmosinae, in which groups the males alone are winged. Similarly apterous females occur frequently in the Proctotrupoidea and in certain of the Ichneumonidae and Braconidae. Apterous members of both sexes of the same species are rare but are known, for example, in the Diapriid *Platymischus*, and in certain members of the Ichneumonid subfamily Cryptinae.

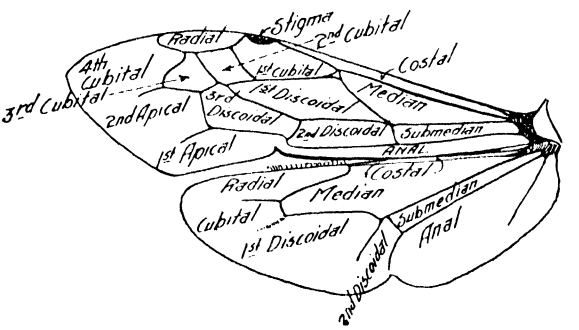


FIG. 506.—*Chlorion*. Left wings with the cells named according to the older nomenclature
After Rohwer, *loc. cit.*

The Legs exhibit various modifications: in all the parasitic groups, excepting the Pelecinidae, the trochanters are commonly said to be two-segmented, though the second piece, known as the trochantellus, belongs to the femur. In the Apocrita the spur or calcar at the apex of the fore tibia is knife-like in character, and fits against a semicircular emargination of the basitarsus. This cavity is beset with fine comb-like teeth, and the antennae are repeatedly passed through the apparatus, which functions as a preening organ. The Sphecoidea, together with a number of other solitary wasps, are often termed the 'Fossores', and their legs are adapted for digging and running, or for nest-building. In the Apoidea, the legs are comparatively simple in certain primitive genera but, in the higher forms, the posterior pair is adapted for pollen-carrying. The posterior tibia is more or less dilated and either bears a large pollen brush or *scopa* or is margined with long hairs, being thus modified to form a *corbicula* or pollen basket. The basitarsus is flattened on its inner aspect, and provided with several rows of short stiff spines which form a brush; by means of the latter the bee gathers the pollen adhering to the hairs of its body. When a sufficient quantity has accumulated on the brushes, it is scraped off over the edge of the hind tibia of the opposite side and stored in the pollen basket. As a rule the tarsi of Hymenoptera are 5-segmented, and an arolium is present between the claws.

The Abdomen is restricted physiologically to the region which commences with the 2nd segment, the 1st abdominal segment being the propodeum already referred to. The region behind the propodeum may be called the *gaster*. The number of segments that can be identified in the gaster varies

very greatly: the maximum number of nine can be distinguished in the Tenthredinidae. As a rule, in the higher groups, there are six exposed segments in the females and seven or eight in the males. In a number of groups, the 9th gastral tergite bears small, lateral, setigerous processes, the *pygostyles*. In the Symphyta the 1st gastral (2nd abdominal) segment is always unmodified and forms a broad base of attachment. In the Apocrita this region is wholly or partially constricted to form a narrow neck-like zone, which is termed the *petiole* or *pedicel*. In the honey bee the latter is so short as to be visible only when the abdomen is deflexed. Almost every transition can be found between this condition and the extremely attenuated bristle-like petiole of *Sphex*, *Sceliphron* and other genera. A ventral pollen brush or *scopa* occurs in some Apidae. *The ovipositor* (Fig. 507) is a well-developed organ with considerable uniformity of structure although modified in different groups for sawing, boring, piercing, stinging or, in some groups (e.g. *Formica*) reduced. Its general anatomy is well illustrated in the hive bee (Snodgrass, 1925). Morphologically, the ovipositor is composed of three pairs of gonapophyses, which have been shown by Zander to arise from a similar number of abdominal processes in the larva—one pair on the 8th segment and two pairs on the 9th. In the adult, the 7th sternite is usually exposed and little modified. The 8th sternite is reduced but on each side is found a *first valvifer* (triangular plate) to which is attached the long *first valvula*. The latter is the active part of the ovipositor, forming the saw in the Symphyta, the effective ovipositor in the Parasitica, and the lancets of the sting in the Aculeata. The sternite of the 9th segment is also reduced and on each side is found a *second valvifer* (oblong plate) to the anterior end of which is attached the *second valvula*. The 2nd valvulae of each side are immovably joined to one another and form the sting sheath, enclosing the 1st valvulae. The fused 2nd valvulae have along most of their length a pair of ridges projecting into corresponding grooves in the 1st valvulae. Thus the latter can move in and out without being detached from their sheath. These two pairs of valvulae together constitute the *terebra*. In the sawflies, both pairs of valvulae are provided with transverse ridges which terminate below in the serrations of the saw. In the Apocrita, the 2nd valvulae normally bear analogous 'barbs' but the 1st valvulae are smooth. The barbs are specially well developed in *Apis* so that the sting normally remains behind in the wound which it causes. The *third valvulae* (gonostyli, sting palps) each arise from the posterior end of the 2nd valvifer. They are usually less sclerotized than the other valvulae and more or less covered in bristles. The 9th abdominal tergite in all more specialized forms is more or less retracted and desclerotized. In the Aculeata, for instance, it is divided into two lateral plates (quadrate plates) by a membranous area.

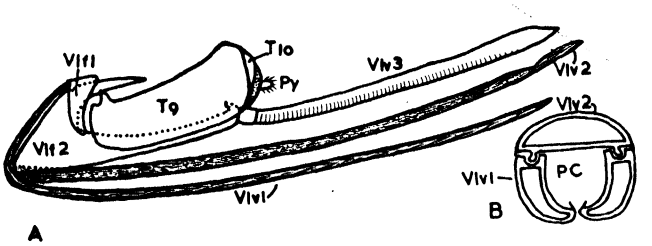


FIG. 507.—A. Ovipositor of *Nemeritis* (Ichneumonidae), from the left side. B. Section of the terebra of *Apis*

PC, poison canal; *Py*, pygostyle: *T9*, *10*, abdominal tergites; *Vlf 1*, *2*, 1st and second valvifers; *Vlv 1*, *2*, *3*, 1st, 2nd and 3rd valvulae.

The two pairs of valvifers and, in higher forms, the quadrate plates function as levers, and can be moved by powerful muscles. By means of the rotation of the valvifers, the terebra is driven through the tissues of the victim when oviposition or stinging take place. A pair of filiform *acid glands* opens, either separately or by means of a common duct, into a large poison-sac. Their secretion is a complex mixture of which the most important constituents are, probably, a protein and certain enzymes. The latter act on the tissues of the victim to release histamine which is responsible for many of the resulting symptoms (summary in Wigglesworth). In *Formica* and its allies the active agent is chiefly formic acid. The poison-sac discharges into the bulb formed by the expanded bases of the 2nd valvulae and, situated close to its opening, is the aperture of an unpaired *alkaline gland*, the function of whose secretion is not clear. Bordas (1897) has studied this glandular system in different groups of Hymenoptera. He finds that in the Ichneumonidae the acid gland consists of numerous filiform tubes and that an accessory poison gland is present as it is, also, in the Crabroninae (Sphecidae).

In the male, the 9th abdominal sternite is always developed though concealed and the genitalia lie above it. The latter consist of a basal ring often partly divided longitudinally; a pair of two-segmented forceps to whose inner edge is attached a complicated plate, the *volsella*; and a pair of central penis valves, connected by membranes to form a tube and acting as the intromittent organ. Morphologists are not agreed as to the homologies of these structures. Snodgrass (1941), who has made a valuable survey of the male genitalia in the order, holds that all the structures are secondary differentiations of an aedeagus. Others, such as Michener (1944), hold that the outer forceps are derived from true abdominal appendages.

B. INTERNAL ANATOMY

The Alimentary Canal (Fig. 509) is of a tolerably uniform character throughout the order and presents but few notable deviations in its morphology (Bordas, 1894). In ants there is an *infrabuccal chamber* below the floor of the mouth: it takes the form of a spheroidal sac and opens into the mouth-cavity by means of a short narrow canal. According to Wheeler (1910) this chamber is used by the ant as a receptacle for the fine particles of solid and viscous food, rasped off or licked up by the tongue. Any juices that may be contained in this nutriment are sucked back into the pharynx, and the solid residue thrown out as a pellet, which retains the form of the chamber in which it was moulded. The mouth-cavity leads into the *pharynx*, which is an organ of suction, and is moved by powerful dilator muscles. The *oesophagus* is a long narrow tube, especially in forms with an elongate petiole, but is relatively short in *Apis* and *Vespula*. Among the Aculeata the oesophagus dilates in the anterior portion of the abdomen into a thin-walled crop or *honey-stomach*. The latter is lined with a sclerotized membrane and its walls contain muscle fibres: it serves as a reservoir for the liquid that has been imbibed, regurgitating it when required. In replete honey ants, the

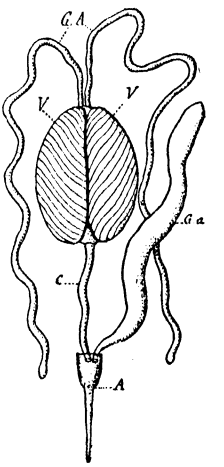


FIG. 508.—*Vespula germanica*, poison glands

G.A, acid gland; *V*, poison sac with canal *c*; *G.a*, alkaline gland; *A*, terebra. *After* Bordas, 1897.

crop is remarkably distensible and, when full, largely determines the shape of the gaster. The crop is succeeded by the *proventriculus*, which is a very characteristic part of the gut in Hymenoptera and forms the neck-like region between the crop and true stomach. In *Apis* it is invaginated into the posterior wall of the crop, and has a X-shaped aperture provided with four triangular lips. The posterior opening of the proventriculus into the stomach is guarded by a well-developed valve. The function of the proventriculus, and its method of action, have given rise to discussion: it apparently serves to pump food from the crop into the stomach and, when closed, to prevent its regurgitation. The *stomach* or *ventriculus* is the largest part of the alimentary canal in *Apis* and *Vespula*, and is bent into a U-shaped loop. In some Sphecoids, Formicoidea and the Parasitica it is reduced to a small elliptical chamber. In the female of *Doryctes*, which lives but a short time and takes no nourishment, its anterior portion has undergone atrophy (Seurat). A peritrophic membrane is present and consists of a number of thin concentric lamellae. In most Hymenoptera, the *ileum* is a short simple tube but, in *Apis*, its length is much increased, and this region of the gut is looped upon itself. The *rectum* forms an enlarged terminal chamber, and its walls are furnished with three rectal papillae in ants, four in *Doryctes* and six in *Apis* and most other Hymenoptera.

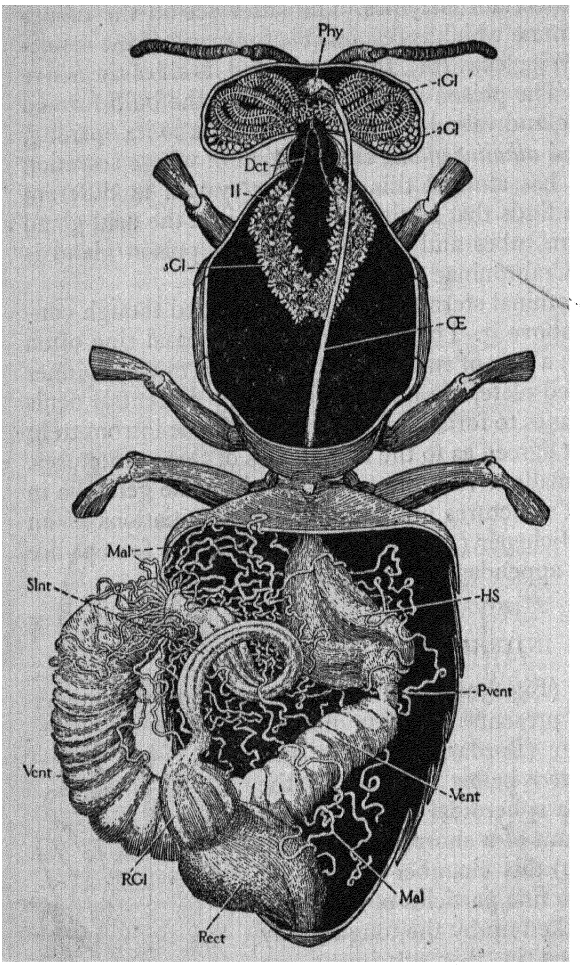


FIG. 509.—Alimentary canal of worker bee

1*GL*, lateral pharyngeal gland; 2*GL*, cephalic salivary gland; 3*GL*, thoracic salivary gland with *Il* its reservoir and *Dct* its duct; *Phy*, pharynx; *OE*, oesophagus; *HS*, honey stomach; *Pvent*, proventriculus; *Mal*, Malpighian tubes; *Vent*, ventriculus; *Slnt*, small intestine; *Rect*, rectum and *RGl*, its papillae. *After* Snodgrass, *U.S. Bur. Entom. Tech. Ser. Bull.* 18 (reduced).

The *Malpighian tubes* are extremely variable in number and, in the Aculeata, they vary from 100 to 125 in the Vespidae; from 20 to 30 in *Megachile* and its allies; and from 6 to 20 among ants. They all open separately into the ileum, and are often disposed in groups. Thus, in *Bombus* and *Apis* there are about 100 of these tubuli and, in the former genus, they are arranged in four bundles; in the Chrysididae there are about 40 Malpighian tubes arranged in three bundles; and in the Eumeninae they number from 40 to 70, which are disposed in two groups. Among the Parasitica, these organs are

often much less numerous: in *Blastophaga* they number from 8 to 14 (Grandi), in *Doryctes* 9, in the Ichneumonidae there are generally from 50 to 60, and in the Tenthredinidae 20 to 25. Among Hymenopterous larvae there are four Malpighian tubes in *Apis* and the Formicoidea, but in most of the parasitic families there is only a single pair of these organs.

Salivary Glands (Bordas, 1894, etc.) are well developed in the bee and consist of two pairs—one situated in the head and the other in the thorax (Figs. 509, 510). Their four ducts unite to form a common canal which opens on the hypopharynx. The *cephalic salivary glands* (postcerebral glands of Bordas; system No. 2 of Cheshire) lie against the posterior wall of the head. The *thoracic salivary glands* (system No. 3 of Cheshire) correspond with the ordinary salivary glands of most other insects. The contents of each gland are discharged into a reservoir, whose duct unites with its fellow to form the main salivary duct which, also, receives those of the cephalic glands. In the drones and queen there is a mass of gland cells situated just above the ocelli. These are the post-ocellar glands of Bordas but, according to Snodgrass, they are detached lobes of the cephalic glands. In addition to the foregoing, there is a pair of large *lateral pharyngeal glands* (supracerebral glands of Bordas; system No. 1 of Cheshire) which are the source of the royal jelly, which is fed to the larval and adult queens and drones by the workers. Each is in the form of a long coiled chain of follicles packed away in the antero-dorsal region of the head; these glands are absent in the drone and rudimentary in the queen. Opening into the floor of the pharynx, between the ducts of the lateral pharyngeal glands, is a transverse row of cells which forms the *ventral pharyngeal gland* of Snodgrass (sublingual gland of Bordas). A sac-like *mandibular gland* opens at the inner angle of each jaw: its function has not been ascertained, but it is larger in the queen than in the worker, and poorly developed in the drone. A second or *internal mandibular gland* has been described by Bordas in the worker of *Apis*, and also found in *Bombus* and *Vespa*; it is a delicate racemose mass, opening near the posterior inner edge of the mandible.

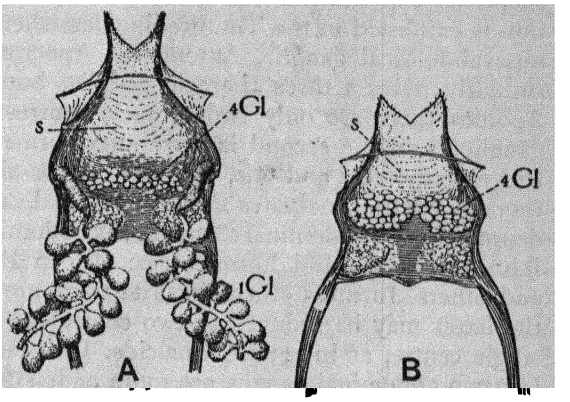


FIG. 510.—Pharyngeal plate (*S*) and associated glands of A, worker and B, drone of hive bee

1*GL*, base of lateral pharyngeal gland; 4*GL*, ventral pharyngeal gland. *After* Snodgrass, *loc. cit.*

The Heart is well developed, and is usually composed of four or five chambers, with a corresponding number of pairs of alary muscles. In *Apis* the chambers are situated in the 3rd to 6th abdominal segments and, in ants, in the 4th to 8th segments. The heart is continued forwards as the aorta which, in the bee, is folded into about eighteen loops in the region of the petiole. In the latter insect both dorsal and ventral diaphragms are well developed.

The Muscular System is one of great complexity and the reader is referred to articles by Janet (1897, etc.) for ants, Duncan (1939) for *Vespula*, Snodgrass (1942) for *Apis* and Alam (1951–53) for *Stenobracon*. In the

dealated queens, among ants, the wing muscles are broken down by phagocytes, which take up and convert their substance, and somewhat later discharge it in the form of fat and albuminoid globules into the blood. In this manner the histolysis of the muscles provides nutrient material which contributes to the growth of the eggs (Janet).

The Nervous System.—The brain has been studied among the higher members of the order and more especially by von Alten (1910), Jonescu (1909), Kenyon (1896), Thompson (1913) and Viallanes (1886). It is principally characterized by the high degree of differentiation of the mushroom bodies and their related fibre-tracts. In ants, for example, there is considerable variation in their development, not only among different species, but also in different castes of the same species. According to Viallanes, the highest type of brain is found in *Vespula* where the calyces are complexly folded.

The ventral nerve-cord is considerably less specialized than in the cyclorrhaphous Diptera. According to Brandt (1879) the most generalized condition is exhibited in the Tenthredinoidea where there are three thoracic and nine abdominal ganglia. Among the Apocrita the majority of the species similarly possess three thoracic ganglia, but among the Crabroninae and Apoidea there are only two thoracic centres. The first is the prothoracic ganglion and the second is a complex formed by the fusion of the meso- and metathoracic and one, or more, of the abdominal ganglia. The second thoracic centre innervates the 2nd and 3rd pairs of legs, the wings, propodeum, and 2nd abdominal segment. Six abdominal centres are present in many Ichneumonoidea and Formicoidea, also in *Ammophila*, *Cerceris*, *Odynerus*, and others. In most other Apocrita there are fewer abdominal ganglia, and the latter may be reduced to two centres as in *Cynips quercus-folii*, or to a single centre, as in certain Chalcids. In the females of many Aculeata the last two abdominal ganglia are more or less fused: thus in *Mutilla europaea* and *Megachile* there are five such ganglia in the latter sex and four in the male. In *Bombus* the worker and female have six ganglia and the male five. In the worker of the hive bee there are five ganglia, while the female as well as the male has but four. In *Vespula* the worker similarly has five ganglia, but the male and female are exceptional in having six. In *Blastophaga* there are two abdominal centres in the female, while in the male they are fused into a common mass (Grandi).

The Male Reproductive System.—The testes are separate in the Symphyta and also in *Apis* and *Bombus*. According to Bordas (1894) they are in close contact in *Vespula* and fused together in other Hymenoptera studied by him. Each testis is enclosed in a double membrane and may consist of 250–300 follicles as in *Vespula*, *Bombus* and *Apis*; these follicles are much less numerous in ants, and are usually reduced to three in other Hymenoptera. The vasa deferentia enlarge to form vesiculae seminales which are usually cylindrical or sac-like in form. In *Vespula* and *Apis* they are particularly voluminous, while they are tubular and convoluted in *Athalia*, *Cimbex* and *Bombus*. The two ejaculatory canals, which leave the vesiculae, receive the ducts of a pair of accessory glands. The latter are large and sac-like in almost all members of the order. In *Apis* the ejaculatory canals are rudimentary, and the accessory glands open into the common ejaculatory duct.

The Female Reproductive System (Fig. 511).—The ovaries are composed of polytrophic ovarioles; in *Apis* the latter are very numerous but their number is inconstant. In *Blastophaga* the ovarioles are very attentuated

and closely packed together; according to Grandi there are 130–182 to each ovary. In *Cimbex* there are usually 20–30 ovarioles in each ovary; in *Aphelinus* there are five, while in other Chalcids and in the Ichneumonoidea there are commonly four. In *Doryctes*, however, each ovary is greatly developed and consists of a single pair of ovarioles; in *Aphidius* the latter are wanting and the follicles are simply enclosed in a sac-like membrane. Among ants the number varies, in different genera and species, between two (*Leptothorax emersoni*) and about 250 (*Eciton schmitti*): in the workers, however, the number is very much lower, there is often a single ovariole to each ovary and rarely there are as many as twelve. The two oviducts unite to form the vagina and, in *Apis*, the latter is dilated posteriorly as the bursa copulatrix. A median spermatheca is generally present together with a pair of colleterial glands: the latter may open into a median reservoir as in *Cimbex* (Severin) or into the duct of the spermatheca as in *Apis*.

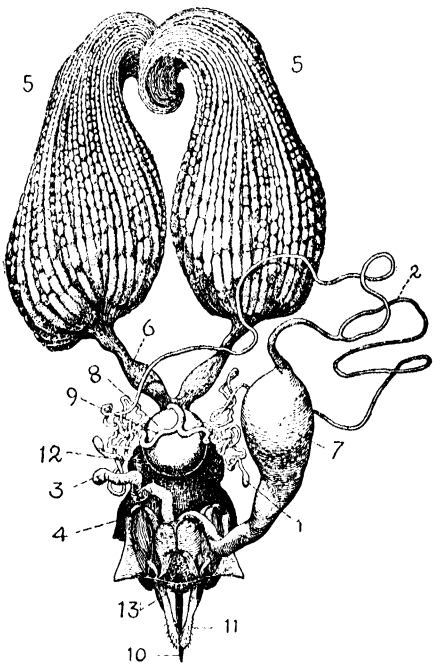


FIG. 511.—Reproductive organs, etc., of queen bee

1, acid gland and 2, its duct; 3, alkaline gland; 4, bursa copulatrix; 5, ovary; 6, oviduct; 7, poison sac; 8, spermatheca and 9, its gland; 10, terebra; 11, sting palp; 12, vagina; 13, 9th sternum. Adapted from Snodgrass, *loc. cit.*

Metamorphoses

THE EGG

The eggs of Hymenoptera are usually ovoid or sausage-shaped and, in the parasitic groups, they are frequently provided with a pedicel. The latter structure may arise from either pole of the egg (Adler) and is of very general occurrence among the Cynipoidea. In the gall-forming species of the latter group it may be five or six times the length of the egg itself. Stalked eggs are also found among the Chalcidoidea and Proctotrupoidea: in *Blastophaga* the pedicel may measure more than twice the length of the egg. In the majority of cases the function of this appendage is obscure, but in *Blastothrix* it protrudes through the body-wall of the host, and functions as a kind of respiratory funnel, which enables the newly hatched larva to breathe the outside air (see p. 148). In *Schedius kuvanae* the eggs are deposited within those of the gipsy moth, with their pedicels protruding to the exterior (Howard and Fiske), and it is probable that the latter organs fulfil a similar function in this instance also. A reduced pedicel is found in other Chalcids as well as in certain of the Ichneumonoidea; it is met with both in the case of eggs which are laid externally to their hosts, and in those which are laid within the latter.

THE LARVA

A typical Hymenopterous larvae is composed of a well-developed head, three thoracic and usually nine or ten abdominal segments. With some

exceptions the tracheal system is peripneustic or holopneustic, either throughout life or in the later instars. Among the Symphyta the head is strongly sclerotized and there are powerful biting mouthparts. Three pairs of thoracic limbs and six or eight pairs of abdominal feet are generally present. Such larvae feed upon plant tissues, and are peripneustic or holopneustic throughout life, with nine or ten pairs of spiracles. Larvae which bore into stems or wood have lost the abdominal feet, but retain the thoracic limbs usually in a more or less reduced condition. Among the Apocrita, the larvae are apodous: evanescent thoracic appendages are present, however, in *Eucoila*, and a single pair is found in larvae of the Platygasteridae, and in these instances they are probably modified survivals of true appendages. As a general rule, the larvae of the Apocrita (Fig. 512) (Clausen, 1940; Short, 1952), are maggot-like in form; the head is less strongly sclerotized than in the Symphyta, and in the parasitic forms it is often greatly reduced and sunk into the prothorax. Degeneration of the organs of special sense is very evident and, in most cases, the larvae are sluggish and move but little. These features are associated with the fact that their possessors live in darkness, and are supplied with an abundance of nutriment in their immediate vicinity, there being no necessity to seek for it. Ocelli are wanting, and the antennae are reduced to short sensory processes, small papillae, or may be atrophied. The mandibles may be either dentate, sickle-shaped or simple pointed spines with broad flattened bases. The labrum, maxillae and labium are fleshy lobes, and the two last-mentioned organs exhibit little or no differentiation into separate sclerites. Both the maxillary and labial palpi are usually represented by small papillae or are

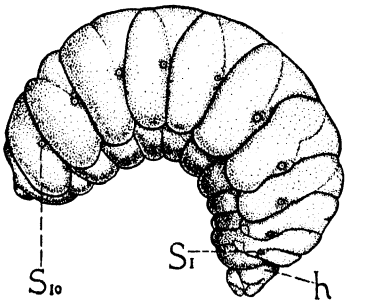


FIG. 512.—Larva of a bee: enlarged *h*, head; *s*, spiracles. From Nelson.

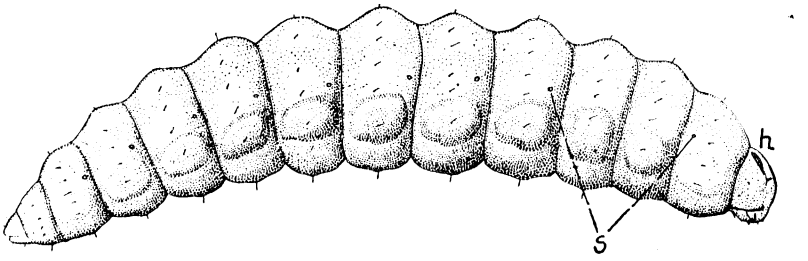


FIG. 513.—Fully-grown larva of an ectoparasitic Ichneumon, *Pimpla pomorum:* enlarged *h*, head; *s*, spiracles.

totally wanting. In almost all the larvae of the Apocrita the stomach is a blind sac and does not communicate with the hind intestine until the final instar, the faecal contents only being evacuated at the conclusion of the larval stage. Well-developed salivary glands are present, often of considerable length, and the ganglia of the ventral nerve-cord are often undifferentiated. In the Aculeata the tracheal system is holopneustic throughout life and generally ten pairs of spiracles are present. In the Parasitica the respiratory system undergoes profound modifications in correlation with varying modes of life (Seurat, 1899). Thus among the ectoparasitic species (Fig. 513) the larvae are hatched

with a peripneustic tracheal system. The typical number of spiracles is nine pairs but they are not always borne on the same segments in different species. The Chalcid *Aphelinus* has eight pairs of spiracles and the Ichneumon *Pimpla pomorum* has ten pairs. In the Proctotrupid *Lygocerus* the larva is hatched with two pairs and there are seven pairs in the last instar. Among the endoparasitic forms the young larvae are commonly apneustic, but this condition is rarely retained throughout life. In the apneustic condition the cuticle is extremely thin and admits of the interchange of gases by means of diffusion. At this stage the larva is haemophagous but it subsequently becomes carnivorous, devouring the various internal organs of its host. When it assumes this mode of life, a certain number of spiracles open on the surface of the body, and in the final instar there are usually nine pairs present (Thorpe, 1932).

Hypermetamorphosis occurs among many of the Parasitica and examples of this type of development are known in five of the major divisions of the order (Richardson, 1913). At least ten distinct primary larval forms are known in addition to the usual larval type already described. Any attempt at the classification of these forms at present can only be a tentative one pending the growth of more detailed knowledge. The principal types of primary larvae are as follows (Figs. 514, 515). (1) The PLANIDIUM (Fig. 514) is an active larva invested with strongly sclerotized imbricated segmental plates and provided with spine-like locomotory processes. It develops from an egg which is laid away from the host and is a migratory form adapted to seek out the latter. This type is known in the Chalcid families Eucharitidae and Perilampidae. (2) The CAUDATE TYPE is well exhibited in certain Ichneumonidae, Braconidae, and in a few of the Chalcidoidea, notably *Aphidencyrtus aphidivorus*. It is somewhat vermiform in shape with a caudal outgrowth of variable length (vide also p. 148). (3) The CYCLOPOID OR NAUPLIIFORM TYPE occurs in certain of the Proctotrupoidea. It is characterized by the large swollen cephalothorax, very large sickle-like mandibles and a pair of bifurcate caudal processes of variable form. In its general facies it bears a resemblance to the nauplius of Crustacea. (4) The TELEAFORM TYPE is found in certain other Proctotrupoidea and in several of the Chalcidoidea; it derives its name from the primary larva of *Teleas*. The cephalic extremity is prominently hooked or curved; posteriorly the body is prolonged into a caudal process, and the trunk is armed with one or more girdles of setae. Apparently modified examples of this larval type have been described by McColloch

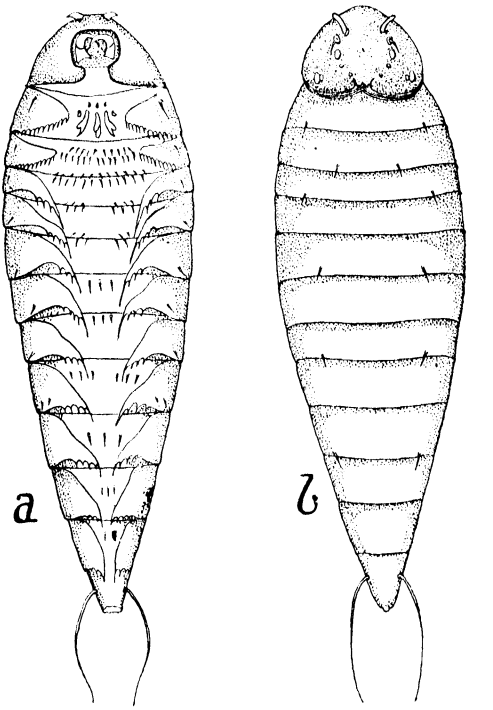


FIG. 514.—Planidium of *Perilampus*
a, ventral; *b*, dorsal. *After* H. S. Smith, *U.S. Bur. Ent. Tech. Ser.* 19, pt. 4.

in *Eumicrosoma* and by Silvestri in the Chalcids *Poropoea* and *Anaphoidea*. (5) The VESICLE-BEARING TYPE occurs in *Apanteles* and *Microgaster* and is characterized by the proctodaeum being everted to form a swollen anal vesicle. (6) The EUCOILIFORM TYPE is known in the Eucoilinae: it differs from the teleaform type in possessing three pairs of long thoracic appendages, and in the absence of the cephalic process and the girdles of setae. (7) The POLYPOD TYPE, with 8 to 12 pairs of trunk appendages, occurs in *Ibalia*, the Braconid *Microdus* and in *Phaenoserphus*: in *Eucoila* and allies it follows the protopod stage. The subsequent stages in development in those species in which hypermetamorphosis occurs exhibit wide variation: thus the second larval instar of *Teleas* is of the cyclopoid type, but the final instar in all cases is the ovoid maggot-like type of larva characteristic of the Apocrita.

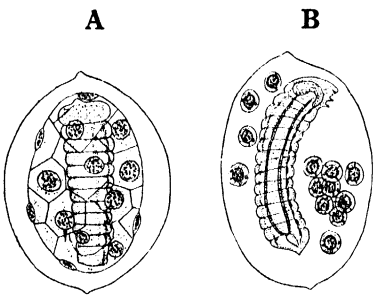


FIG. 516.—*Chalcis* (*Smicra*) *clavipes*. A, Egg with embryo surrounded by trophamnion. B, young larva and disintegrated trophamnion

After Henneguy, *Les Insectes*.

The presence of a trophic membrane or trophamnion (Fig. 516) enclosing the embryo in certain endoparasitic Hymenoptera, has been already alluded to (p. 208). It has been found in diverse species, comprising members of each of the main parasitic groups, but is evidently not homologous in all cases, and very different methods of formation have been described. This membrane is believed to play an important part in the nutrition of the embryo.

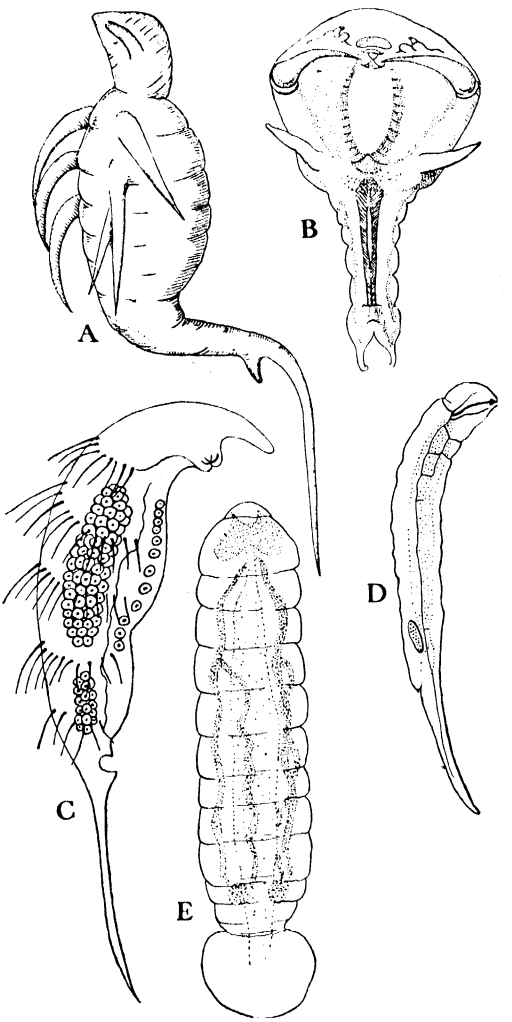


FIG. 515.—Primary larvae of various parasitic Hymenoptera

A, eucoiliform (*Eucoila*); *after* Keilin & Pluvinel. B, cyclopoid (*Trichacis*) *after* Marchal. C, teleaform (*Teleas*), *after* Ayers. D, caudate (*Mesochorus*), *after* Seurat. E, vesicle-bearing (*Microgaster*), original. All highly magnified.

THE PUPA

In the Apocrita the prepupa (pharate pupa) is intermediate in some characters between the larva and pupa (Fig. 195B). The prothoracic segment is

distended by the developing pupal head, the wings and legs have assumed the form of those of the pupa, and it is in this stage that the first abdominal segment or propodeum becomes incorporated with the thorax. After the final larval moult, the prepupa passes into the pupa and the latter is of the exarate type, in which the wings and appendages are free and not soldered to the surface of the body (Fig. 195). With the exception of the Cynipidae and Chalcidoidea a cocoon, though often slight, is of general occurrence in the order. In many Tenthredinoidea it is parchment-like; in others it is formed of agglutinated soil particles; while in *Cimbex* the cocoon is formed of an outer and inner coat, and attains a higher degree of development than in other Hymenoptera. In many of the Aculeata the cocoon is little more than a silken lining to the larval cell, and in some of the ants it is totally wanting. Among the Braconidae dense masses of silken cocoons are often formed by the members of a species which issue from a single individual host.

Classification of Hymenoptera

The Hymenoptera are divisible into the suborders Symphyta and Apocrita. It has long been customary to separate the Apocrita into two main divisions, viz. the Aculeata or stinging forms and the Parasitica (Terebrantia) which are parasites of other insects. The distinctions between these divisions are so difficult to draw and subject to so many exceptions that it is more practical and probably more correct to recognize rather a series of superfamilies. Biologically, there is also no clear distinction. A number of the Parasitica are plant feeders and many Aculeata are parasites. In the Aculeate families Sapygidae, Dryinidae and Chrysididae, the ovipositor retains its egg-laying function as in the Parasitica: in other Aculeates, the ovipositor is converted into a sting and the egg reaches the exterior at its base.

The standard works on European Hymenoptera are those of André (1879–1913) and Schmiedeknecht (1930). Dalla Torre (1892–1902) published a catalogue of the species of the world but this is now very out of date. A valuable catalogue of the North American species was published by Muesebeck *et al.* (1951). It is difficult to construct a key which will identify all the wingless and other highly modified species. The following attempt is based as far as the Symphyta are concerned on that of Benson (1938); for the Apocrita those of Bradley (in Comstock, 1929) and of Brues & Melander (1945) have been largely drawn on.

A. Abdomen broadly attached to the thorax, no marked constriction between the 1st and 2nd abdominal segments. Larva (except *Orussus*) with thoracic and generally abdominal legs **Suborder SYMPHYTA** (CHALASTOGASTRA) . 1

B. Abdomen deeply constricted between the 1st abdominal segment (propodeum) and the 2nd. Larva apodous **Suborder APOCRITA** (CLISTOGASTRA) . 14

1. Antennae inserted below the eyes and below the apparent clypeus. Hind wing without any enclosed cells . . . . . ORUSSIDAE (p. 698)

–. Antennae inserted between the eyes, well above the clypeus. Hind wing usually with one or more enclosed cells 2

2. 3rd antennal segment very long 3

–. 3rd antennal segment not abnormally long 5

3. 3rd antennal segment followed by a thin filament of 9–25 segments. Vein Rs in fore wing generally forked. Pronotum with hind margin almost straight XYELIDAE (p. 697)

–. Antennae with at most 4 segments. Vein Rs in fore wing simple. Pronotum with hind margin deeply emarginate 4

4. Antennae with a small 4th segment. Fore wing with cross-vein 2r present. Mid and hind tibia without preapical spurs . . BLASTICOTOMIDAE (p. 699)
–. Antennae with 3 segments, 3rd sometimes bifid. Fore wing with cross-vein 2r absent. Mid and hind tibiae often with preapical spurs ARGIDAE (p. 699)

5. Fore wing with cross-vein 2r present 6
–. Fore wing with cross-vein 2r absent 13

6. Pronotum with hind margin almost straight 7
–. Pronotum deeply emarginate behind 10

7. Abdomen flattened. Ovipositor not projecting. Fore tibia with 2 apical spurs 8
–. Abdomen cylindrical or laterally compressed. Ovipositor projecting. Fore tibia with 1 apical spur 9

8. Antennae with flagellar segments distinctly produced. Fore wing with Sc not developed. Mouthparts as long as head-capsule . MEGALODONTIDAE (p. 697)
–. Antennal flagellum simple. Fore wing with Sc present. Mouthparts not as long as head-capsule . . . . . PAMPHILIIDAE (p. 697)

9. Abdomen constricted between 1st and 2nd abdominal segments. Cenchri absent. Fore tibial spur simple . . . . . CEPHIDAE (p. 698)
–. Abdomen not constricted. Cenchri present. Fore tibial spur pectinate SYNTEXIDAE (p. 698)

10. Antennae clubbed. Sides of abdomen carinate . . CIMBICIDAE (p. 699)
—. Antennae at most subclavate. Sides of abdomen not carinate . . . 11

11. Postgenae not meeting behind the oral fossa. Scutellum with the posterior part separated off as a 'postscutellum'. Fore tibia with 2 apical spurs TENTHREDINIDAE (p. 699)
—. Postgenae meeting behind the oral fossa. Scutellum not so divided. Fore tibia with 2nd spur small or absent 12

12. Cervical sclerites longer than broad. Last abdominal segment of ♀ without horn-like projection. Maxillary palpi with 4, labial with 3 segments XIPHYDRIIDAE (p. 698)
—. Cervical sclerites broader than long. Last abdominal segment of ♀ with a horn-like projection. Maxillary palpi with 1, labial with 2–3 segments SIRICIDAE (p. 697)

13. Hind wing with no enclosed 1st medial or anal cells. Antennae often modified, serrate or clubbed . . . . . PERGIDAE (p. 699)
—. Hind wing with m-cu cross-vein enclosing medial cell; anal cell closed . 13*a*
13*a*. Antennae with more than 9 more or less serrate or plumose segments . DIPRIONIDAE (p. 699)
—. Antennae with 9 segments or all segments simple. Part of Tenthredinidae or Xiphydriidae 11

14. Winged species 15
—. Wings absent or very rudimentary. 29

15. Hind femur with a trochantellus, except some Cynipids which have no pterostigma in the fore wing. Hind wing with no anal lobe (except Evaniidae in which the gaster is attached to the top of the propodeum). Last visible tergite and sternite of ♀ not opposed, so that the ovipositor which is often elongate is partially exposed, tergite 8 fully exposed and resembling tergite 7 . . 16
—. Hind femur with a trochantellus, fore wing with a pterostigma, hind wing with enclosed cells, attachment of gaster to propodeum normal. Last visible tergite and sternite of ♀ opposed, so that the short or vestigial ovipositor is hidden 20
—. Hind femur without or with a very feebly marked trochantellus, in doubtful species a pterostigma is present in the fore wing. Hind wing usually with an anal lobe. Last visible tergite and sternite of ♀ opposed, so that the short ovipositor is mainly or entirely hidden, tergite 8 retracted and partly desclerotized (except Dryinidae) 21

16. Fore wing nearly always with a distinct pterostigma, to which the proximal part of the costal vein extends, venation usually relatively complete. Antennae usually long, with 16 or more segments. Abdomen in ♀ with at least the central

part of tergite 9 exposed and pigmented, tergite 10 separately developed, pygostyles present 17

—. Fore wing with no pterostigma, proximal part of costa not developed, venation usually more reduced. Antennae usually short, with less than 18 and usually less than 14 segments. Abdomen with spiracles on segments 1 and 8 only, in ♀ with tergite 10 indistinguishably fused with 9. 18

17. Gaster attached near top of propodeum. Abdomen with spiracles on segments 1 and 8. Fore wing with costal cell wide . **EVANIOIDEA** (p. 704)

—. Gaster attached at bottom of propodeum (a little above this in a few Braconidae). Abdomen with spiracles on segments 1–8. Fore wing with costal cell narrow (except Megalyridae and Stephanidae) **ICHNEUMONOIDEA** (p. 701)

18. Pronotum lateroventrally pointed and closely coadapted to the mesepisternum, posteriorly extending back to the tegulae. Fore wing with cell R_1 more or less complete. Antennae not elbowed. Trochantellus usually not developed. Abdomen without pygostyles, in ♀ tergite 9 retracted and desclerotized **CYNIPOIDEA** (p. 705)

—. Pronotum ventrally rounded, not closely coadapted to the mesepisternum, posteriorly usually distinctly separated from the tegulae. Fore wing with cell R_1 not defined by proper veins or absent. Antennae elbowed. Trochantellus present. Abdomen with pygostyles, in ♀ central portion of tergite 9 exposed and pigmented . . . . . **CHALCIDOIDEA** (p. 708)

20. Hind wing without an axillary or anal lobe. Head large, mandibles with 4 strong teeth, antennae with more than 20 segments. Abdomen not petiolate, ovipositor vestigial . . . . . **TRIGONALOIDEA** (p. 701)

—. Hind wing with an axillary as well as an anal lobe. Antennae with 13 segments in ♂, 12 in ♀, with a seta at end of most segments. Tarsal segments 2 and 3 expanded in ♀. Abdomen with long petiole. Ocelli enlarged RHOPALOSOMATIDAE (p. 730)

21. Hind wing with no cells enclosed by veins or antennae with 14 or more segments 22

—. Hind wing with 1 or more cells enclosed by veins; antennae with 13 or fewer segments. Abdominal spiracles on segments 1–8 23

22. Hind wing with no anal lobe. Pronotum obtuse below but with a narrow posteroventral process which meets its fellow from the other side beneath the fore coxae. Abdominal spiracles on segments 1, 1 and 8, or 1–6 **PROCTOTRUPOIDEA** (p. 714)

—. Hind wing with an anal lobe or if this is inconspicuous or absent, the integument is largely metallic. Pronotum obtuse below and not closely attached to the mesepisternum. Abdominal spiracles on segments 1–7 or (Dryinidae) 1–8 **BETHYLOIDEA** (p. 716)

23. Pronotum produced back to or almost to the tegulae, with no conspicuous lobe concealing the anterior thoracic spiracle 24

—. Pronotum not produced back to the tegulae but at a lower level forming a conspicuous lobe over the anterior thoracic spiracle 28

24. 1st segment of gaster forming a scale or node or the first 2 segments nodiform and deeply separated from the 3rd, both above and below 25

—. 1st segment of gaster not scale-like, if nodiform, then the next segment is closely coadapted to the 3rd 26

25. Male abdomen ending in an upturned sternal spine (♀ apterous) **SCOLIOIDEA** (Apterogyninae) (p. 718)

—. Male abdomen not ending in an upturned sternal spine. Fertile females winged but wings soon shed. . . . . **FORMICOIDEA** (p. 720)

26. Fore wing usually longitudinally folded in repose, with 1st discoidal cell usually very long, longer than the submedian cell. Eyes nearly always internally emarginate. Glossa and paraglossa nearly always ending in pigmented pads **VESPOIDEA** (p. 730)

—. Fore wing not longitudinally folded in repose, first discoidal cell shorter, usually much shorter than submedian cell. Eyes rarely internally emarginate. Glossa and paraglossa not ending in pigmented pads 27

27. Mesopleuron divided obliquely by a suture running from near upper posterior corner, downwards and forwards. Pronotum obtuse below and loosely overlapping the mesopleuron. Legs long, hind femur especially so, mid tibia with two spurs . . . . . **POMPILOIDEA** (p. 729)
—. Mesopleuron not so divided. Pronotum usually acute below and coadapted to the mesopleuron. Legs usually short and stout . **SCOLIOIDEA** (p. 718)

28. Pubescence simple. Hind tarsi not broadened . **SPHECOIDEA** (p. 733)
Pubescence at least in part (e.g., near anterior thoracic spiracle) plumose or branched. Hind tarsi usually more or less widened and often densely pubescent **APOIDEA** (p. 735)

29. Gastral sternites considerably membranous, tending to dry into a longitudinal fold 30
—. Gastral sternites fully sclerotized 31

30. Gaster sessile or subsessile or if petiolate, the petiole not curved and expanded at the apex, tergites 2 and 3 more or less fused . . BRACONIDAE (p. 703)
—. Gaster petiolate, petiole more or less curved and expanded at apex, tergites 2 and 3 nearly always separate . . . . . ICHNEUMONIDAE (p. 702)

31. Pronotum not extended back to the tegula and not coadapted to the mesepisternum which is provided with a distinct prepectus. Antennae elbowed **CHALCIDOIDEA** (p. 708)
—. Pronotum extending back to the tegulae, prepectus not distinctly present 3

32. 1st or 1st and 2nd segments of gaster forming a scale or node, well separated from posterior part of gaster. Antennae elbowed 33
—. If gaster is petiolate, the petiole is more or less cylindrical and the antennae are not elbowed 34

33. Meso- and metathorax and propodeum fused. Spur of fore tibia strongly curved, its convex edge pectinate . . MUTILLIDAE (*Apterogyna* ♀) (p. 719)
—. Some of the posterior thoracic sutures often present. Spur of fore tibia less curved and not externally pectinate . . . . **FORMICOIDEA** (p. 720)

34. Hind coxae large, legs relatively long, prothorax not coadapted to the mesepisternum which is divided by an oblique suture. Antennae with 12 segments in ♀, 13 in ♂ . . . . . **POMPILOIDEA** (p. 729)
—. Hind coxae and legs relatively smaller 35

35. Head pyriform, long axis vertical, the 10-segmented antennae arising from a prominence. Gaster not petiolate . . . EMBOLEMIDAE ♀ (p. 717)
—. Head differently shaped or the gaster petiolate 36

36. Antennae with 10 segments or fewer 37
—. Antennae with more than 10 segments 38

37. Pronotum not coadapted to the mesepisternum, fore tarsi nearly always chelate, antennae with 10 segments . . . . . DRYINIDAE ♀ (p. 717)
—. Pronotum coadapted to the mesepisternum, fore tarsi not chelate **PROCTOTRUPOIDEA** (p. 714)

38. Gaster compressed and integument smooth and shining. Antennae not geniculate . . . . . **CYNIPOIDEA** (p. 705)
—. Gaster not compressed, integument often sculptured or pubescent. Antennae usually geniculate 39

39. Head more or less markedly longer than broad with the long axis in life horizontal. Thoracic sutures normally complete . . . . BETHYLIDAE (p. 717)
—. Head more or less globular or long axis vertical 40

40. Antennae with 12 segments in ♀, with 13 in the few apterous males **SCOLIOIDEA** (p. 718)
—. Antennae with some other number of segments or if with 12, the antennae arising from a prominence and the gaster petiolate, or the sides of the gaster acutely margined . . . . . **PROCTOTRUPOIDEA** (p. 714)

Suborder I. SYMPHYTA

Included in this division are all the more primitive members of the Hymenoptera which are recognized by the broadly sessile abdomen and the fact that its first segment is only partially amalgamated with the thorax. The imagines do not exhibit the highly specialized habits and instincts so prevalent among the Apocrita and the ovipositor is adapted for sawing or boring: except in *Orussus* parasitism is wanting. The peculiar structures known as the *cenchri* are raised bosses on the metanotum which engage with a scaly area on the underside of the fore wings and keep them in place when at rest (Zirngiebl, 1936). They are found in all families except the Cephidae. The larvae (Yuasa, 1922) have a well-developed head and 13 trunk segments: three pairs of thoracic legs and frequently six or more pairs of abdominal limbs are present. The tarsus and claw of each thoracic leg are fused into a single piece while the abdominal limbs are devoid of crochets. A single pair of ocelli is present and the maxillary and labial palpi are usually 4- and 3-segmented respectively. Spiracles are always present on the prothorax and first eight abdominal segments: metathoracic spiracles are also present in the Cephidae, and in *Sirex* and *Tremex*, but are vestigial or wanting in the larvae of other Symphyta.

The Symphyta fall into two groups, the Orthandria including the first eight families, and the Strophandria with the remaining six. The first group show the male genitalia in normal orientation except in a few Xyelidae; in the second they are inverted with the ventral surface uppermost. The British species are being revised by Benson (1951–52).

Superfamily **Xyeloidea**

FAM. XYELIDAE.—This family has the most generalized venation among Hymenoptera (Fig. 504). The larvae are also noteworthy since they retain feet on all the abdominal segments. The imagines may be easily recognized by the greatly elongated 3rd antennal segment which is followed by a flagellum: the ovipositor is moderately or very long. *Xyela* and *Macroxyela* are typical genera: the only common British species, *X. julii*, is found where *Pinus* and *Betula* occur together. The larva lives in the staminate flower of the former, whereas the adults visit the flowers of *Betula*.

Superfamily **Megalodontoidea**

FAM. PAMPHILIIDAE.—These are robustly-built insects with a short ovipositor and a primitive venation (Fig. 503). The larvae (Fig. 517), on the other hand, have no abdominal feet: they are sometimes gregarious and often live in webs or rolled leaves. *Neurotoma* and *Pamphilius* are British genera: their species are mostly rather infrequent in occurrence.

The **Megalodontidae** are rather similar insects but have flabellate antennae in the adult. The larvae live gregariously in webs spun on herbaceous plants.

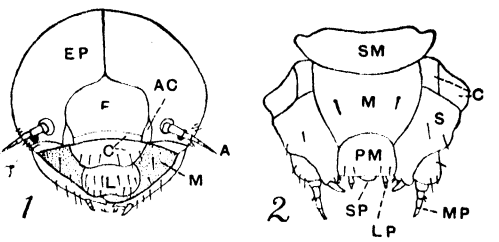


FIG. 517.—*Pamphilius dentatus*, larva. 1, frontal view of head; 2, maxillae and labium

AC, antecoxal piece of mandible; *SP*, spinneret (other lettering as in Fig. 6 (p. 19) and Fig. 10 (p. 23)). Adapted from MacGillivray.

Superfamily **Siricoidea**

FAM. SIRICIDAE (Wood-wasps or Horn-tails).—A family of large-sized insects with conspicuous coloration, being often black and yellow or metallic blue. The

abdomen terminates in a spine or horn, which is short and triangular in the males and lanceolate in the females. The ovipositor is exceedingly strong and, when at rest, projects backwards in the horizontal plane, and has the appearance of a powerful sting. This instrument is used for boring and drilling, and not for sawing as in the Tenthredinidae. Holes are made through the bark into the new wood of various forest and shade trees and a single egg is deposited in each hole. The larvae on hatching burrow into the heart wood and often cause considerable damage. Pupation takes place in the larval gallery and a cocoon of silk and gnawed wood is constructed. The larva has a tolerably large head and three pairs of reduced thoracic limbs: the last trunk segment terminates in a horny process which aids in locomotion. The best known species in the British Isles is *Urocerus gigas* which lives in Pinaceae, and its life-history appears seldom to occupy less than two years. It usually only attacks trees which have passed their full vigour and are not perfectly healthy, but sound felled trees are sometimes selected. The metallic blue *Sirex noctilio* is also not infrequently met with, but it is not truly indigenous. For further information on the British species of the genus, see Chrystal (1928). In the allied genus *Tremex* the larva affects broad-leaved trees in N. America.

The species of the family **Xiphydriidae** lack the spine [illegible] apex of the abdomen; their larvae bore in the wood of deciduous trees; two [illegible] *Xiphydria* are rather uncommon in Britain (Chrystal & Skinner, 1932). Th[illegible]ra of the family were revised by Konow (1905). The family **Syntexidae** includes a single N. American species with a wood-boring larva.

Superfamily **Orussoidea**

FAM. ORUSSIDAE.—This very small family is evidently a relic of an ancient group, and is distributed over most parts of the world. It is represented in Europe and N. America by the single genus *Orussus* and the species *O. abietinus* has been supposed to occur in Britain. Structurally the members of this family show many peculiar features. The wings have a reduced venation (Fig. 518) quite unlike that of any Symphyta, since there are no closed submarginal cells in the hind wing. In the position of the antennae, and the form and attitude of the long ovipositor when at rest, the family is unique among Hymenoptera. The only known larva is apodous and probably an ectoparasite of Buprestidae. It is described by Rohwer & Cushman (1917), who also emphasize the unique features of the family. On account of its adult characters, and the form and habits of the larva, they place the family in a separate suborder, the Idiogastra—intermediate between the Symphyta and Apocrita. Apart from its specializations however, it shares many characters with the Siricidae (cf. Cooper, 1953).

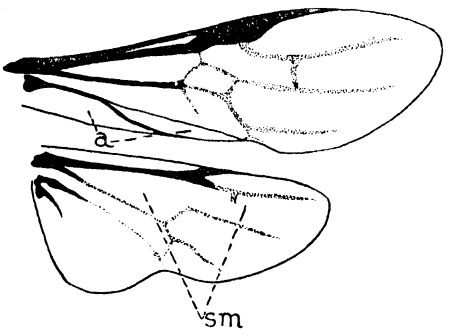


FIG. 518.—Right wings of *Orussus abietinus*
a, divided anal cell; *sm*, submarginal area. Adapted from MacGillivray.

Superfamily **Cephoidea**

FAM. CEPHIDAE (Stem Saw-flies).—The Cephidae are a small family of slender, narrow-bodied insects with a thin integument (Fig. 519). The prothorax is exceptionally large and movably articulated with the following segment. They are mostly black or darkly coloured, either with or without narrow yellow bands. In length they seldom measure more than 18 mm. and are usually smaller. The larvae bore into the stems and shoots of various plants and are apodous, with the exception of three pairs of reduced tubercle-like thoracic limbs. They are also characterized by the vestigial ocelli, the well developed metathoracic spiracles and the presence of vestigial subanal appendages. The abdomen terminates in a small retractile point or spine which arises from a fleshy protuberance on the last segment, above the anus. The pupae are usually enclosed in transparent cocoons within the stems of the food-plant. For an enumeration of the larval characters in different genera vide Middleton

(1918). Less than a dozen species occur in the British Isles, the best known being *Cephus pygmaeus*, the Wheat-stem Borer. Although destructive in many parts of Europe, and introduced into N. America, it is rarely injurious in Britain. The eggs of this species are laid in the stem of the wheat plant, and the larva bores its way upwards through the latter, ultimately weakening it below the ear: for an account of its biology and parasites see Salt (1931). *Janus integer* (= *flaviventris*) lays its eggs in the centre of the pith of the shoots of currants and its larvae bore through the stems: its metamorphoses are figured by Marlatt (1894). For a systematic account of the group see Benson (1946).

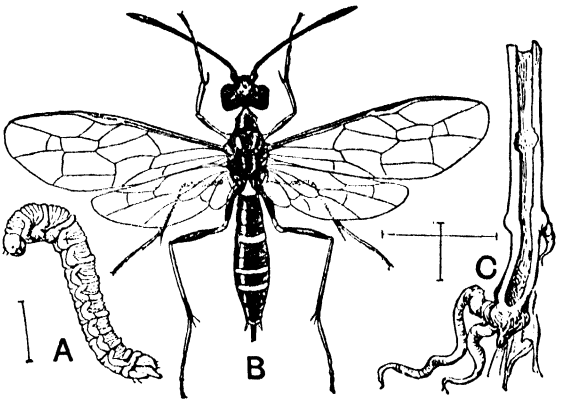


FIG. 519.—*Cephus cinctus* (= *occidentalis*)
A, larva; B, female; C, larval gallery in grass-stem. *After* Marlatt, *U.S. Dept. Agric.*

Superfamily **Tenthredinoidea**

FAM. ARGIDAE.—A family of more than 400 species of world-wide distribution, easily recognized by the structure of their antennae. The larvae have 6–8 abdominal legs and feed freely, mostly on woody Angiosperms. In the S. American *Dielocerus* the female sits over and protects her young which spin their cocoon in a communal covering.

FAM. BLASTICOTOMIDAE.—The single European species, lately found in Britain, is *Blasticotoma filiceti*. The larva, which has no abdominal legs, bores in the stems of various ferns.

FAM. CIMBICIDAE.—A small family of stout, often large insects with strongly clubbed antennae. The larger species are mostly attached to various trees and the larvae, which sit partly curled up and are covered with a waxy powder, are characteristic.

FAM. DIPRIONIDAE.—*Diprion* (= *Lophyrus*) and its allies include a number of important pests of coniferous trees. *Gilpinia hercyniae*, attached to *Picea*, has been introduced into Canada where large areas of forest have been defoliated. Males are very rare in this species. *Diprion pini* is the common British species on *Pinus*. The characteristic spotted larvae live gregariously and are very conspicuous.

FAM. PERGIDAE.—There is great diversity of structure within this family which occurs mainly in Australia and S. America. The females of *Perga* brood over their young. The larvae have no abdominal legs and feed gregariously on the leaves of *Eucalyptus*. The larvae of *Phylacteophaga* mine the leaves of the same plant.

FAM. TENTHREDINIDAE.—This family with about 4,000 species (nearly 400 British) includes the bulk of the suborder and exhibits considerable diversity of structure and habit. The adults are most often obtained by sweeping or shaking the vegetation; many frequent flowers and some are carnivorous, preying upon small flies and beetles. Great variation exists as to the proportion of individuals of the sexes and in only a few species are the males as numerous as the females. Cameron estimated that males were unknown in one-third of the British species. Parthenogenesis is common in the family and in some species males, in others females, and in a third group individuals of both sexes are produced from unfertilized eggs. Thus in *Nematus ribesii* only males have been reared from the unfertilized eggs. The impregnated females give rise to individuals of both sexes, but females predominate. In such species as *Croesus varus* or *Monostegia abdominalis* the parthenogenetic eggs produce females and no males are known (Benson, 1950).

The eggs are usually laid in young shoots or in leaves and the saw, or cutting instrument, of the ovipositor is toothed in various ways in conformity with the nature of the oviposition and also as a specific character. Its serrations are large and stout in species which lay their eggs in woody twigs; very fine in those which oviposit in leaf-tissue; or scarcely evident at all in *Nematus ribesii*, which simply attaches its eggs each by means of a small flange into a minute slit on the underside of a leaf. In most species,

during oviposition the blades of the ovipositor move alternately, one being thrust forward while the other is withdrawn, until an incision or pocket of the required depth is formed (cf. Keir, 1936). Both the first and second valvulae are more or less complexly serrated towards their apices while the third valvulae serve to protect the whole terebra. The larvae often bear a close general resemblance to those of the Lepidoptera. They are exclusively phytophagous in habit and affect almost all orders of Phanerogamia and certain of the Filices. Trees and bushes, however, support a larger number of species than herbaceous plants. The larvae (Yuasa, 1922) exhibit much diversity of habit and a large number are nocturnal feeders: many are solitary while others are gregarious. The vast majority live exposed, but some live internally in stems, fruit or galls and a certain number are leaf-miners. Many closely simulate their environment and are cryptically coloured, while others are very conspicuous

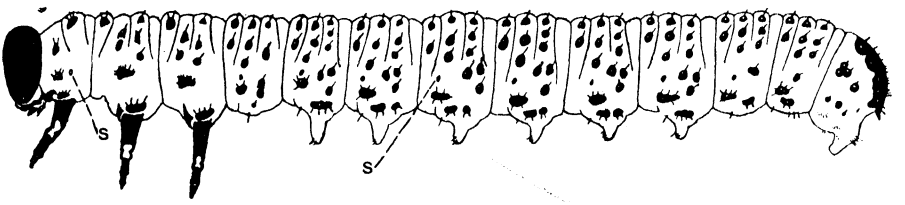


FIG. 520.—Larva of *Nematus ribesii*
s, spiracles. *After* MacGillivray, *Can. Entom.*, 45.

with bright colours. In numerous species the larvae are covered with a whitish powdery exudation: in *Caliroa* they are sluglike and the body is obscured by a darkly coloured slime or exudation and species of *Monophadnoides* are invested with bifurcate spines. The body-segments of saw-fly larvae are usually subdivided, by means of transverse folds, into annulets whose number appears to be constant for each species (Fig. 520). Three pairs of thoracic limbs are present and almost all species carry abdominal feet also. Unlike those of the Lepidoptera there are usually more than five pairs of the latter organs and they are devoid of crochets. The number of these appendages varies from 6 to 8. In many cases the larvae emit secretions which are produced by special glands. *Caliroa* has a pair of ventral digit-like glands opening between the head and prothorax: many larvae are provided with glands resembling osmeteria, which open by means of a slit-like aperture on the sternum of each of the first 7 abdominal segments. Pupation, as a rule, takes place in an elongate-oval silken cocoon which may or may not be mixed with soil particles; in other cases an earthen cell is constructed.

Suborder II. **APOCRITA**

Included in this suborder is the vast majority of Hymenoptera, all of which are recognizable by the abdomen being basally constricted or petiolate. The imagines are almost always highly specialized in their habits and are often social, living in large communities. The ovipositor is adapted for piercing in the Parasitica and usually for stinging in the Aculeata. The larvae are apodous, and the head is generally well developed but, among certain of the parasitic families, it is greatly reduced. The larval habits are extremely diverse. Thus many of the Cynipoidea and a few of the Chalcidoidea are phytophagous. Others of the Cynipoidea, all the Ichneumonoidea, and almost all the Chalcidoidea, are carnivorous, being either ecto- or endoparasites. The Sphecoidea and Vespoidea are largely predacious, and the Apoidea are nourished upon nectar and pollen.

The British Aculeata are described and figured in the work of Saunders (1896). Among the Parasitica, the Cynipoidea are dealt with by Cameron (1882–92) and the Ichneumonoidea by Marshall (1885–99) and Morley (1903–14), the Evanioidea by Crosskey (1951), but no monographic works exist on the remaining British parasitic groups. Clausen (1940) has summarized the biology of the Parasitica.

The literature on the biology of the Aculeata has assumed enormous proportions. Among the more important works are those of Fabre (1879–1903), Ferton (1901–21), Friese (1922–23), G. W. & E. G. Peckham (1898), Roubaud (1916), Grandi (1926–31), Williams (1919), and Wheeler (1910). The latter authority (1923) has given an admirable annotated bibliography of the subject to which the reader is referred.

The first five superfamilies are unambiguous Parasitica and the last six Aculeata, but annectent forms occur in the Proctotrupoidea and Bethyloidea.

Superfamily **Trigonaloidea**

FAM. TRIGONALIDAE.—A small family of rare but widely distributed insects. The multiarticulate antennae and the presence of the trochantellus ally them to the Parasitica, but the ovipositor (though reduced) and the wing-venation are more of an Aculeate type. They appear to be an archaic but also highly specialized group. In some species very numerous eggs are laid on leaves and are then eaten by caterpillars or saw-fly larvae within which they attack other Hymenopterous or Dipterous parasites. *Trigonalys maculatus*, however, is a direct parasite of *Perga* and some species seem to be parasites of social wasps (Clausen, 1940). The family has been monographed by Schulz (1907) and the anatomy of the single, rare British species *Pseudogonalos hahni*, is discussed by Bugnion (1910).

Superfamily **Ichneumonoidea** (Fig. 521)

With the possible exception of the Chalcidoidea this is the largest superfamily of the order. At the present time probably less than 16,000 species have been described but undoubtedly many times this number inhabit the world. Without exception all are parasites preying upon some stage in the life-history of other insects, or occasionally upon other Arthropoda. It will, therefore, be readily appreciated that the group, as a whole, is of the greatest importance, not only on account of the role which it plays in the economy of nature, but also from the fact that the majority of the species are beneficial to man.

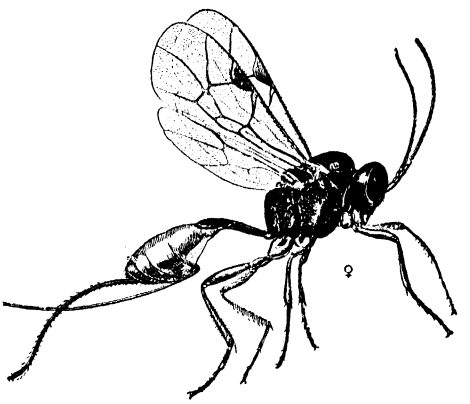


FIG. 521.—*Thersilochus conotracheli*, female enlarged
After Cushman, *J. agric. Res.*, 6, 1916.

Table of families:

1. Costal cell narrow or obliterated. Sternites of gaster often partly membranous. 2
–. Costal cell broad. Sternites of gaster evenly sclerotized. 3

2. Fore wing with cross-vein 2 *m-cu* present (except a few genera with the gaster three times as long as head and thorax and propodeum prolonged beyond the insertion of the hind coxa) or (*Neorhacodes*) indicated. Hind wing with cross-vein *r-m* meeting Rs after it leaves Sc + R . . . ICHNEUMONIDAE (p. 702)
–. Fore wing with cross-vein 2 *m-cu* absent. Hind wing with cross-vein *r-m* meeting Sc + R before Rs leaves it. . . . . BRACONIDAE (p. 703)

3. Mesoscutum with a central furrow or groove but without notauli. Anterior thoracic spiracle lying in the prothorax. Ovipositor long . . MEGALYRIDAE (p. 704)
–. Mesoscutum without this central furrow. Anterior thoracic spiracle concealed by the posterior lobe of the prothorax 4

4. Antennae multiarticulate. Head tuberculate above. Hind femur with teeth. Ovipositor long . . . . . STEPHANIDAE (p. 704)
–. Antennae with 14 segments. Head not tuberculate above. Hind femur without teeth. Ovipositor concealed **PROCTOTRUPOIDEA** (MONOMACHIDAE) (p. 715)

FAM. ICHNEUMONIDAE (Ichneumon Flies).—The vast majority of these insects are parasites, or less frequently hyperparasites, of Lepidoptera. After the latter come the Hymenoptera, and more especially the family Tenthredinidae, but all groups including the Parasitica may be attacked. A considerable number of Ichneumonidae are known to utilize Coleoptera as their hosts, but Diptera are much less frequently selected. A still smaller number parasitize Arachnida, and a few attack Aphididae and also *Hemerobius*, *Chrysopa* and *Raphidia*. Most species of the family are probably seldom restricted to any individual specific host, and those so accredited are becoming reduced in number with increasing knowledge. In their behaviour, the Ichneumons are among the most highly evolved of all solitary insects. The remarkable instincts exhibited in the discovery of their hosts and in providing for their offspring, their mating habits, behaviour in captivity, etc., afford a wide field for investigation. The imagines are most active on warm sunny days and are partial to flowers, especially Umbelliferae. Many species hibernate as adults but it appears to be the female, the male perishing before the advent of winter. Apterous and brachypterous forms are comparatively frequent in the subfamily Cryptinae, and it is often a matter of difficulty to discriminate them from similarly wingless Braconidae. In the Cryptinae, however, the abdominal segments are soft and telescopic whereas, among the Braconidae, the middle segments do not overlap one another. Ichneumon larvae (Beirne, 1941) are composed of a variably shaped head and usually 13 body segments. Spiracles, when present, consist typically of nine pairs, which are situated on the pro- or mesothorax, and first eight abdominal segments. Among endoparasitic larvae, there are frequently striking differences between the earlier and later instars. One of the most characteristic features of the newly hatched larvae of many species is the presence of a prominent caudal prolongation or tail. Owing to the fact that it disappears when the tracheal system becomes open to the exterior, this appendage has been regarded as an accessory respiratory organ, but this seems to be incorrect (Thorpe, 1932). Seurat, on the other hand, ascribes to it a locomotory function. The head in the young larva is large, and often strongly sclerotized, the segments between that region and the caudal appendage are sometimes greatly compressed, and the respiratory system is apneustic. The second instar is usually of a transitional nature between the first and third. The tail, though greatly reduced, is still evident, and the head has also undergone reduction and is less strongly sclerotized. In the third instar the larva generally becomes maggot-like, with a greatly abbreviated head, and the tail, as a rule, has disappeared or is vestigial. Towards the end of this stadium Timberlake states that, in *Limnerium*, the tracheal system communicates with the exterior by the spiracles. The number of instars present is obviously extremely difficult to determine: according to Cushman there are five in *Thersilochus*, and the same number is stated by Smith to be present in *Calliephialtes*. Ectophagous larvae are always devoid of the caudal appendage, the head is well developed and sclerotized, a variable growth of body hairs is evident, and the tracheal system is peripneustic from an early stage. When fully fed, Ichneumon larvae construct silken cocoons often composed of iridescent strands. Some of the most remarkable members of the family belong to the genera *Thalessa* and *Rhyssa* whose larvae are ectoparasites of those of the Siricidae. The adults are notable on account of the great length of the ovipositor and for their specialized habits of egg-laying. *Thalessa* has an ovipositor which may attain a length of six inches, with which it pierces or drills the wood of trees in order to reach the burrows occupied by *Tremex*. The British *Rhyssa persuasoria* similarly parasitizes *Urocerus*, and it has been recorded to reach its host by inserting the terebra along the burrows of the latter and also by passing it through the bark and solid wood. An interesting account of the habits of both genera is given by Riley (1889). The familiar reddish-brown species of *Ophion*, so often attracted to lights, are common parasites of Noctuid larvae. *Hemiteles areator* has been bred from a remarkable range of hosts comprising many Lepidoptera, various Hymenoptera including other Ichneumonidae, and also from several Coleoptera and Diptera. *Agriotypus* is an endoparasite of Trichopterous larvae, and the adults have been observed to dive and swim beneath the water while seeking their host (vide Clausen, 1931). Ashmead places this genus in a family of its own on account of the hardened abdominal sterna and the spined scutellum. Among the more important life-history studies of individual species of Ichneumonidae the reader should

consult the old though important work of Ratzeburg (1844), particularly for the larval development of *Anomalon*; among others, the papers of Cushman on *Calliephialtes* and *Thersilochus*, Newport (1852–53) on *Netelia*, Timberlake (1913) on *Limnerium*, and Imms (1918a) on *Pimpla* may be mentioned. Morley (1903–14) has monographed the British species, and Schmiedeknecht (1902–11) has produced a general systematic treatise on the family.

FAM. BRACONIDAE.—These insects are closely related in structure and habits to the Ichneumonidae but are readily separated by the absence of 2 *m-cu* in the fore wings. A further distinction is the general presence of the first sector of M + Rs which is absent in the Ichneumonidae (Fig. 522). Also, with the exception of the subfamily Aphidiinae, there is no articulation between the 2nd and 3rd gastral segments. Braconidae are easily distinguished from the Stephanidae by the absence of the costal cell. With regard to their hosts a great variety of insects are selected; the Lepidoptera are the most commonly parasitized, and more than one hundred examples of an individual species of Braconid may issue from a single caterpillar. Braconid larvae are composed of thirteen body segments and, in the first instar, the head is often large and sclerotized (Short, 1952). As in the preceding family, the most frequent number of spiracles in the adult larva is nine pairs, of which the first is placed as a rule on the mesothorax, and the remainder on the first eight abdominal segments. The endoparasitic forms are often provided with a caudal appendage similar to that found in Ichneumonid larvae. In *Apanteles*, *Microplitis*, *Microgaster*, and probably in other closely allied genera, this appendage is wanting, and the proctodaeum is evaginated to form a swollen anal vesicle, which is an accessory respiratory organ. Weissenberg (1908), from the analogy of the hind gut of other parasitic larvae, considers its most important function to be that of excretion. Pupation may occur within the host as in *Rhogas* and *Aphidius* or, more usually, externally as in *Apanteles* and many other genera. The pupa is enclosed in a cocoon which, in the last-named genus, is composed of fine threads of white, yellow, or buff-coloured silk. In *Microgaster* the cocoon is of a glistening papyraceous nature. Very frequently members of a species emerging from the same host construct their cocoons in a mass, often enveloped by a common web. They may be closely compacted to form a cake, the individual cocoons being regularly arranged so as to resemble honeycomb. The biology of *Apanteles* has been studied by many observers, notably Grandori (1911), Seurat (1899), Muesebeck (1918) and others. It is a common endoparasite of Lepidopterous larvae, *A. glomeratus* being an abundant enemy of *Pieris*, a single larva of which may support nearly 150 examples. When mature the larval parasites gnaw their way through the skin of the host, and construct sulphur-yellow cocoons, irregularly heaped together. The biology of *Microgaster* is very similar and *M. connexus* is a common parasite of *Porthesia similis* (Gatenby, 1919). The species of *Alysia* and their allies are distinguished by the peculiar attachment of the mandibles, the apices of the latter being directed outwards and not meeting when closed. Those Braconids which exhibit this curious feature are separated by Ashmead into a distinct family—the Alysiidae. Almost all their species are parasitic upon Dipterous larvae and the biology of *Alysia manducator* has been followed by Altson (1920). It is a common endoparasite of *Calliphora*, *Lucilia*, etc.; the young larva has a caudal appendage, and becomes maggot-like with nine pairs of open spiracles in the last instar. One of the most remarkable Braconids is *Sycosoter lavagnei* which is an ectoparasite of the Scolytid *Hypoborus ficus* (Lichtenstein & Picard, 1917): both sexes are dimorphic, having winged and apterous forms, but in the male the alate forms are the commoner.

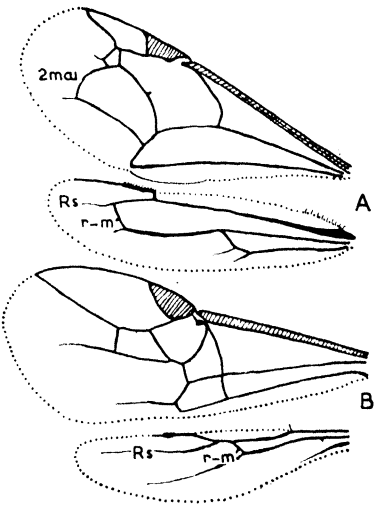


FIG. 522.—Left wings of A an Ichneumonid and B a Braconid, to show the absence of 2 *m-cu* in fore wing of the latter, and the different positions of *r-m* in the hind wing

The Aphidiinae are parasites of aphides, more especially of the apterous

viviparous females and, as a general rule, only a single larval parasite develops within the body of an individual host (cf. Vevai, 1942). The life-history of *Aphidius testaceipes*, which is a common enemy of *Toxoptera graminum*, has been followed by Webster & Phillips (1912). These observers state that the aphid may be attacked in any of its instars but if parasitized before the second ecdysis the host fails to reach to maturity. On the other hand, if the *Aphidius* deposits its egg in an aphid which has passed the second ecdysis the parasitism does not prevent its attaining the adult stage. If the aphid has passed the third ecdysis before becoming parasitized, it is capable in all cases of producing a small number of young before succumbing. When about to pupate the *Aphidius* larva makes a ventral fissure in the body-wall of its host, and cements the latter down to the object upon which it finally rests. The dead parasitized aphids are familiar straw-coloured objects and each bears a circular hole through which the adult parasite issued. Species of *Praon* leave their host prior to pupation and construct for themselves a separate shelter, which is usually surmounted by the empty body of its victim (Fig. 523). The British species of Braconidae have been monographed by Marshall (1885–99), and Lyle has contributed notes on their biology (1914–29).

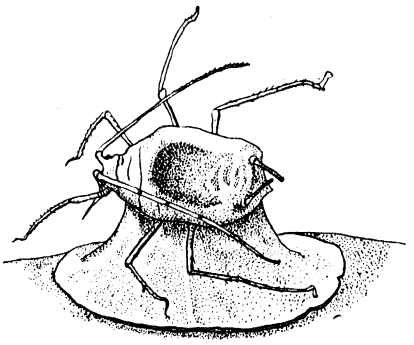


FIG. 523.—Cocoon of *Praon* beneath the body of its dead host (an aphid)
After Howard.

FAM. STEPHANIDAE.—The members of this small family have very slender antennae composed of 30 or more segments, and the abdomen and the ovipositor are likewise elongate. The antennae are situated far forwards near to the clypeus, the hind femora are usually swollen and spined beneath, and the hind wings are most frequently without basal cells. About 100 species have been described (Elliott, 1922) and they appear to be parasites of wood-boring insects.

FAM. MEGALYRIDAE.—The nineteen Australian species of the genus *Megalyra* are thought to be parasitic on wood-boring beetles. The single S. African species of *Dinapsis* has been put in a separate family. The position of the group in the Parasitica needs much more study.

Superfamily **Evanioidea**

The three families placed in this group agree in the abnormal attachment of the petiole, at a point just behind the scutellum, but are otherwise rather diverse. Crosskey (1951) deals with the British species and Kieffer (1912) has monographed the group.

Key to the families:

1. Fore wing with 2 *m-cu* cross-veins, 2 *r-m* present. Antennae inserted just above the clypeus. Hind wing with no anal lobe . . . . . AULACIDAE
–. Fore wing with 1 or no *m-cu* cross-vein, 2 *r-m* absent. Antennae inserted well above the clypeus 2

2. Gaster short, compressed, with a long abrupt petiole and a short, unexserted ovipositor. Propleuron short. Hind wing with an anal lobe . . . EVANIIDAE
–. Gaster long, gradually clavate, ovipositor exserted, often long. Propleuron forming a long 'neck'. Hind wing with no anal lobe . . . . GASTERUPTIIDAE

FAM. EVANIIDAE.—A few hundred species of this family are known from all the main geographical regions. All seem to be parasites of the oothecae of cockroaches, *Evania appendigaster* on *Periplaneta*, *Brachygaster minuta* on *Ectobius* and *Zeuxevania splendidula* (Genieys, 1924) on *Loboptera*. In some genera the wing-venation becomes almost completely lost.

FAM. AULACIDAE.—There are rather more than 100 species of this widespread but generally uncommon family. *Aulacus* attacks the larva of *Xiphydria* but other members of the family attack Coleoptera (Buprestidae, Cerambycidae).

FAM. GASTERUPTIIDAE.—The insects of this family are distinguished by a neck-like prolongation of the propleuron, swollen hind tibia, and long gaster, and sometimes by a long ovipositor. There are about 300 species found in all parts of the world. They seem to be parasites chiefly of solitary bees (Höppner, 1904), less often of Sphecoids or other wasps.

Superfamily **Cynipoidea**

Included in this superfamily are about 1,600 species of small, and often minute, insects which are usually black or darkly coloured. Biologically, they are of great interest as the various species are either gall-makers, inquilines or parasites, the first-mentioned exhibiting the phenomena of heterogony and agamogenesis. The eggs are provided with a usually elongate pedicel, the larvae are apodous and maggot-like, and there is no cocoon. In the great majority of the imagines the second gastral tergum is larger than the remainder and in many cases forms almost the whole of the dorsal surface of the gaster. The trochantellus is more or less indicated but, as Kieffer points out, it is often no more than the contracted base of the femur. Authorities differ with regard to the division of the group into families; four families are dealt with in the pages which follow. Kieffer (1914) has written an admirable short account, which is accompanied by a full bibliography; Cameron's monograph (1882–92) refers to the British species. For a catalogue of the world's species vide Dalla Torre & Kieffer (1910) and the recent revisional treatise of Weld (1952) who gives a key to the families and genera.

Key to families:

1. Largest segment of gaster the 4th, 5th, or 6th, with 2 or more small tergal plates preceding it. Larger species with cell R_1 closed in the fore wing . . 2
–. Largest segment of gaster the 2nd or 3rd or these fused, with at most 1 tergal plate preceding it. Usually smaller species 3

2. Fore wing with cell R_1 at least 9 times as long as broad. Hind basitarsus twice as long as the remaining segments together . . . . . IBALIIDAE
–. Fore wing with cell R_1 much shorter. Hind basitarsus not twice as long as the remaining segments . . . . . LIOPTERIDAE

3. Second tergite not forming half the gaster . . . . . FIGITIDAE
–. 2nd or 2nd and 3rd tergites the longest and usually forming at least one-half the gaster . . . . . CYNIPIDAE

FAM. CYNIPIDAE.—The greater number of species belong to the subfamily Cynipinae, all of which produce galls for the purpose of providing shelter and nutriment for their offspring or are inquilines in such galls. Their larvae are consequently internal feeders and are maggot-like in form, with well-sclerotized dentate mandibles. The head is small and is followed by twelve body segments, and there are nine pairs of spiracles. The antennae and both pairs of palpi are vestigial. Pupation takes place within the larval cell and a cocoon is wanting. The forms of galls produced by these insects are almost endless and all parts of plants may be affected, from the roots to the flowers. In every case the female insect lays an egg or eggs in the tissues of the growing plant, in the interior of which the subsequent development takes place. As a rule this mode of life is accompanied by the production of a gall. Many theories have been advanced to account for the phenomena of gall-formation, but the problem appears to be still far from being solved, largely on account of difficulties attending the experimental side of the subject. A full discussion of the various views which are or have been held is given in the works of Kieffer. The irritation of the tissues produced by the insertion of the ovipositor is not the initial cause. There also appears to be no evidence that the fluid injected by the female during oviposition is anything more than of the nature of a lubricant. The mere presence of the Cynipid egg in the tissues is not in itself sufficient to produce the gall as, ordinarily, the latter does not commence to develop until the larva has hatched; many months may elapse between the date of oviposition and that of eclosion. All that can be said is that the galls are produced as the result of reactions of the cambium and other meristematic tissues of the plant in

response to the stimulus induced by the presence of the living larva. It is probable also that the latter exudes a secretion which exercises an influence upon the growth of the cells of the plant (Triggerson, 1914). The formation and structure of the galls have been studied by Beyerinck (1882), Cook (1902–04), Cosens (1912), Hough (1953) and others. Viewed in section, a gall is usually seen to be composed of the following layers of tissue passing from without inwards (Fig. 524). The outermost coat is the epidermis and beneath the latter is an extensive development of parenchymatous tissue. The third layer is protective in function and is usually of a hard consistency but is sometimes wanting, while the innermost layer is nutritive and surrounds the cell containing the larva. Cook concludes that the morphology of a gall is dependent, as a rule, upon the insect which produces it rather than upon the plant upon which it is produced. Galls formed by the same genus of insects exhibit great similarity even though produced on widely different plants. Furthermore, those produced on a particular genus of plants by different insects are very dissimilar. In addition to the species which actually forms the gall, the latter frequently supports a definite biological association of other insects. A large number are inquilines, which comprise not only other Cynipidae but also larvae of Diptera, Coleoptera and Lepidoptera. Furthermore, the larvae and pupae of the true gall-maker, and of the inquilines, are very subject to the attacks of hymenopterous parasites, more particularly Chalcids. Kinsey (1920) estimates that 86 per cent. of the known species of gall-wasps produce galls on *Quercus* and are confined to that genus. Another 7 per cent. are restricted to species of *Rosa* and the remaining 7 per cent. are found on plants belonging to 35 genera of Angiosperms, more especially the Compositae. The reason for this very marked selection of a single genus of plants is hard to understand, particularly as oaks have a limited distribution in the present age. It is true that the galls on this genus are more conspicuous than on other plants where they are more liable to become overlooked. According to Kinsey the tribe Aylacini is, in many respects, the most primitive of the gall-wasps. Its members are not confined to a particular plant family but select those belonging to many genera. The various species of *Aulacidea* either induce extremely simple gall formation or live in stems, producing no gall at all. They have not acquired agamic reproduction, the sexes are produced in about equal numbers, and the alternation of generations so characteristic of the higher Cynipinae is absent. Almost every transition may be observed from the simple condition prevalent in *Aulacidea* to the many types of highly complex galls, and the alternation of morphologically and physiologically different generations found in many other genera. The most highly evolved galls are to be looked upon as almost entirely separate organisms, which are only connected to the host plant by means of a narrow neck of tissue. In some cases the galls develop in size and form new tissue after separation from the parent plant. The galls of two successive generations, produced on different parts of the same plant, often present entirely different forms; and the insects of the two generations are frequently so divergent in characters that they have often been allocated to separate genera until their relationships have been detected. Heterogony among Cynipidae is of an exceptionally remarkable nature. In many species males have never been seen at all, out of many thousands of the insects which have been reared, and there appears to be little doubt of their non-existence. In these very highly specialized cases the successive generations are all similar and agamic and a secondary simplification of the life-cycle results. The majority of the Cynipinae have only the alternate generations alike: each agamic generation is followed by a bisexual generation which, in its turn, produces the agamic one. The latter is the overwintering stage while the bisexual generation is produced during summer. A few of the commoner species, which are prevalent in Britain, may be selected as illustrating the principal biological phenomena already referred to. *Neuroterus lenticularis* is a very abundant gall-wasp in England. The galls from which the spring (agamic) generation emerges are lenticular growths

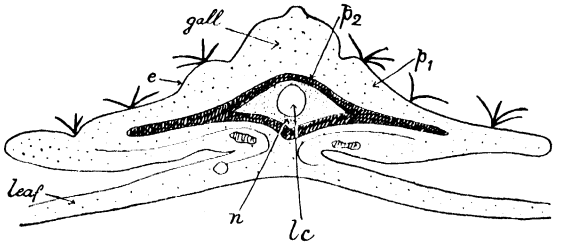


FIG. 524.—Diagrammatic section of gall of *Neuroterus lenticularis*, according to Fockeu

e, epidermis; p_1, parenchyma; p_2, protective layer; *n*, nutritive layer; *lc*, larval cell.

found on the lower surface of oak leaves in October. The insects remain in the galls all the winter, and appear as adults early in April. They consist entirely of parthenogenetic females which deposit their eggs deep down among the catkins and young leaves. The resulting galls occur in May and June and are quite different from those preceding, being spherical and sappy in character. The summer generation which emerges from them was originally referred to a different species, i.e. *Spathegaster baccarum*. Both males and females are produced but the latter largely predominate in numbers. After copulation the eggs are laid at the sides of the veins in the tissues of the young leaves, and the resulting galls are of the lenticular kind found in October. The most conspicuous difference in the females of the two generations is seen in the ovipositor, which is much larger in the agamic than in the summer individuals. *Biorrhiza pallida* is another very characteristic oak species. In the bisexual generation the males are winged, and the females are either apterous or have vestigial wings. This generation emerges from the 'oak apple' galls and the eggs are laid in the roots of that tree. In this situation other galls are produced from which, in spring, the agamic generation (known as *B. aptera*) is produced. The individuals of this brood

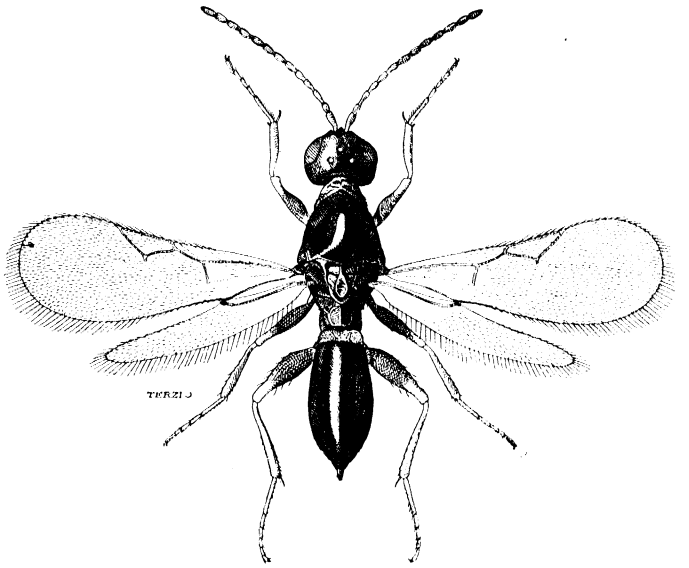


FIG. 525.—*Eucoila cucera*, female. Britain

consist exclusively of apterous females which migrate up the tree and produce the 'oak apple' galls in due course. The genus *Rhodites* is confined to the Rosaceae—*Rosa* and *Rubus* being most usually selected. The familiar and striking bedeguar or 'pincushion' galls are produced on the former genus by *Rhodites rosae*. These galls consist of a mass of moss-like filaments surrounding a cluster of hard cells containing the *Rhodites* larvae. There is no alternation of generations in this species, males are much less frequent than females, and the eggs are known to be capable of parthenogenetic development. The hard spherical 'marble' galls of what is usually known as *Adleria kollari* on oak produce the agamic generation of that species. Marsden-Jones (1953) has now proved what Beyerinck suspected that the bisexual generation is *Andricus circulans*, bred from galls on *Quercus cerris*. The species was introduced into Devonshire about 1830 and soon became abundant: it should now be known as *Andricus kollari*.

The genus *Synergus* and its allies are inquilines though they are easily mistaken for true gall-makers to which they frequently bear an extremely close resemblance. They mostly lay their eggs in cynipid galls found on oak.

The subfamily Charipinae contains species which are mainly hyperparasites of aphides through *Aphidius* or other parasites: less frequently they have similar relations with coccids. An account of the biology of *Charips* is given by Haviland (1921).

The subfamily Eucoilinae includes insects which are parasites of Diptera and the primary larvae are eucoiliform. In *Kleidotoma* the 2nd instar larva is polypod with 10 pairs of trunk limbs (James, 1928). *Eucoila eucera* is an important parasite of *Oscinella rit* and *Cothonaspis rapae* attacks *Erioischia brassicae.*

FAM. FIGITIDAE.—*Aspicera* and its allies are parasites of Syrphidae, while the Anacharitinae have been bred from the Neuroptera. The Figitinae are parasites of Diptera. The primary larva of *Figites* is eucoiliform and is followed by a polypod instar with 10 pairs of trunk limbs (James, 1928).

FAM. IBALIIDAE.—The members of this small family are among the largest Cynipoidea. The genus *Ibalia* is widely distributed in Europe and N. America and its members are endoparasites of Siricidae. The single British species *I. leucospoides* has been studied in great detail by Chrystal (1930). The egg is laid in the *Sirex* larva and the 1st-instar larva is of the polypod type with 12 pairs of trunk limbs: the whole larval period appears to last three years.

FAM. LIOPTERIDAE.—This family includes a few, mostly rather large insects of S. America, Africa and the far East (Hedicke & Kerrich, 1940); their habits are not known.

Superfamily **Chalcidoidea** (Fig. 526)

The superfamily is probably the largest in the order as regards number of species and it also includes some of the smallest members of the Insecta.

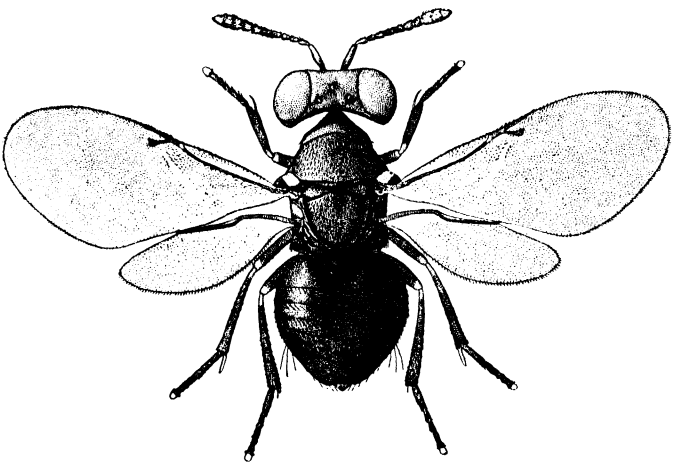


FIG. 526.—A typical Chalcid, *Blastothrix sericea,* female: magnified

The bulk of its species are either parasites or hyperparasites of other insects, and are of even greater economic importance than those of the Ichneumonoidea as a natural means of control. Non-parasitic vegetable-feeding forms are comprised in the families Agaontidae, Torymidae, Perilampidae and Eurytomidae: in the majority of cases they infest seeds but certain members of the last two families are gall-producers. The parasitic species, in a relatively small number of instances, are indirectly injurious from the fact that they destroy beneficial insects such as *Laccifer lacca,* or are hyperparasites of other insects which, in their turn, are destroyers of harmful species. The orders most commonly parasitized are the Lepidoptera, Hemiptera-Homoptera and Diptera. Lepidoptera are more frequently selected than any other major group, enormous numbers of their eggs and larvae succumbing to infestation by various Chalcids: on the other hand their pupae are rarely affected. Certain Pteromalidae, however, prefer to oviposit in larvae just about to pupate or in newly transformed pupae. The Coccoidea are the

most universally attacked of any group of insects, and some species (*Eulecanium coryli*, etc.) are so freely infested that it is often rare to find an immune individual. In temperate regions Chalcids seem to pass through from one to three generations in the year—a higher number is apparently rare. One of the shortest life-cycles occurs in *Euplectrus comstockii*, which develops from the egg to the adult in seven days (Schwarz, 1881), and an equally rapid development is found in *Trichogramma minutum* (= *pretiosa*) which has been reared from the eggs of *Aletia xylina* (Hubbard). Chalcid larvae are composed, as a rule, of a reduced head and thirteen trunk segments. In the ectophagous forms open spiracles are evident at the time of hatching: thus in *Aphytis mytilaspidis* the full number of eight pairs are present at this stage. In other cases, as in *Torymus propinquus*, a reduced number of spiracles is present at the time of eclosion from the egg, additional pairs being acquired subsequently. Among endophagous species the younger larvae are usually apneustic, open spiracles developing later when the destruction of their hosts reaches an advanced stage. In *Blastothrix* and other genera the newly hatched larva is exceptional in being metapneustic (Fig. 527). This condition is an adaptation which allows of the respiration of atmospheric air along the pedicel of the egg, which protrudes externally through the body-wall of the host and functions as a kind of respiratory tube. In *Blastophaga psenes* the tracheal system is apneustic throughout life (Grandi). Hypermetamorphosis is common in the superfamily, and at least five types of primary larvae are known, but probably others await discovery. In the later instars all these types assume an ovoid maggot-like form and, in the majority of species, the latter kind of larva is retained throughout life. Chalcid larvae do not construct any cocoons (except in *Euplectrus*, see p. 713), and pupation usually occurs either within or in close proximity to the remains of their hosts.

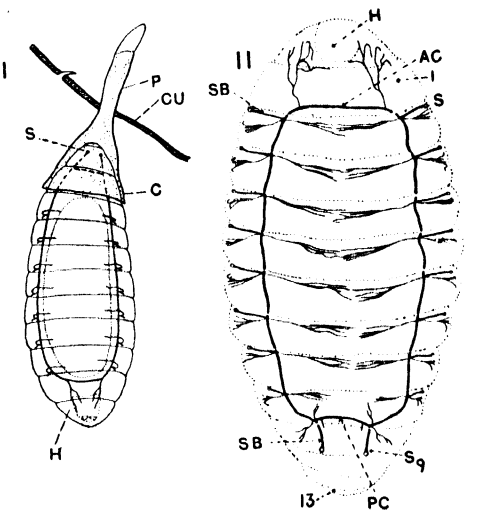


FIG. 527.—*Blastothrix sericea*. I, Newly-hatched larva respiring by means of the pedicel (*P*) of the egg

C, remains of chorion; *CU*, body-wall of host; *H*, head; *S*, spiracles.

II, Larva in last instar

AC, *PC*, anterior and posterior tracheal commissures; 1, 13, 1st and 13th trunk segments. S_1, S_9, 1st and 9th spiracles; *SB*, spiracular tracheae.

For the classification of the Chalcidoidea (now much in need of revision) see Ashmead (1904): a general account of the biology of the group is given by Clausen (1940). Life-history studies of individual species are numerous; in Europe a series of papers has been contributed by Silvestri (*Boll. Lab. zool. Portici*) and a large number by other authors will be found in various American journals and bulletins. Some of the more important of these papers are referred to under the families concerned. A monograph on the British species is greatly to be desired and over 1,400 species have been listed.

Key to the families:

1. Hind wing linear, base forming a stalk. Ovipositor issuing almost at tip of abdomen. Antennae with short scape and no ring-segments. Wings with long fringes MYMARIDAE
–. Not as above 2

2. Axillae advanced strongly in front of anterior margin of scutellum and usually in front of tegulae. Tarsi usually with 3 or 4 segments 3
–. Axillae not or little advanced in front of anterior margin of scutellum. Tarsi with 5 segments (rarely 4 in a few wingless males) 5

3. Hind coxa much enlarged, hind femur compressed. Tarsi 4-segmented. Marginal wing-vein long. . . . . ELASMIDAE
–. Hind coxa not enlarged 4

4. Tarsi with 4 or (Aphelininae and some females of other groups) 5 segments. Fore wing narrower, with pubescence not in rows or lines . . EULOPHIDAE
–. Tarsi with 3 segments. Fore wing broad, pubescence in rows or lines, marginal and stigmal veins forming a single curve . . . TRICHOGRAMMATIDAE

5. Head of female long, oblong, with a deep longitudinal groove above; front and hind legs very stout, the middle ones much more slender. Males nearly always wingless, with stout 3–9-segmented antennae. Fig-insects . AGAONTIDAE
–. Not as above 6

6. Mesepisternum large and almost completely covering the mesepimeron. Mid tibial spur usually enlarged 7
–. Mesepisternum not enlarged, normally of about the same width as the mesepimeron. Mid tibial spur rarely larger than the bigger hind tibial one . 10

7. Mesoscutum with notauli present and usually long. Marginal vein in fore wing usually long 8
–. Mesoscutum more or less convex, notauli not more than feebly indicated . 9

8. Mesoscutum in females more or less strong depressed, in males more or less convex with notauli incomplete. . . . . EUPELMIDAE
–. Mesoscutum convex in both sexes, with fine but complete notauli TANAOSTIGMATIDAE

9. Marginal vein in fore wing at least shorter than Sc + R, often punctiform. Scutellum longer. Mid tibia without long bristles . . . . ENCYRTIDAE
–. Marginal vein in fore wing long, as long as Sc + R. Scutellum transversely linear. Mid tibia with long bristles . . . . . THYSANIDAE

10. Mandibles sickle-shaped, usually with 1 or 2 inner teeth. Thorax very convex, scutellum usually produced backwards. Gaster compressed, usually with a long petiole . . . . . EUCHARITIDAE
—. Mandibles stout, with 3 or 4 teeth at apex. Thorax rarely so formed . . 11

11. Hind coxae large, 5 or 6 times larger than the front ones 12
—. Hind coxae not conspicuously larger than the front ones 17

12. Hind femur simple or with 1 tooth beneath 13
—. Hind femur with a row of teeth beneath 15

13. Insect very elongate, including the legs and ovipositor, prothorax forming a long narrow neck . . . . . LEPTOFOENIDAE
—. Without all these characters 14

14. Notauli present. Gaster not coarsely punctured, ovipositor usually long and exserted . . . . . TORYMIDAE
—. Notauli very feeble or absent. Gaster usually with rows of coarse punctures, ovipositor short . . . . . ORMYRIDAE

15. Hind femur with 4–8 long teeth. Ovipositor long, straight PODAGRIONIDAE
—. Hind femur with rows of short teeth 16

16. Fore wing longitudinally folded. Prepectal plate distinct, adjacent to the tegulae. Ovipositor long, bent forwards over abdomen . . . LEUCOSPIDIDAE
—. Fore wing not longitudinally folded. Prepectus not developed. Ovipositor straight, nearly always very short . . . . . CHALCIDIDAE

17. Pronotum narrower, usually much narrowed in front or transversely linear, rarely as wide as the mesoscutum which is usually reticulate . . PTEROMALIDAE
—. Pronotum wide, quadrate, scarcely narrower than the mesoscutum which is often coarsely punctured 18

18. Gaster rounded or ovate, more or less compressed, 2nd tergite never very large, female last sternite usually produced. Colours black or yellowish EURYTOMIDAE
—. Gaster small, subtriangular, 2nd or fused 2nd and 3rd tergites covering most of its surface. Thorax large but short. Colours more or less metallic PERILAMPIDAE

FAM. AGAONTIDAE (Fig-insects).—A family which includes some of the most remarkable of all Chalcids both as regards their structure and biology. Sexual dimorphism has reached a very highly specialized condition, the males being wingless and greatly modified in other respects, bearing no resemblance to the members of the opposite sex. The species are caprifiers that live within the receptacles and pollinate, or fructify, the flowers of various species of *Ficus*. The number of known species and varieties of fig is said to reach 500 and, in certain of these, the caprification phenomena are known to vary widely, and many of the insects involved are apparently confined to certain definite species of figs. The investigation of the symbiotic relationship between plant and insect offers, therefore, an extremely wide field for investigation. The best known species is *Blastophaga psenes*, which exists in a state of symbiosis within the fruit of *Ficus carica*. It is well known that, in the Smyrna variety of fig, the receptacles contain only female flowers, and pollination is brought about by the agency of this Chalcid. On the other hand, the caprifigs, or varieties which contain male flowers, are the natural hosts of the *Blastophaga*. Caprification, or the process of hanging caprifigs in the Smyrna trees, is an old custom based upon the belief that the figs would not mature unless it were carried out. Much discussion has arisen with reference to whether caprification is essential or not. In California it is agreed that the culture of the Smyrna fig necessitates the simultaneous cultivation of caprifying varieties in which the *Blastophaga* lives. If the latter insect fails to pollinate the Smyrna figs, the fruit falls without maturing (Condit, 1947). The eggs of this Chalcid are laid in the ovaries of the caprifig and give rise to galls therein. The male imago emerges first and, on finding a gall containing a female, commences to gnaw a hole through the wall of the ovary and fertilizes the female while the latter is still *in situ* (Fig. 528). The female leaves the receptacle through the opening at its apex and, laden with adherent pollen, flies to a neighbouring fruit. If the latter be in the right condition she seeks the opening and gains admission into the interior of the receptacle, where she commences oviposition. Should the caprifig, from which she has emerged, be suspended in a tree of the Smyrna variety she enters a fruit of the latter, but subsequently discovers that she has selected a wrong host, as the flowers are of such a shape that they do not allow of oviposition within them. After wandering about for a while, she usually crawls out of the receptacle and incidentally pollinates the flowers. The males mostly die without ever leaving the receptacles in which their development took place.

According to Baker (1913) the active caprifier and normal inhabitant of the receptacles of *Ficus nota* in the Philippines is *Blastophaga nota*, and related to the latter species is a complex Chalcid association. *Agaonella larvalis* and *Sycophaga* are probably inquilines, and *Sycoryctes philippensis*, along with other Chalcids, parasitizes the *Blastophaga*. In India Cunningham (1889) states that the complete development of *Ficus roxburghii* is dependent upon the access of the fig-insects to the interior of the receptacles and, should their entry fail to occur, both male and female flowers abort. Grandi (1920) has investigated the structure and biology of *Blastophaga psenes* and gives a full bibliography. The taxonomic writings of the latter author (1916 et seq.) also deal with the external morphology of many genera. Papers by Mayr and Saunders should also be consulted.

FAM. TORYMIDAE.—A very large family whose affinities lie more closely with the Agaontidae than any other group. Members of the subfamily Idarninae are found associated with fig-insects either as parasites or inquilines. Their males are often apterous, but the abdomen is short and not tubularly lengthened or broadened at the apex as in the Agaontidae. The great majority of Torymidae are parasites of gallicolous insects, but a certain number have been reared from the nests of bees and wasps. Species of *Megastigmus* have been bred from Hymenopterous and Dipterous gall-makers while others are phytophagous, attacking the seeds of Coniferae, *Rosa*, etc. *Syntomaspis druparum* is the apple-seed Chalcid of Europe and N. America.

Monodontomerus parasitizes many insects, *M. obsoletus* having been bred from both Lepidoptera and Hymenoptera. *Torymus* (*Callimome*) chiefly attacks gall-making Diptera and Hymenoptera (Hoffmeyer, 1930–31). The **Ormyridae** have often been united with the Torymidae but are mostly very different looking insects. They are usually parasites of gall-making insects.

FAM. CHALCIDIDAE.—This family is especially well represented in S. America and is less common in cool climates. Nine species are recorded as British. Many of its members are primary or secondary parasites of Lepidopterous larvae or pupae, or of Dipterous puparia. *Chalcis* attacks the eggs of *Stratiomyia*. The **Leucospididae** are now usually regarded as a separate family of parasites of Aculeata. *Leucospis gigas* has been observed by Fabre (1886): it undergoes hypermetamorphosis and is an ectoparasite of *Chalicodoma muraria*. The **Podagrionidae** have been often placed in the Torymidae but seem to be distinct and in some ways nearer to the Chalcididae. The species are parasites of the eggs of Mantids.

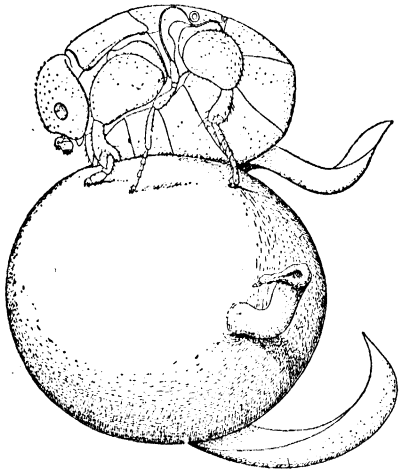


FIG. 528.—Male *Blastophaga psenes* fertilizing the female, the latter within a galled flower of the fig

After Grandi, *Boll. Lab. zool. Portici*, 14, 1929.

FAM. EURYTOMIDAE.—Probably no other family of Chalcids exhibits so wide a diversity of habits as is met with among the members of this group. *Harmolita* (*Isosoma*) produces galls on the stems of wheat, rye, barley and various grasses (Phillips, 1920). *H. grandis* exhibits alternation of generations: the apterous form, *minutum*, occurs in spring, laying its eggs at the base of the young wheat plant, and the larva destroys the tiller affected, or may kill the entire plant. The alate form, *grandis*, is the summer generation which lays its eggs slightly above the nodes. Males are rare and have only been found in the case of the spring brood: *H. orchidearum* is exceptional in that it produces galls on the stems and leaves of certain orchids (*Cattleya*). *Bruchophagus funebris* is likewise phytophagous and passes its developmental stages in the seeds of clover and alfalfa. Species of *Eurytoma* and other genera attack the seeds of plum, grape, Ampelopsis, etc. Other members of the family live in the nests of bees and wasps or are parasites of gall-forming Diptera and Hymenoptera; a few are egg-parasites of Orthoptera, while several species of *Eurytoma* attack a wide selection of hosts.

FAM. PERILAMPIDAE.—A small family distinguishable from the preceding by the large thorax and small triangular abdomen. The biology of *Perilampus hyalinus*, a hyperparasite of the larva of *Hyphantria* and other hosts, has been studied by Smith (1912; 1917). The newly hatched larva is an active planidium which bores its way into the *Hyphantria*, in whose body-cavity it remains until it meets with either the larva of the Tachinid *Varichaeta* or of the Ichneumon *Limnerium*, which are primary parasites. Upon discovering one or other of the latter hosts it becomes endoparasitic: subsequently it makes its way out, undergoes hypermetamorphosis into a white maggot-like larva and becomes an ectoparasite of the same host.

FAM. EUCHARITIDAE.—Included herewith are certain remarkable metallic blue or green Chalcids characterized by the configuration of the scutellum which is frequently produced backwards in the form of powerful spines. So far as known they attack ants, usually as ectoparasites, and are mainly found in the tropics. *Orasema* attacks members of the genera *Pheidole* and *Solenopsis*. According to Wheeler (1907) it parasitizes the prepupa just after the last exuviae have been stripped off by the worker ants. Its newly-hatched larva is a planidium and is found attached near to the head of the host. As a result of the parasitism the hosts undergo degeneration and fail to become imagines. For the biology of *Schizaspidia* see Clausen (1923).

FAM. PTEROMALIDAE.—This family is the largest among Chalcids and its members, like those of the Encyrtidae, affect almost all orders of insects either as parasites or hyperparasites. *Pteromalus puparum* is common and widely distributed: it especially parasitizes *Pieris rapae* and *brassicae* and an account of its biology is given by Martelli (1907). *P. deplanatus* has been recorded as occurring in great

swarms in buildings but there is no satisfactory explanation of the habit (Scott, 1919). *Nasonia brevicornis* (*Mormoniella vitripennis*) is a common pupal parasite of *Musca domestica*, *Calliphora* and other Calyptratae (Altson, 1920). *Spalangia muscidarum* is likewise a pupal parasite of *Musca*, *Stomoxys* and *Haematobia*, its larva undergoing hypermetamorphosis (Richardson, 1913). *Asaphes* and *Pachyneuron* parasitize aphides, etc., and the Eunotinae mainly affect coccids, *Scutellista cyanea* being an important factor in the control of the Black Scale (*Saissetia oleae*) in California and of *Ceroplastes rusci* in Italy.

The Miscogasterinae are not now treated as a distinct family, since they intergrade with other Pteromalids. Many of the species are Dipterous parasites. The Cleonyminae have also been reduced to a subfamily. The species are often relatively large and attack wood-boring beetles. The **Leptofoenidae** are perhaps no more than specialized members of the last subfamily; they are some of the most extraordinary of all Chalcids in appearance and are found on dead wood in tropical America and Australia.

FAM. ENCYRTIDAE.—The Chalcids comprised in this extensive family live as parasites of the ova, larvae or pupae of various insects. Although the Hemiptera-Homoptera and Lepidoptera are most frequently selected hardly a single order of insects is immune from their attacks. Certain genera are definitely restricted with reference to their selection of hosts. Thus *Aphycus* is an ecto- or endoparasite of Coccoidea, particularly of *Eulecanium*; *Blastothrix* almost exclusively parasitizes *Eulecanium* and *Pulvinaria* while *Ageniaspis* is mainly confined to the Lepidopterous genera *Lithocolletis* and *Yponomeuta*. The family is of more than ordinary interest and importance from the fact that certain species of *Ageniaspis*, *Litomastix* and *Copidosoma*, which parasitize Lepidoptera, are known to exhibit polyembryony. They deposit their eggs in those of the hosts but the larvae of the latter emerge in the normal manner and contain the developing parasites in their body-cavity where embryonic fission takes place (vide p. 192). Several members of the family have been the subject of detailed biological studies and reference should be made to papers on *Ageniaspis* by Bugnion (1891) and Marchal (1904), on *Encyrtus* (*Comys*) by Embleton (1904), on *Aphycus* and *Blastothrix* by Imms (1918), on *Copidosoma* by Leiby (1922) and Doutt (1947) and *Litomastix* by Silvestri (1906). The work of Mercet (1921) on the Spanish species is well illustrated and is a valuable taxonomic monograph.

Several smaller groups have more recently been segregated from the Encyrtidae and are regarded as separate families. The **Eupelmidae** includes a few genera with a very wide host-range, having been bred from the eggs of Lepidoptera (*Anastatus*), from Cecidomyidae, Coccoidea and various Coleoptera (*Eupelmus*), and from Arachnids (*Arachnophaga*). The **Thysanidae** includes the genus *Thysanus* (*Signiphora*), very curious small insects with bristly tibiae which are parasites of Coccoidea, or more rarely Diptera. The **Tanaostigmatidae** include a few Encyrtid-like species, some of which attack Coleoptera. *Eutrichosoma*, another beetle parasite, has also been made the type of a family.

FAM. EULOPHIDAE.—A very large family consisting for the most part of very small species. The Aphelininae are important parasites of the Diaspine coccids and of aphids, their larvae being either ectophagous or endophagous. *Aphytis mytilaspidis* is a common ectoparasite of the Mussel Scale and its structure and biology have been fully studied (Imms, 1916). *Prospaltella berlesei* has been introduced into Italy for the purpose of controlling *Diaspis pentagona* and there is now a voluminous literature on the subject. The species of this subfamily exhibit extraordinary specializations in parasitic behaviour (summary of Flanders' work in Clausen, 1940). The female larva is the direct and almost always internal parasite of a scale insect. The male larva is an obligatory hyperparasite, either of other scale-parasites or frequently on its own species. The male larva is most often an external feeder, though sometimes internal. Fertilized and unfertilized females behave differently, the latter showing interest only in scales which are already parasitized. The Tetrastichini affect nearly all orders of insects either as primary or secondary parasites: the majority parasitize gallicolous Diptera, Hymenoptera and Coleoptera. *Tetrastichus asparagi* is an egg-parasite of *Crioceris asparagi* and, according to Johnston (1915), from 1 to 10 larvae occur in a single egg. The beetle larvae emerge from the infested eggs but fail to pupate, although a pupal cell is constructed, and the adult parasites issue from the latter. *Melittobia* is a common ectoparasite of the pupae of *Bombus*, *Osmia* and other Aculeata (Balfour-Browne, 1922) as well as of certain Diptera, more especially *Calliphora*. Members of the subfamily Eulophinae are principally primary or secondary parasites of leaf-mining Lepidoptera. *Euplectrus* is exceptional in that a cocoon is

present. Thomsen (1927) has shown that it is constructed from the products of the Malpighian tubes which are modified in the hind gut and discharged through the anus.

FAM. TRICHOGRAMMATIDAE.—The 3-segmented tarsi separate this family from all others and, according to Ashmead, it is related to the Eulophidae, connecting the latter with the Mymaridae. Over 100 species are known, all are egg-parasites, and they include some of the most minute examples of the Insecta. *Trichogramma* usually parasitizes Lepidoptera and Howard mentions that as many as 20 individuals will develop within a single egg. In Europe *T. evanescens* is a parasite of *Donacia* and certain Odonata (Gatenby, 1917) and of many Lepidoptera. *T. minutum*, in America, has been extensively used in connexion with biological control. *Prestwichia aquatica* has been reared from the eggs of *Notonecta*, *Ranatra*, *Dytiscus* and *Hygrobia*, while *Hydrophylax aquivolans* parasitizes those of *Ischnura*. The last-named Chalcid swims beneath the water by the aid of its wings. *Poropoea stollwerckii* affects the eggs of *Attelabus* and, according to Silvestri, it passes through five larval forms (see also Bakkendorf, 1934).

FAM. ELASMIDAE.—A few dozen small black species with enlarged, compressed hind legs. The group has a wide distribution and parasitizes either Lepidoptera or secondarily their parasites.

FAM. MYMARIDAE (Fairy Flies).—The species of this family are all exceedingly minute and are exclusively egg-parasites. They are mostly black or yellowish and devoid of metallic colours. Some authorities have placed them among the Proctotrupoidea but Ashmead holds their position to be in the present superfamily. One of the most remarkable genera is *Polynema* which parasitizes Hemiptera: *P. natans* utilizes *Notonecta* as its host and both sexes swim readily beneath the water by means of their wings. *Alaptus* includes probably the smallest of all insects, *A. magnanimus* measuring only 0·21 mm. in length. *Anaphes conotracheli* has been reared from the eggs of weevils and *Litus krygeri* from those of *Ocypus olens*. One group in which the gaster has a long petiole has recently been placed in a separate family, the **Mymarommidae** (Debauche, 1948).

Superfamily **Proctotrupoidea (Serphoidea)**

The members of this superfamily are slender insects mostly of small size and all are parasites. Many attack the eggs of other insects, other species are endoparasites of larvae or pupae, some are hyperparasites and a small number are inquilines. The majority of species form a cocoon of a silky or parchment-like nature but in the aphid-infesting genera the pupa is protected by the body of the host. The wings exhibit the greatest diversity of venation and in many forms they are almost veinless, while apterous species are frequent. By some authorities these insects are considered to be closely allied to the Chalcids but according to Ashmead they are in every respect more intimately related to the Vespoidea. The whole group is in great need of study at all levels. The British species have scarcely been investigated, but a standard work is that by Kieffer (1914–26).

The following table of families though primarily intended for winged forms will also serve for the apterous species if the venational characters are ignored:

1. Sides of gaster acute or distinctly margined 2
–. Sides of gaster rounded. 3

2. Antennae with 10 or, rarely, fewer segments. Fore wing without marginal or stigmal veins, usually also without submarginal vein . . PLATYGASTERIDAE
–. Antennae with 11 or 12 segments, or with 7–8 and an unsegmented club; if with 10 the stigmal vein is present . . . . . SCELIONIDAE

3. Antennae inserted far above the clypeus on a frontal shelf or strong prominence. Antennae with 11–15 segments . . . . . DIAPRIIDAE
–. Antennae inserted much lower down and not on a shelf or prominence. . 4

4. Mandibles short with 3 large, outwardly-directed teeth, not meeting when closed. Gaster with 2 (♀) or 4 (♂) visible segments, ovipositor long and directed forwards under the gaster . . . . . VANHORNIIDAE
–. Mandibles normal 5

5. Propodeum extending back far behind the hind coxae, gaster long and slender. Hind wing with at least 1 closed cell . . . . . MONOMACHIDAE
–. Propodeum not extending back beyond the hind coxae. Hind wing without a closed cell 6

6. Antennae with 14 or more segments 7
–. Antennae with 13 or fewer segments 9

7. Hind basitarsus much shorter than 2nd segment. 1st segment of gaster as long as head and thorax together, gaster in ♀ very long and narrow, with segments of equal length, in ♂ clavate. Large insects . . . . PELECINIDAE
–. Hind basitarsus longer than second segment. Petiole much shorter . . 8

8. Antennae with 14 segments. Abdomen strongly compressed . ROPRONIIDAE
–. Antennae with 15 segments. Abdomen not compressed . . HELORIDAE

9. Antennae inserted at middle of face, with 13 segments. Fore wing with a closed, usually very small radial cell . . . . . PROCTOTRUPIDAE
–. Antennae inserted very low down, at clypeal margin, with 9–11 segments. Radial cell in fore wing not closed . . . . . CERAPHRONIDAE

The **Pelecinidae** occur in the Americas and though their structure is in many ways specialized, they are closely allied to the next family, especially in the structure of the anterior thoracic spiracle which in both groups lies entirely in the prothorax. *Pelecinus polyturator*, which is rather common in temperate N. America, is 50–60 mm. long in the female and has been bred from the larvae of *Lachnosterna* (Scarabaeidae). The **Proctotrupidae** may be recognized by the sheath (apparently composed of the pygostyles) which terminates the female abdomen; in the male, a pair of spine-like processes, the parameres, are often visible. Their larvae appear to be mainly parasitic upon those of Coleoptera (cf. Eastham, 1929). The **Monomachidae** are found in S. America and Australia. Their structure is in many ways aberrent and their early stages are not known. The **Vanhorniidae** includes a single N. American species bred from the larva of an Eucnemid (Col.). The **Roproniidae** includes a few N. American species of which the habits are not known. The **Heloridae** are a small but widely distributed family known to parasitize the Chrysopidae (Clancy, 1946). The **Diapriidae** are primarily Dipterous parasites; *Diapria conica* attacks *Eristalis tenax* (Sanders, 1911) and *Cinetus* (= *Belyta*) *fulvus* has been bred from *Arachnocampa luminosa*. The **Ceraphronidae** attack insects of several orders but are probably most generally secondary parasites of aphids or coccids through various Braconid and Chalcid primaries. The biology of *Lygocerus* has been followed by Haviland (1920), the species observed being ectoparasites of the larvae and pupae of *Aphidius* which lives as an internal parasite of various aphides. There appear to be four larval instars and the first-stage larva is ovoid, with a reduced head and no tail-like appendage. Only two pairs of spiracles are present and these are placed between the 1st and 2nd segments and on the 4th segment respectively: at a later stage seven pairs of spiracles are present. The **Scelionidae** are very numerous and widely distributed and are all parasites of eggs, most often of Lepidoptera, Hemiptera or Orthoptera (s.l.), occasionally of spiders. The biology of *Telenomus* has been studied by Balduf (1926), Costa Lima (1928) and Jones (1937), and that of *Eumicrosoma* by McColloch & Yuasa (1914–15). Species of the former genus lay in the eggs of Lepidoptera or Heteroptera, of the latter in those of *Blissus leucopterus*. In *Mantibaria* (= *Rielia*) *manticida*, an exceptionally advanced type of parasitism is presented (Chopard, 1922; Hervé, 1945). Its development takes place in the eggs of *Mantis religiosa* and the adult parasites make their way to the imagines of the host upon whose bodies they settle down. In this situation they cast off their wings and lead an ectoparasitic life. Where the mantis is a female, and has commenced oviposition, the *Mantibaria* migrates to the genital region in order to lay its eggs in the viscid mass of the ootheca while the latter is being formed. Parasites which settle upon male mantids are short-lived and perish along with their hosts. Examples of less obligatory phoresy are recorded in other Scelionids.

The **Platygasteridae** (Fig. 529) form the largest family of the Proctotrupoidea

and its species mainly parasitize Cecidomyidae (Marchal, 1906). Their eggs are usually laid within those of their host, but the development of the latter is not arrested since the larval parasite does not develop until after the eclosion of the larval Cecidomyid. Such species as *Platygaster herrickii* exhibit polyembryony (Hill & Emery, 1937). The localization of the parasitic larvae in the host is variable. Thus,

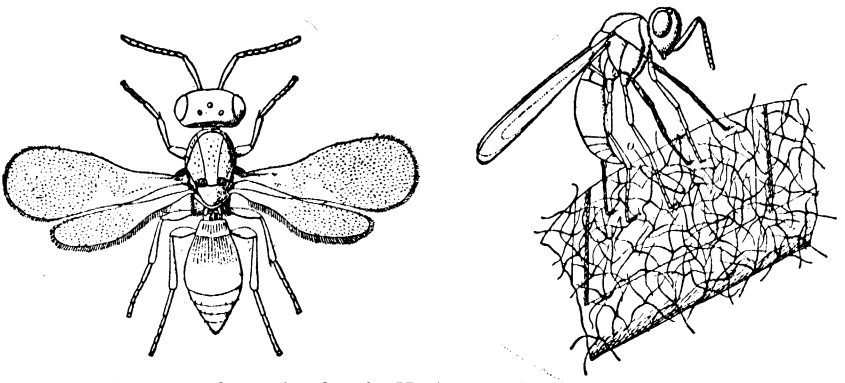


FIG. 529.—I, *Platygaster dryomyiae*, female; II, the same in the act of oviposition in an egg O, of *Dryomyia* (Cecidomyidae) on a leaf

After Silvestri, *Boll. Lab. zool. Portici*, 11, 1921.

Synopeas rhanis lives free in the body-cavity of the larva of *Dasyneura ulmariae*: *Platygaster minutus* lives in the gut of *Mayetiola destructor* while *Trichacis remulus* forms cysts in the ventral nerve cord of the same host-species. On the other hand, larvae of *Platygaster dryomyiae* (Fig. 30) and *Inostemma piricola* live in cysts in the brain of their hosts. The females of the last-mentioned genus possess on the 1st segment of the gaster a long horn-like growth which curves forwards over the thorax. This peculiar projection lodges the greatly elongate ovipositor with which eggs are inserted within those of *Contarinia pirivora* in the blossom-buds of the pear.

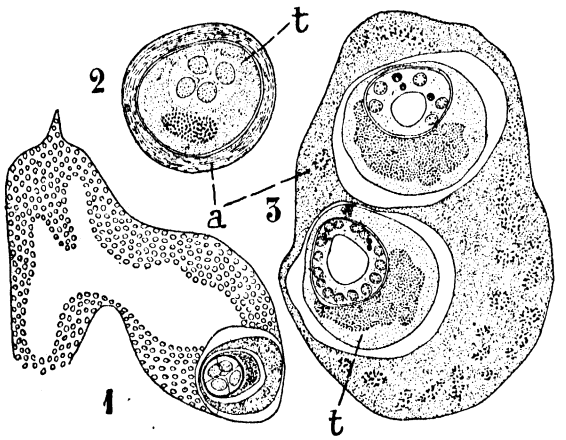


FIG. 530.—*Platygaster dryomiae*. 1, Embryo in morula stage in the brain of larva of *Dryomyia* (sagittal section). 2, An embryo with trophamnion *t* and adventitious layer *a*. 3, Two embryos in the blastula stage enclosed in a common adventitious layer

After Silvestri, *loc. cit.*

Superfamily **Bethyloidea**

At first sight this assemblage of families seems very diverse but, except for the Dryinidae which are difficult to place anywhere, there are annectent forms between the extreme types. In particular, the metallic coloured Mesitiinae in the Bethylidae are difficult to separate from the Cleptidae and the Chrysididae (cf. Reid, 1941). In the whole group, sexual dimorphism in number of antennal segments is absent, in contrast to typical Aculeates. A note on the affinities of the Dryinidae will be found under the Pompiloidea (p. 729). The British species have partly been described by Richards (1939) and for the Chrysididae and Cleptidae the work of Berland & Bernard (1938) should be consulted.

Table of families:

1. Antennae with more than 19 segments. Female apterous, male winged, hind wing with anal lobe . . . . . SCLEROGIBBIDAE
–. Antennae with less than 14 segments 2

2. Antennae with 10 segments 3
–. Antennae with 12–13 (in one genus of Bethylids 11) segments, inserted low down on face. Sexual dimorphism usually slight 4

3. Antennae not inserted on prominence but near to dorsal margin of clypeus. Female nearly always with chelate fore tarsi (except *Aphelopus*) and often brachypterous or apterous . . . . . DRYINIDAE
–. Antennae inserted on prominence high above clypeus. Female apterous, with simple fore tarsi, head pyriform, narrowed below. Male winged with relatively complete venation . . . . . EMBOLEMIDAE

4. Gaster with 2–4, rarely 5, exposed segments, venter concave. Pronotum short but wide. Propodeum normally with sharp lateral keels or teeth. Antennae with 13 segments. Colours metallic, sculpture usually coarse . . CHRYSIDIDAE
–. Gaster with 6–8 exposed segments, venter convex. Pronotum nearly always longer 5

5. Gaster with 7–8 exposed segments. Anal lobe of hind wing conspicuous, apterous species not rare. Head usually prognathous. Colours rarely metallic. Pronotum usually parallel sided . . . . . BETHYLIDAE
–. Gaster with 6 exposed segments. Anal lobe of hind wing ill-defined by a slight notch, species fully winged. Head orthognathous. Colours metallic. Pronotum narrowed anteriorly . . . . . CLEPTIDAE

The **Sclerogibbidae** though a small group have a wide distribution and are apparently all parasites of Embiids (vide Richards, 1939a). The **Dryinidae** are mostly recognized in the female by the chelate fore tarsi (Fig. 531); females of many species (*Gonatopus*, etc.) are apterous. All are parasitic upon the nymphs of Homoptera and more especially of the families Fulgoridae, Cercopidae, Membracidae and Jassidae. Their biology is of exceptional interest and most of what is known thereon will be found in writings of Perkins (1905–07), Fenton (1918), Kornhauser (1919) and Keilin & Thompson (1915). During the larval stages they are endoparasites in the abdomen of the host and, sooner or later, an external gall-like cyst or thylacium containing the parasite is developed as a rule from the moulted larval skins. This cyst protrudes after the manner of a hernia, its position on the host is variable, and one or several may be present on a single individual. In many cases the cyst may be as large as the abdomen of the host, and is usually black or yellow in colour. Pupation takes place either on the food-plant of the Homopteron or in the soil. The effect of the parasitism is often very marked and the changes induced are regarded by Giard as an instance of 'castration parasitaire'. They vary according to the species of insect attacked and, in some cases, they are evident externally owing to the imperfect development of the genitalia of the host. Over 300 species of Dryinidae are known and the greatest number has been described from Europe: in Britain *Aphelopus* frequently parasitizes species of Typhlocybinae. In this genus the cyst is formed from a proliferation of the host tissues.

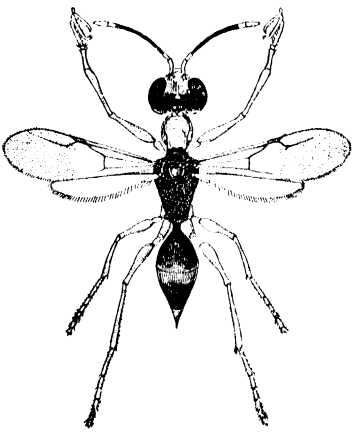


FIG. 531.—*Echthrodelphax fairchildi*, female

After Perkins, *Ent. Bull.*, 11, *Hawaiian Sugar Pl. Assn.*

The **Embolemidae** include a very few Holarctic species of considerable rarity and unknown habits.

The **Bethylidae** are a family of mostly small black insects, to some extent forming a link between the Proctotrupoidea and the Scolioidea, though nearer the latter group. Reduction of the wings is rather frequent, especially in the females. A few

forms, e.g. *Sclerodermus*, are dimorphic in each sex. So far as is known the species parasitize Lepidopterous and Coleopterous larvae and their biology has chiefly been observed by Bridwell (1918; 1919a; 1920) and Williams (1919a). *Epyris* stings Tenebrionid larvae and lays a single egg on each. *Sclerodermus* utilizes various Coleopterous larvae distributing her eggs over the prey, while *Goniozus* and *Bethylus* attack concealed Lepidopterous larvae. Parthenogenesis has been recorded, the unfertilized eggs producing males.

The **Chrysididae** (Cuckoo or Ruby-tailed Wasps) are of a brilliant metallic coloration, generally green, green and ruby, or blue, with a very hard coarsely-sculptured integument. They are easily recognizable by the structure of the gaster, which is peculiar in several ways, and very little longer than the head and thorax. It is convex above, and flat or concave beneath, so that it is capable of being readily turned under the thorax and closely applied to the latter. In this manner the insect rolls itself into a ball when attacked, leaving only the wings projecting. There are, with few exceptions, only three or four segments visible dorsally. The terminal segments in the female are modified to form a retractile tube within which the ovipositor is concealed (Fig. 532). The imagines only fly during hot sunshine, and are usually seen in the neighbourhood of the nests of various solitary bees and wasps within which their transformations take place. The family is very widely distributed and the genus *Chrysis* includes over 1,000 species. About 21 species of Chrysididae are British, one of the commonest being *Chrysis ignita* (vide Morice, 1900). So far as known all the species are parasites, and the Eumeninae and Megachilidae are especially subject to their attacks. As a rule their larvae prey on those of the host but Chapman (1869) has observed the larva of *Chrysis ignita* feeding upon a caterpillar stored by its host (*Odynerus*). *Chrysis shanghaiensis* is exceptional in that it lays its egg on the mature caterpillar of *Monema* (Cochlidiidae) inside its cocoon (Parker, 1936).

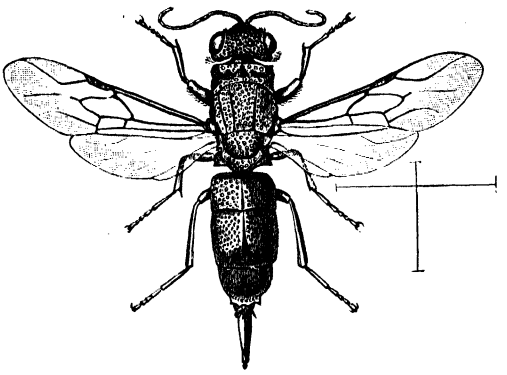


FIG. 532.—*Chrysis ignita*, female. Britain
After Sharp, *Camb. Nat. Hist.*

The **Cleptidae** include a few species superficially resembling Chrysidids but with a less specialized abdomen. The larva of *Cleptes* develops on mature saw-fly larvae in their cocoons but little is known of their habits in detail. There are two British species. *Mesitiopterus* has been bred from a Phasmid egg (Milliron, 1950).

Superfamily **Scolioidea**

Within this group are found the most primitive members of the true Aculeata. While many of them are parasites, usually of Coleopterous larvae or of other Aculeates, a primitive form of nesting activity is seen in the Scoliids and some species of *Tiphia* are the only Aculeates in which more than one egg is laid on a single victim. There is a clear affinity with the Bethylidae, some of which also exhibit rudimentary nidification. Sexual dimorphism is usually marked and in the Thynninae is carried to very great lengths.

Table of families:

1. Antennae with conspicuous pubescence, as long or longer than width of segments (♀ unknown) . . . . . PLUMARIIDAE
–. Antenna without this conspicuous pubescence 2
2. Meso- and metasternum together forming a continuous plate overlying the bases of the mid and hind coxae. Male last sternite produced into 3 spines. Female fully winged, wing-membrane striolate. . . . . SCOLIIDAE
–. Meso- and metasternum not forming a plate overlying the bases of the mid and hind coxae. Male last sternite rarely with 3 spines. Wing-membrane not striolate 3

3. Second gastral tergite with lateral 'felt lines' (except *Rhopalomutilla* in which the dorsum of the female thorax and propodeum forms a single plate and the male hind wing lacks the anal lobe). Male nearly always winged and usually without an anal lobe. Female apterous . . . . . MUTILLIDAE

–. 2nd gastral tergite without lateral felt lines. Dorsum of female thorax and propodeum never fused into a single plate. Male wings with an anal lobe or body smooth, shining and nearly bare 4

4. 1st and 2nd gastral tergites not separated by a constriction, 1st and 2nd sternites with only a feeble constriction between them. Mesosternum simple. Female fully winged . . . . . SAPYGIDAE

–. 1st and 2nd gastral segment separated by a deep constriction or the mesosternum with 2 laminae which overlie or project between the bases of the mid coxae. Females often apterous . . . . . TIPHIIDAE

FAM. PLUMARIIDAE.—A few male specimens have been caught in S. America (*Plumarius*) and S. Africa (*Myrmecopterina*) but nothing is known of their biology.

FAM. SCOLIIDAE.—This extensive family includes some of the largest members of the Hymenoptera. They are hairy insects whose prevailing colour is black marked with spots or bands of yellow or red, and the wings are often dark with a metallic iridescence. They are mainly inhabitants of warm countries, and the larvae are ecto-parasites of larval Scarabaeidae or much more rarely Curculionidae. The habits of some European species were observed by Fabre who found that the females penetrate the soil in order to discover the larvae upon which they deposit their eggs. Thus *Scolia hirta* (= *bifasciata*) selects those of species of *Cetonia*, *S. flavifrons* is confined to *Oryctes*, and *Elis sexmaculata* (= *interrupta*) chooses *Anoxia*. *Scolia manilae* has been successfully used to control *Anomala orientalis* in Hawaii.

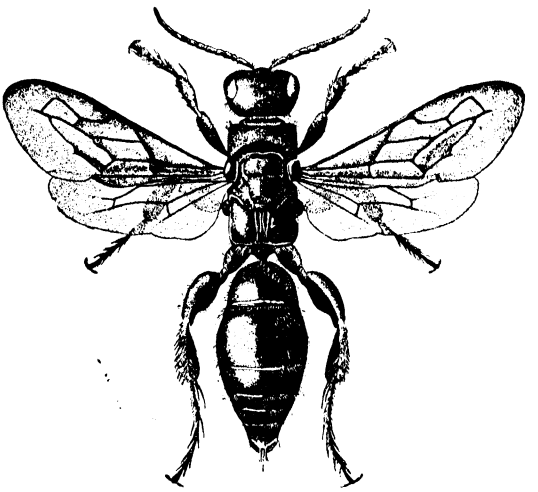


FIG. 533.—*Tiphia transversa*, N. America. Female
After Davis, *Bull. Illin. nat. Hist. Survey*, 13, Art. V (reduced).

FAM. TIPHIIDAE.—This is another large family whose members vary much in structure and habits and perhaps include survivors from the ancestral stock from which several of the higher groups of Aculeates arose. *Tiphia* (Fig. 533) includes two British species and exotic species have been much studied with a view to their use in biological control (Clausen *et al.*, 1932). *Pterombrus* in America and the widespread *Methoca* attack the larvae of Cicindelidae. The latter genus, with one British species, *M. ichneumonides*, has ant-like apterous females and the males are rarely seen (Champion, 1914; Pagden, 1926). *Myrmosa* and its allies also have apterous females but are superficially more like Mutillids. They parasitize various ground-nesting Aculeata.

The Thynninae is a subfamily of some size in S. (one species in N.) America and Australia. The majority of species lay their eggs on the larvae of Scarabaeidae, but *Diamma* attacks *Gryllotalpa*. The females are apterous and in most species are carried about by the male in a prolonged mating flight, during which the female obtains food from flowers. An illustrated account of the biology of several Chilean species of *Elaphroptera* has been published by Janvier (1933). The subfamily Sierolomorphinae includes a few N. American and one Hawaiian species of unknown habits. The lack of an anal lobe in the hind wing has led some authors to place them in a separate family.

FAM. MUTILLIDAE.—Some thousands of species are placed in this family, most of them with a characteristic common facies. The female is apterous with the thorax and propodeum usually fused into a single plate. The male is nearly always winged and usually rather different structurally from the female. Both sexes are black

or reddish in colour, often with spots or bands of silvery pubescence and a generally velvety appearance. The hosts are mostly aculeate Hymenoptera but various other orders are also attacked and one species has been bred from *Glossina* (Mickel, 1928). There are two British species, *Mutilla europaea* a parasite of *Bombus*, and *Smicromyrme rufipes* a parasite of Pompilids and Sphecids.

FAM. SAPYGIDAE.—The species of this family are parasites of Aculeates, particularly bees. The first-stage larva has big mandibles and destroys the host larva; in later instars the mandibles are smaller and the stored food is devoured (Fabre). *Polochrum* attacks *Xylocopa*, and in Britain, *Sapyga clavicornis* is mainly a parasite of *Chelostoma florisomne* (Megachilidae).

Superfamily **Formicoidea** (Ants)

The ants constitute a single very large family—the Formicidae which embraces, according to Wheeler, about 3,500 described species. They are all social and, with the exception of a few parasitic forms, have a well-differentiated worker caste (Fig. 534). The demarcation between the head, thorax and abdomen is highly accentuated. Myrmecologists usually term the narrow (often scale-like) segment or two segments following the propodeum, the *pedicel* and the more posterior broad segments, the *gaster*; it is more convenient in the Hymenoptera generally to keep the latter term for the whole post-propodeal abdomen and to speak of the differentiation of a petiole of one or two segments.

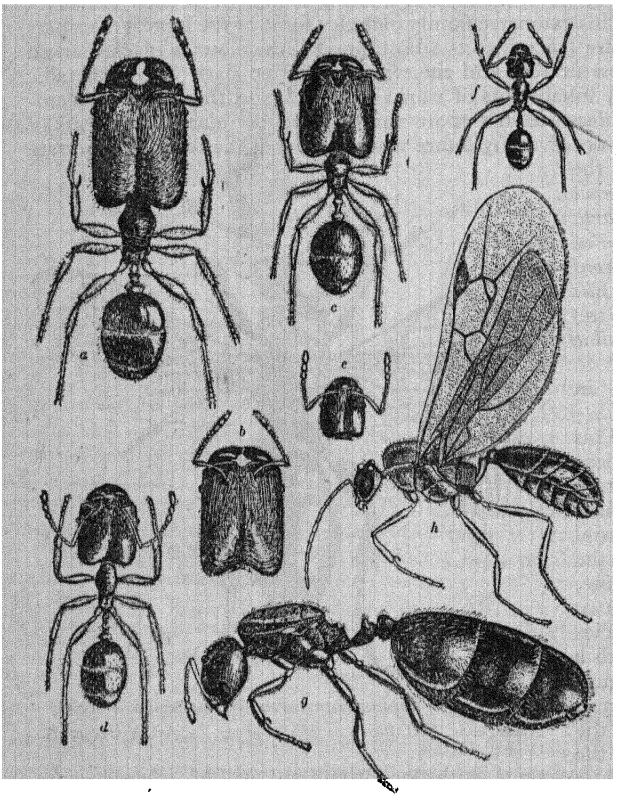


FIG. 534.—*Pheidole instabilis*

a, Soldier; *b–e*, intermediate workers; *f*, typical worker (micrergate); *g*, deälated female; *h*, male. *After* Wheeler, *Ants*.

The head varies enormously in shape, and the mandibles present an almost bewildering variety of form, and are subjected to many uses. The labrum is vestigial, the maxillae are composed of the usual sclerites, and their palpi are 1- to 6-segmented. The laciniae are membranous and toothless, thereby indicating a liquid diet. In the labium both submentum and prementum are evident, together with a median glossa: at the base of the latter is a pair of small paraglossae beset with rows of setae. The labial palpi are 1- to 4-segmented. The antennae are composed of 4 to 13 segments and usually the male has one more segment than the female or worker. Compound eyes and three ocelli are well developed in the males, but in the females, and

especially the workers, the eyes are usually reduced or vestigial. The abdomen is the seat of a stridulating organ which consists of an area of extremely fine parallel striae on the mid-dorsal integument of the first broad segment of the gaster (Fig. 97). The sharp edge of the preceding segment overlaps this area, and is deflexed, so that it may scrape backwards and forwards when the segments are moved on each other, thereby producing a highly pitched sound. A large and well developed sting is present in the females and workers of the subfamilies Ponerinae, Dorylinae and most Myrmicinae, but is vestigial or absent in the remainder.

Ants, as Wheeler observes, have acquired an extensive and uniform experience with all developmental stages of their progeny which they not only feed and clean, but also transport from place to place as conditions may demand. The eggs are small, hardly more than 0·5 mm. long even in the largest species, but the popular expression of 'ants' eggs' is often applied to the cocoons or even to the larvae or pupae. The larva consists of a head and 13 trunk segments: eyes are wanting and in a few cases vestigial antennae are present. There are ten pairs of spiracles, situated on the meso- and metathorax and the first eight abdominal segments. The body is almost always invested with hairs which assume many forms and are most abundant in the first instar. In many genera of the Ponerinae there are girdles of large segmentally repeated tubercles. Different species adopt very different methods of nourishing their larvae. Many feed them only on regurgitated liquid while carnivorous species give them portions of other insects, the harvesting ants utilize fragments of seeds, and the fungus growers nourish their larvae with fungus-hyphae. Wheeler states that a cocoon is constantly present in the most primitive ants and equally constantly absent in large groups of highly specialized forms.

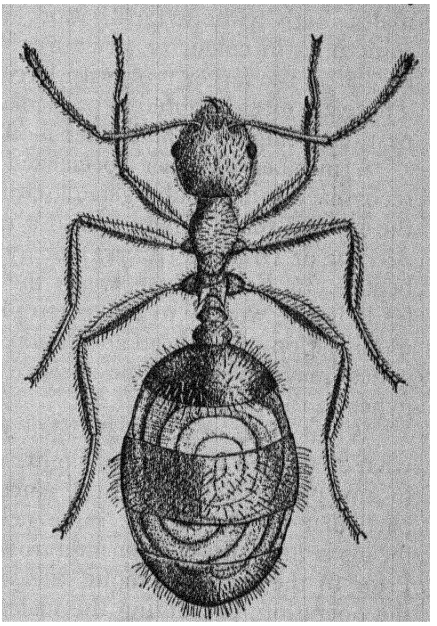


FIG. 535.—Worker of *Pheidole commutata* parasitized by *Mermis*
After Wheeler.

Polymorphism attains its highest expression among ants and a large number of types have been recognized, some normal, others, like the individual illustrated in Fig. 535, pathological. The normal phases are male, queen and worker. The male is the least variable of the three castes and retains many scolioid features. The sense-organs, wings and genitalia are highly developed but the mandibles are often weak. The head is smaller and rounder than in the females and workers of the same species, and the antennae longer and more slender. A remarkable type of male occurs in the Dorylinae, characterized by its large peculiar mandibles, long cylindrical abdomen and the specialized genitalia. In a few species (e.g. of *Ponera*), the male is apterous.

The queen is a female characterized by her large stature and well-developed reproductive organs. She is usually larger than the male and worker

of the same species and attains a great size in certain exotic forms. The antennae and legs are often shorter and stouter than in the male, the mandibles are well developed and the gaster large. Where the queen is relatively small (e.g. *Formica rufa*), some special method of colony-foundation, such as temporary social parasitism (p. 728) is often adopted.

The worker is a female characterized by the absence of wings, the reduced thorax and small gaster. The eyes are small and the ocelli either absent or minute. A receptaculum seminis is usually wanting and the ovarioles are greatly diminished in number. In some species, no eggs are laid by workers, in others eggs are laid but rarely hatch and are used as food for the young larvae (Brian, 1953). In *Oecophylla*, according to Ledoux (1950) two kinds of egg are laid, small ones giving rise to queens and workers, large ones to males, both without fertilization. Workers are usually variable in size and sometimes in colour or structure. Where they are dimorphic without intermediates, the larger type with large head and mandibles is termed a *soldier*. These are often adapted to particular functions such as fighting, guarding the nest, crushing seeds and other food particles, etc.

A number of other specialized types of worker and queen have been recognized in particular genera, either as the only type or in coexistence with the normal form. There is also a range of types modified by parasitism by *Mermis* or *Orasema* (p. 712), or by the presence in the nest of certain guest beetles. In *Formica sanguinea*, the influence of the Staphylinid *Lomechusa* leads in the worker to a hypertrophy of the labial glands and a consequent modification of the head and thorax (Novák, 1948). These so-called 'pseudogynes' may develop in the absence of the beetle provided there are pseudogynes in the nest.

When both sexes are winged mating nearly always takes place during what is termed the nuptial flight. As a rule one or other sex predominates in any particular colony and, since the nuptial flight for the colonies of a particular species in the same neighbourhood takes place synchronously, means is thus afforded for intercrossing with individuals of different colonies. Prior to the marriage flight, the workers become much excited and direct the operation, preventing the males and females from leaving the nest until the right time. There is good reason to believe that meteorological conditions exercise an important influence in this matter. There exist in the literature many references to great nuptial swarms of ants which sometimes cloud the air like smoke. On descending to earth the impregnated female divests herself of her wings, and the deälated individual commences to excavate a small chamber, within which she remains in seclusion until her eggs are mature, and ready to be laid. During the whole of this period, which may extend for months, the chamber is sealed up, and the female draws entirely upon the nutriment afforded by her fat-body and degenerating flight muscles. An exception however is seen in a few of the Ponerines in which the queen forages for food. When the first larvae appear, they are fed by the secretion of her salivary glands until they pupate. As soon as the workers are mature they break through the soil and establish a communication between the brood chamber and the outer world. They then go abroad and forage for food, and share it with their parent. The latter is now relieved from the care of the brood, and she limits her activities to egg laying, imbibing liquid food directly from the mouths of the attendant workers. In this capacity, she lives on solely for the purpose of egg-production, sometimes to an age of fifteen years. The number of ants in a fully developed colony appears to vary between

wide limits. Yung has made actual counts in the case of *Formica rufa* and found that the numbers vary between about 19,900 and 93,700; in *Formica pratensis* Forel estimated that the largest mound may contain as many as 500,000 individuals, a figure which Yung regards as excessive.

The nests or formicaries present an almost bewildering variety of architecture. Not only has every species its own plan of construction, but this plan may be modified in various ways in adaptation to special local conditions. The Dorylinae can hardly be stated to construct nests, and usually have their abode in some available recess beneath a stone, or log, or they may even temporarily occupy nests of other ants. A large number of ants construct nests in the soil and these habitations consist of a number of more or less irregular excavations, either with or without a definite superstructure around the entrances. The excavations are divided into galleries, or passages of communication, and chambers leading off from the latter. The chambers are used as nurseries for the brood, as granaries for storing seeds, as fungus-gardens and for other purposes. In some species there is nothing to indicate the situation of a subterranean nest, the excavated soil being carried some distance away and scattered irregularly. In others it is heaped up in the vicinity of the entrance, or entrances, to the nests, to form a crater, which varies in size and construction among different ants. Such craters are often difficult to distinguish from mound or hill nests. The latter are usually much larger and are formed not only of excavated soil but also of straws, twigs, pine-needles, leaves, etc., and are perforated with galleries and chambers. Such mound nests are well exhibited in the European *Formica rufa*. Perhaps the largest number of ants' nests is excavated beneath stones or logs. In the tropics many ants take advantage of cavities found in stems, petioles, thorns and bulbs, or even in the spaces enclosed by the overlapping leaves of certain epiphytes. Cavities in the bark, the dead wood, and stumps of trees are also frequently utilized, and even old deserted Cynipid galls. Suspended nests are of frequent occurrence, hanging from trees in tropical and subtropical forests. These are constructed of earth, carton, or silk and contain anastomosing galleries and chambers. *Oecophylla smaragdina* forms leaf nests, the leaves being fastened together by means of a silken web. The observations of Doflein and others have proved that the silk is provided by the larvae of the species concerned. They are held by the workers in their jaws and used, as it were, as shuttles in weaving the silken tissue of the nest.

About eight subfamilies of the Formicidae are recognized (cf. Wheeler, 1922) and of these the most primitive are the Ponerinae (Fig. 536). They are characteristic of the tropics and are the dominant group of ants in Australia. The only genus found in Britain is *Ponera* which is represented by two species, and in *P. punctatissima* the males are ergatoid. The nests of the Ponerinae are subterranean and are usually only occupied by a few dozen individuals. The three castes differ very little in size; the workers are monomorphic, they feed their larvae with portions of other insects, and the pupae are enclosed in cocoons. The 'bull-dog' ants (*Myrmecia*) of Australia attain a length of 2–2·5 cm. and, as Wheeler remarks, they bite and sting with such ferocity that few observers care to study them at close quarters.

The Dorylinae include the driver and legionary ants of the tropics; they are likewise carnivorous, but the workers are blind and highly polymorphic, varying from large soldiers with toothed mandibles, through intermediates, to the smallest workers. The females are very little known and seldom found: they are very large, blind and wingless like the workers. Schnierla (1949)

has shown that the queen periodically lays large numbers of eggs and each time this happens her abdomen becomes enormously swollen. The males are likewise very large, with sickle-shaped mandibles, and peculiar genitalia. These insects do not construct permanent nests but merely bivouac in temporary quarters, and wander from place to place in long files. Their sorties are only made on sunless days or at night and are for predatory and migratory purposes. The periodicity of the migrations depends on the periodic oviposition and occurs when many larvae require feeding. Belt mentions columns of *Eciton* which he followed for two or three hundred yards without coming to the end. Their prey consists of insects and spiders of various kinds, but

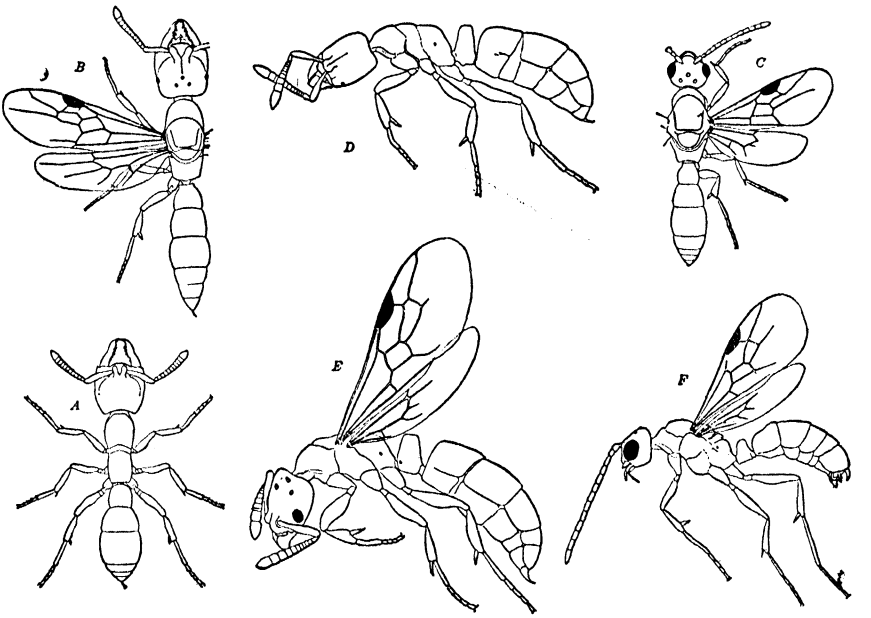


FIG. 536.—Ponerine ants. A, B and C, worker, female and male of *Stigmatomma pallipes*; D, E, F, worker, female and male of *Ponera pennsylvanica*

After Wheeler, *Ants.*

Savage records that *Anomma* will succeed in killing large animals if the latter be penned up, and he mentions having lost monkeys, pigs and birds by these insects.

The Ponerinae and Dorylinae, together with the small subfamily Cerapachyinae and many of the lower Myrmicinae are carnivorous ants which represent the savage or hunting stage in the evolution of those insects. The remaining groups of ants have partly abandoned this habit and adopted a vegetarian diet. Wheeler has called attention to the fact that an abundance of food is necessary for the maintenance and fullest development of social life. In warm arid countries insect food is either very scarce, or competition to secure it very keen among ants and other animals. A number of the former have become vegetarians as their last resource in the struggle for existence. Under such circumstances, the seeds of herbaceous plants provide an accessible nutritious food, and the outcome of this is the harvesting habit which is prevalent in many species. The four higher subfamilies, however, have an extremely varied diet, since they not only imbibe the secretions of nectaries, the honey-dew or products of aphides and other Homoptera, but also feed

upon fungi, fruit, seeds and other substances. The harvesting habit appears to have arisen sporadically, and often in distantly related genera, but all of which pertain to the subfamily Myrmicinae. In species of *Messor*, for example, the ants have been observed to gather the seeds both from the ground and from the plants, remove their envelopes, and cast the chaff and empty capsules on the kitchen middens outside the nest. In confirmation of Pliny and Plutarch, Moggridge mentions that the ants bite off the radicle to prevent germination. The latter process is also arrested by the ants bringing the seeds when damp to the surface, spreading them in the sun, and then carrying them back to the special chambers or granaries wherein they are stored.

The Myrmicine tribe of the Attini, which is peculiar to tropical and subtropical America, are all fungus growers and fungus eaters, and number about 100 species. The fungi are cultivated in special chambers of the nest termed fungus gardens (Fig. 537) and, according to Moeller (1893), these gardens are practically pure cultures of the fungi concerned, being assiduously 'weeded' and tended by the ants. Neither free aerial hyphae, nor any form of fruit body develop, but whether this is due to their elimination by the ants, or to environmental conditions, is uncertain. A fungus garden is a sponge-like mass of comminuted leaf fragments or, in some cases, of insect excrement. The fungi grow rapidly on this substratum and produce numerous swellings or bromatia. The latter form the food of the ants and their larvae and have never been produced in cultures. The systematic position of these fungi is unsettled: several genera have been described which have been referred to the Ascomycetes and Basidiomycetes. The formation of a new fungus-garden is undertaken by the queen who, before departing for the mating flight, fills her infrabuccal pocket (p. 685) with fungal hyphae. This pellet is expelled within the newly made nest-chamber and the growing hyphae are nourished, at first, by the faeces of the insect, who may even sacrifice some of her eggs for the same purposes (see also the papers of Weber, 1937, etc.).

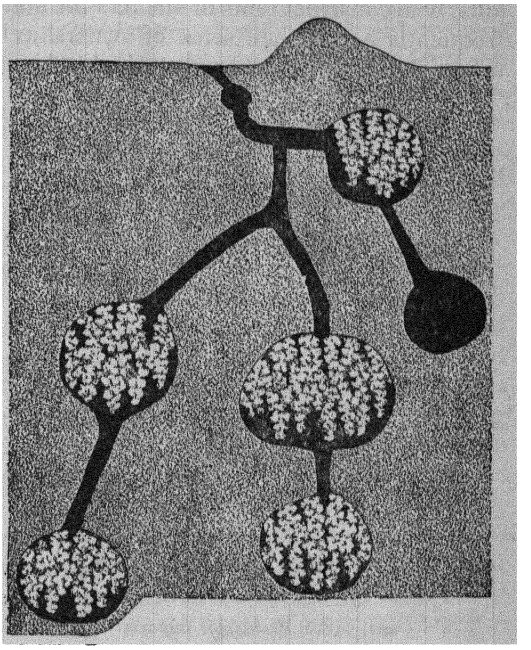


FIG. 537.—Diagram of a large nest of *Trachymyrmex septentrionalis* showing, near surface, small original chamber of queen, chambers with pendent fungus-gardens and newly excavated chamber

After Wheeler, *Ants*.

The small tropical subfamily Pseudomyrminae is notable for its highly specialized larvae. The head in these larvae is surrounded by the hood-like thorax and lies far back on the ventral surface, where it is in contact with the first abdominal segment. The latter somite bears a pocket, or trophothylax, and food received from the workers is deposited in this pouch, from which it

is gradually drawn into the mouth and swallowed. As previously mentioned (p. 675) trophallaxis is highly developed, the larvae supplying their nurses with the secretions of their remarkable exudatoria.

Ants have become associated with a large number of phytophagous insects which possess the habit of excreting liquid of a kind which is exceedingly palatable. In return, the ants render many of such insects certain services, and the relations thus established may be regarded as a kind of symbiosis (Nixon, 1951; Bünzli, 1935). The insects most concerned belong to various families of the Homoptera, viz. aphides, coccids, Membracidae, Psyllidae, etc., together with the larvae of the Lycaenidae (Hinton, 1951). In the case of many aphides and coccids, for example, they are afforded protection by the ants, who construct tents or shelters for housing them. With aphides the ants frequently betray their sense of ownership by at once carrying them away to safety should the nest be disturbed. This solicitude on the part of the ants may extend to the eggs of the aphides also, and numerous observers have noted ants collecting and storing aphid eggs in autumn and tending the nymphs when they emerge. The latter are carried and placed upon stems or roots which may be situated either within the nest or at some distance outside the latter. Nearly 70 species, representing 29 genera, of Lycaenidae are mentioned as having larvae that are attended by ants, and the relationship in some cases may be exceedingly intimate.

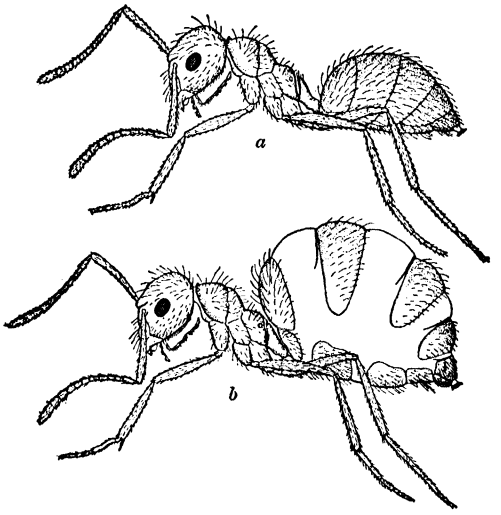


FIG. 538.—*Prenolepis imparis*

a, worker in ordinary condition; *b*, replete. *After* Wheeler, *Ants*.

In the subfamilies Formicinae and Dolichoderinae the habit of collecting nectar and honey-dew has become highly developed. The workers of these insects have a pliable integument, which often allows of great distension when their crops are gorged with food. In a few species, the gorging may take place to such an extent that the inflated crop may cause the sclerites of the gaster to be so far forced apart that they appear as islands upon the tense intersegmental membranes: individuals which exhibit this habit are known as *repletes* (Fig. 538), and the species possessing this physiological caste are termed honey ants. In *Prenolepis* all the workers are thus able to distend themselves, and regurgitate the sweet substance which they collect to their larvae or their sister ants. The true or perfect repletes are developed only in the nest, where they remain and store the sweets brought to them by the foragers, thus functioning as living casks or bottles. The contents of the latter are regurgitated when required for feeding the community. Repletes occur among the ants of N. America, S. Africa and Australia but the caste is wanting in the British species.

The relations of ants to aphides and Lycaenid larvae represent only one of the many phases of symbiosis. The others are extremely diversified and the ants are, as a rule, passive or indifferent, and the other insects associated

with them are mostly of the nature of inquilines. When the latter regularly inhabit the ants' nests, either throughout life, or during some stage in their development, they are known as myrmecophiles or ant-guests. Our knowledge of these organisms is due to the efforts of many workers, notably Wasmann, Escherich, Janet, Silvestri and others. Wasmann, in 1894, enumerated 1,246 species of myrmecophilous Arthropoda, the greater number being insects, and more especially Coleoptera. Since that time many more species have been brought to light, and we are now acquainted with probably over 2,000 species, including at least 1,200 different Coleoptera. In Britain there are about 300 species, upwards of 70 being Coleoptera (Donisthorpe, 1927a). The relations of these myrmecophiles to the ants are extremely diversified, and the following classes are recognized by Wheeler. 1. The *synechthrans*, which live in the nests as scavengers or predators and are treated with marked hostility. They have to elude the ants in order to obtain their food, which usually consists of dead or diseased ants, the brood, or refuse of various kinds. They constitute rather a small group, comprising a number of agile carnivorous Staphylinidae belonging to the genera *Myrmedonia*, *Quedius*, *Xantholinus*, *Myrmoecia*, *Lamprinus*, etc. The first-mentioned genus is represented by numerous species on all the continents. 2. The *synoeketes*, or indifferently tolerated guests, live in the nests without attracting the notice of the ants, or without arousing any obvious animosity. They are either too small, or too slow of movement, to attract attention, or have no specific odour which differentiates them. Among this large and heterogeneous assembly the most regular synoeketes are the curiously flattened larvae of the Syrphid genus *Microdon*. Verhoeff has observed the fly ovipositing in the nest and it was repeatedly driven away by the ants (*Formica sanguinea*), but kept returning until the eggs were finally laid. In addition to *Microdon*, synoeketes of British ants include Collembola of the genus *Cyphoderus*, larvae of the Chrysomelid beetle *Clytra*, species of *Dinarda*, various Phoridae, etc. A very large number of these guests is associated with the Doryline ants, accompanying the latter from place to place on their wanderings, and some of the Staphylinids, for example, exhibit an extraordinarily close mimetic resemblance to their hosts. The curious Lepismid *Atelura* is common in the nests of various European ants and, according to Janet, its members obtain most of their food by running up and imbibing some of the liquid while it is being regurgitated by one ant to another. The remarkable wingless crickets of the genus *Myrmecophila*, and the diminutive cockroaches of the genus *Attaphila*, lick the ants in order to imbibe the cutaneous secretions of the latter, and often mount the bodies of their hosts in the process. 3. The *symphiles*, or true guests, are species which are amicably treated, licked, fed, and even reared by the ants. They are much less numerous than the synoeketes, and consist largely of Coleoptera. Although they belong to many different families of the latter order, they exhibit marked adaptive convergence which is shown in the similarity of coloration, antennal characters, mouthparts, and gland structure. These features are developed in order to solicit food from the ants, and to ingratiate themselves by means of special exudations. These true guests are assiduously licked by the ants, and it has long been known that they usually bear tufts of reddish or golden-yellow hairs. The latter are regarded by Wasmann as being the most characteristic organs of the symphiles, and he has shown that they are situated on various regions of the integument, where numerous glands open, and that they have the function of diffusing some aromatic secretion. It is thus evident that the symphiles repay their hosts for their

hospitality by secreting a substance which is highly attractive to them. Some of the most remarkable among the ant-guests are the members of the *Lomechusa* group of the Staphylinidae. These insects are tended with the greatest fidelity by the ants, who also rear the *Lomechusa* larvae like their own brood notwithstanding the fact that the guest larvae devour large numbers of both the eggs and young of their hosts. The Paussidae and Clavigeridae, which are remarkable for the bizarre forms assumed by their antennae, also include among their ranks various symphiles. 4. The remaining groups of myrmecophilous insects are *parasites*. The latter include various larval Chalcids such as *Orasema* and other Eucharitid genera, the Phorid *Metopina* and the Gamasid mite *Antennophorus*. The endoparasites include members of all the great groups of parasitic Hymenoptera, the Strepsipteran *Myrmecolax* (p. 829), several Phoridae and Conopidae, and the Nematode *Mermis*.

So far reference has only been made to the relations of ants to other organisms. There are, however, many instances of social symbiosis between different species of ants. Thus two species of ants belonging to different genera may occupy a compound nest and live amicably together though keeping their broods separate. Other cases have been brought to light by Forel in which small ants nest in close proximity to larger species, and either feed upon the refuse food of the latter, or waylay its workers and compel them to deliver up their booty. True inquiline species are also known which can only live in association with a host of another species and share its nest. Social symbiosis leads us to the condition termed temporary social parasitism. In the latter type of existence the queen seeks adoption in the colony of another species and trusts to the alien workers to rear her first brood of young. The full benefits of this form of parasitism can only be secured by elimination of the queen of the host species. The workers of the latter gradually die out and the nest is ultimately entirely peopled by the parasitic ants. Parasite and host are always members of the same or closely allied genera.

From temporary social parasitism the next step is exhibited by slavery. Slave-making ants are confined to the northern hemisphere and are members of four genera only. One of the best known species is the blood-red ant (*Formica sanguinea*) of Europe and N. America, which utilizes as its slave certain other species of its genus, viz. *F. fusca* and its allies. An army of *sanguinea* workers start out and, having found a suitable nest, they do not kill the workers of the slave species unless they should offer resistance, their main object being to capture the pupae and bring the latter back to their nest. It appears probable that a number of the captured pupae is eaten since the number of slaves in a *sanguinea* nest is smaller than the number of cocoons captured. The survivors from the latter emerge and become slaves in the colony of the captors. Wasmann regards this species as a facultative slave-maker, since independent slaveless nests do occur, and there is nothing to show that the slaves are anything more than auxiliary rather than essential workers, in the colony which has adopted them. Obligatory slave-makers or 'amazons' are members of the genus *Polyergus*. The European *P. rufescens* is one of the best known, and its normal slaves belong to the same species as those selected by *sanguinea*. The *Polyergus* never excavates its nest, or cares for its young, and is entirely dependent on the slaves hatched from the worker cocoons pillaged from the alien colonies. The European ant *Anergates atratulus* is a highly specialized social parasite; it possesses no workers, and selects as its host *Tetramorium caespitum*. The *Anergates* queen enters the nest of the latter, and the eggs which she lays gives rise to a progeny

which is tended and fed by the host workers. Ants which exhibit this parasitic habit are known to eliminate the queens of their host species which accept the alien substitutes. This mode of life is associated with degeneration; the males of *Anergates*, for example, are sluggish, wingless worker-like individuals, and even more or less pupa-like; the females are also modified and have rather poorly developed eyes.

Ants are frequently a great nuisance to man and many species are serious agricultural pests in the tropics owing to their cultivation of coccids. One of the best known of the noxious species is the Argentine ant (*Iridomyrmex humilis*) which has overrun the warmer parts of the United States and become a serious household pest.

The literature on ants is voluminous but much of what is known concerning these insects will be found in the works of Wheeler (1910; 1922; 1923) which are accompanied by very full bibliographies. The two masters of European myrmecology are Forel (see especially 1921–23) and Emery (1910–25), a mere list of whose writings would occupy several pages. Almost equally numerous are the various papers of Wasmann, particularly with reference to myrmecophilous insects. British ants number 36 species and these are admirably dealt with by Donisthorpe (1927).

Superfamily **Pompiloidea**

This is a large and in most respects very homogeneous group. Several thousands of species are already described but this is clearly only a fraction of those awaiting discovery, especially in the tropics. The Pompilids all prey on spiders, usually storing them in simple subterranean nests or, less commonly, building mud-cells. A few have become parasitic on other Pompilids and the Ceropalinae, all which have this peculiarity, have diverged rather widely from the remainder. In 1941, Reid showed that the anomalous genus *Olixon* is structurally very close to certain brachypterous Pompilids described by Arnold from Africa. Later specimens of the genus *Harpagocryptus* have become available and these are closely allied to *Olixon*. Perkins bred *Harpagocryptus* from external sac-like structures on the body of an Australian *Trigonidium* (Gryllidae). Very recently Krombein has suggested that the anomalous *Rhopalosoma* (p. 730) also has affinities with this group on the grounds of resemblances in the male genitalia. In other respects, however, it is widely different. Finally, the Dryinidae (p. 717) which develop in sacs on Homoptera might conceivably have some affinity with this superfamily; again there are certain resemblances in the male genitalia but little resemblance in any other part of the body.

FAM. POMPILIDAE (Psammocharidae).—The Pompilidae are distributed over almost the whole world; twelve genera, including about 40 species, are found in the British Isles. In these insects the abdomen is devoid of a definite pedicel, the hind pair of legs is very long and the males are more slenderly built and usually smaller than the females (Fig. 539). All are fossorial and predatory wasps, their size is very variable and certain species may attain a length of three inches. Included in the genus *Pepsis* are some of the largest of all Hymenoptera. They are remarkable for their extreme activity and possess great powers of running. The nests of these insects are usually burrows in the ground, but *Pseudagenia* constructs earthen vase-like receptacles which are attached to walls or stones. Their prey consists of spiders and some of them, by means of their highly developed stinging powers, are able to overcome even the largest of these Arachnids. One of the giants of the family is *Pepsis femoratus* which stores its burrows with the great Tarantula spiders. The habits of the Pompilidae have been observed by Fabre (1891), the Peckhams (1898), Ferton (1901–21),

Williams (1919) and others (for a summary of British species, see Richards & Hamm, 1939; for a wider survey, see Iwata, 1942). There appears to be a good deal of variation in the degree of perfection in the art of stinging among different species. Fabre states that *Calicurgus*, correctly *Cryptocheilus*, first stings its prey between the poison fangs of the latter, and subsequently near the junction of the cephalothorax and abdomen, thereby producing complete immobility. The observations of the Peckhams on species of *Pompilus* indicate that in this genus stinging is a much less refined process: in some cases the spider is stung in such a way that it is killed outright, while in others it may live for 40 or more days, but in all cases it is reduced to a sufficiently helpless condition to afford a safe repository for the egg of the wasp.

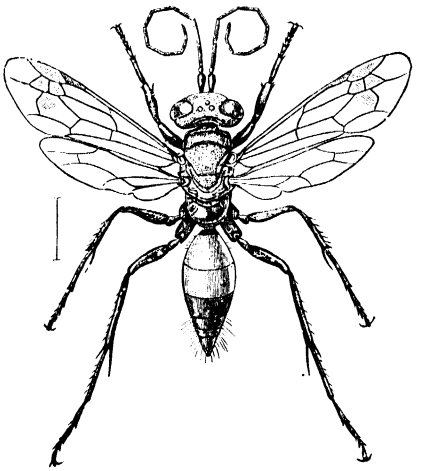


FIG. 539.—*Calicurgus hyalinatus*, female, Britain

After Sharp, *Camb. Nat. Hist.*

FAM. RHOPALOSOMATIDAE.—A few species of nocturnal habit, superficially somewhat like the Ichneumonid genus *Ophion*, found in all except the Australian regions. The Nearctic species of *Rhopalosoma* are external parasites of crickets (Gurney, 1953) and no nest is made. The affinities of the group have always been a puzzle but they seem to fall either here or amongst the Scolioids.

Superfamily **Vespoidea**

The true wasps are usually placed in a single family, the Vespidae, with somewhat uniform structure. In the vast majority of genera the eyes are reniform, the glossa and paraglossa terminate in sclerotized pads, the wings can be folded longitudinally and have a characteristic venation. In the very specialized Masarinae, some of these characters may be absent. The solitary Eumeninae form one of the largest subfamilies in the Hymenoptera and are found in all regions. The social wasps are placed in five subfamilies, some of which may have been independently derived from solitary ancestors.

FAM. VESPIDAE.—This large and important family is divided into eleven subfamilies of which six are solitary and four of these are found in Europe. The Masarinae are recognized by the presence of only two 'cubital' cells and often by their strongly clubbed antennae. Their glossa is often greatly elongate and retractile into the prementum, and they are adapted for the collection of pollen and nectar which they store in subterranean burrows or mud-cells. There are about 150 species found in all the main regions.

The Eumeninae comprise most of the solitary wasps of temperate regions. They exhibit many variations in nest-building habits: certain species dig tunnels in the ground, and others construct tubular nests in wood or stems, partitioning the tunnels into cells divided by mud-walls. There is, furthermore, a number of species which are mason or potter wasps, constructing oval or globular vase-like nests of mud or clay, fastened to twigs and other subjects. The latter types are often of the daintiest description and are said to have served as models for early Indian pottery. The species of *Odynerus* (*s.l.*) construct varied kinds of nests, while some regularly take advantage of a deserted nest of another wasp, or of a nail-hole or key-hole, rather than build cells of their own. All the species of the family are predacious upon small Lepidopterous larvae, or more rarely, upon those of the Tenthredinidae and Chrysomelidae. The prey when captured is stated by Fabre to be stung into insensibility and a dozen or more larvae may be stored in a single cell. The wasp deposits each egg by means of a suspensory filament from the roof of the cell where it hangs in close proximity to the food thus collected and, after the chamber is sealed, the parent betrays no further care for its offspring. The group is a large one well-represented in

most regions of the globe and its habits are discussed by Roubaud (1916), Williams (1919), Iwata (1942) and others. Six genera occur in Britain, viz. *Eumenes* and *Odynerus* (*s.l.*). In the former the first abdominal segment is very long, and narrowed into a petiole (Fig. 540) while in *Odynerus* the petiole is scarcely evident.

The Vespinae are Asiatic and Holarctic. This subfamily, in temperate regions, includes the papermaking wasps which are social in habit, and live in large communities each composed of a fertilized female or 'queen', workers and males. The colonies exist for a single season only, the males and workers perishing during autumn, while the impregnated females hibernate and each founds a new colony the next spring. The three forms of individuals are generally alike in coloration, but the queens are considerably larger than the workers and males: the males may be readily distinguished by having seven evident gastral segments and thirteen segments to the antennae, whereas only six gastral segments and twelve antennal segments are found in the queens and workers. Vespinae are largely predacious in habit and feed their larvae upon other insects, portions of which they previously masticate: both fresh and decaying meat and fish are also utilized. The adult wasps are very partial to nectar, ripe fruits and honey-dew and this same diet is given to the very young larvae for a short period. Their mouthparts have not attained the length and perfection found among bees, and hence wasps are unable to obtain the secretions of deeply seated nectaries. Although, at times, they cause injury to fruit they render service as scavengers and in reducing the numbers of other insects, more especially Diptera and Lepidopterous larvae. The British species of the family belong to the genus *Vespa* (the hornet) and *Vespula*, and our knowledge of these insects has been greatly extended by the researches of Janet (1893, etc.), Marchal (1896) and Weyrauch (1936, etc.) (cf. Duncan, 1939). Great variety of nest construction is found in this genus and the British forms exhibit three distinct types of nidification. Thus *Vespula vulgaris*, *germanica*, and *rufa* make underground nests; *V. norvegica* suspends its nests in bushes, etc., while *Vespa crabro* usually nests in hollow trees. *Vespula austriaca*, sometimes put in a third genus, is a parasite of *V. rufa* and lacks the worker caste. The stings of these insects are always painful and many of the tropical species are very fierce and easily roused, their stings sometimes involving dangerous consequences to animals and human beings. One of the largest species of the genus is the Himalayan *V. ducalis* whose queens attain a length of 40 mm. with a wing-expanse of over 80 mm.

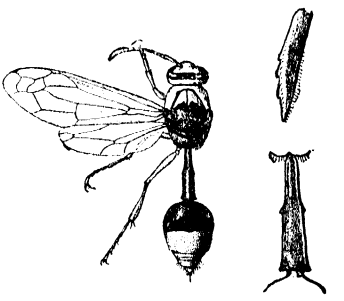


FIG. 540.—*Eumenes petiolata*. Female × $\frac{5}{6}$. India
After Bingham (F.B.I.).

After hibernation the female wasps are roused into activity by the warmth of early spring, and commence to seek out likely situations for their nests. Having discovered suitable places they proceed to gather the material for nest-construction. This consists of weather-worn but sound wood, particles of which are rasped off by means of the mandibles, and worked up with the aid of saliva to form a substance known as 'wasp-paper'. In the case of *V. germanica* and *vulgaris*, layers of the substance are applied to the roof of the cavity in the ground destined to hold the nest. From the centre of the disc thus formed, a pedicel is hung with its lower end widened out. Upon the latter the first cells, up to about thirty in number, are constructed: they are hexagonal in form, open below and closed above. An umbrella-like covering is suspended from the roof of the cavity to protect the comb and, in the angle of each cell nearest the centre of the comb, an egg is deposited, being fixed by means of a cement-like substance. In a few days, according to temperature, the larvae hatch and are fed by the parent until ready to pupate. Prior to transforming, the larva spins a cocoon within the cell and closes the mouth of the latter with a tough floor of silk. The contents of the gut are now evacuated for the first time, and transformation into the pupa takes place. After a period of four to six weeks from the time of egg-laying, the adult wasps bite their way through the floors of their cells and emerge. These individuals are always workers, and very soon the entire care of the young and the nest-building is taken over by them, the parent female devoting herself solely to egg-laying. When the nest is fully formed (Fig. 541) it is more or less spherical in form externally, and is invested by several layers of coverings which protect it from rain and also serve to prevent loss of heat from within. New cells are added at the

periphery of those already formed and, when one layer of comb has attained a suitable size, new tiers or layers are built below and interconnected with vertical pillars. This goes on until about seven or more combs are constructed and the spaces between the several combs, and between these and the innermost covering of the nest, are just sufficient to allow of the free movement of the occupants of the nest. Each cell of the comb is used for rearing the brood twice or perhaps three times, and it will therefore be seen that the number of cells does not accurately represent the total population of a colony. Janet found in a nest containing seven combs 11,500 cells of which 11,000 had been used twice and the remainder thrice. An average-sized nest probably has a population of about 5,000 individuals towards the end of the season. Near the end of summer larger cells are constructed and these 'royal' cells are destined for the females or 'queens' of the next generation. The fertilized eggs produce either females or workers, but the mechanism of caste-determination is unknown. The workers, though probably never fertilized, usually lay some eggs and in the absence of the queen large numbers. Males are always produced from unfertilized eggs whether the latter be laid by the female or workers.

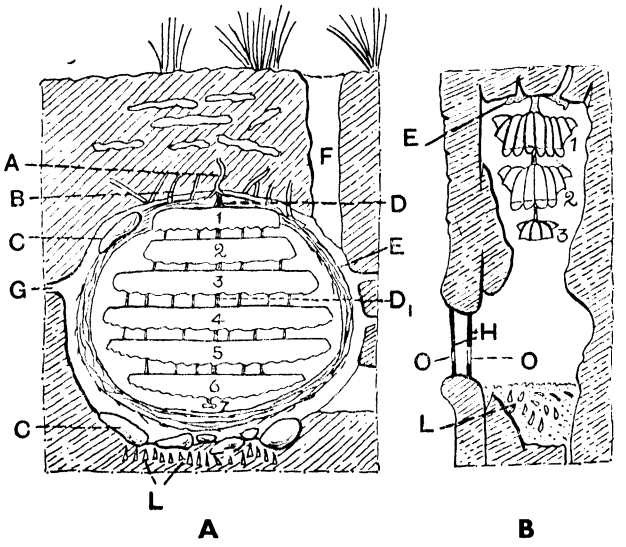


FIG. 541.—A, section of subterranean nest of *Vespula germanica*; B, section of nest of *Vespa crabro* in a tree hollow

A, root to which first attachment *D* was made; *B*, secondary attachment; *C*, pieces of flint; D_1, suspensory pillar; *E*, envelope, in **B** its vestiges; *F*, entrance; *G*, side gallery; *H*, lamellae closing opening to tree hollow; *O*, entrance orifices in lamellae; *L*, saprophagous dipterous larvae. The numerals refer to layers of comb in order of construction. Adapted from Janet.

In addition to their normal occupants a large number of other insects has been observed in wasps' nests, either as parasites or inquilines. In the soil beneath the nest, which contains excreta and other organic matter, larvae of *Acanthiptera inanis* are often abundant. Larvae of *Volucella inanis*, *zonaria* and *pellucens* appear to act as scavengers, devouring excreta, etc., but sometimes also the occupants of the cells: among true parasites the most important is *Metoecus paradoxus* which destroys the larvae. Newstead (1891) has recorded a number of other insects and several species of Acari from nests of *V. germanica* and *V. vulgaris*. *Polistes* (subfamily Polistinae) is the only other type of European social wasp. The colonies are much smaller than those of *Vespula*, and each nest is composed of a single tier of cells suspended by means of a central pedicel without any external envelope. The cycle is essentially like that of *Vespula* and a few species have also become parasites (Weyrauch, 1937). The genus is very large and found in all regions. Of the extra-European social groups the Stenogastrinae, of the Orient and Australia, are the most primitive. Some species are solitary and others social: the latter make fragile naked combs, the colony comprises but few individuals, and the larvae are fed by progressive provisioning. The Polybiinae are the largest social group: they are tropical and largely S. American. In species of *Belonogaster* in Africa the colonies are small and there is little differentiation of caste, the older females being the egg-layers and the younger individuals are foragers: new colonies are provided for by rudimentary swarming. In other genera true queens and workers can usually be recognized: the colonies are often immensely populous and pleometrotic (with more than one egg-laying queen), while swarming is a regular phase in their life. In *Brachygastra*, honey forms part of the nest provisions. The Ropalidiinae are a small group found in the tropics of the old world: they construct combs (usually naked) and there is little or no distinction into queens and workers.

Among the principal works on the family is De Saussure's monograph (1852–58) and the writings of Janet, Marchal, Roubaud (1916) and Bequaert (1918): for a useful account of the biology of the British Vespidae vide Latter (1904). Their evolution and economy are also discussed by Richards, O. W. & M. J. (1951).

Superfamily **Sphecoidea**

This superfamily is composed of solitary wasps, mostly fossorial but occasionally constructing free mud-cells. Much more rarely resin is used as a building material. They are predacious and store their nests with Lepidopterous larvae, Hemiptera, Orthoptera, Arachnida, etc., or very rarely are parasitic on their allies. Parental care for their larvae occurs in species of *Bembix* and *Ammophila* but in most genera, once the cells have been provisioned, and an egg deposited in each, they are sealed down and the parent exhibits no further concern for her offspring. The prey is probably always stung and the result in most cases is to induce rapid paralysis of the motor centres, thereby eliminating all or almost all power of movement. The often repeated assertion that the prey is stung in the ganglionic nerve centres is not an ascertained fact, but an inference drawn from the effects of stinging, and the positions in which the sting is inserted into the bodies of the victims. In a number of cases the prey is stated to be killed outright, but it retains its fresh condition for a variable period up to several weeks, a fact which suggests the possibility that the injected venom exercises an antiseptic influence. Many interesting and original observations on the habits and instincts of the European species of the group are detailed in the writings of Fabre, Ferton and Adlerz; a number of N. American species have been studied by G. W. & E. G. Peckham and by Rau (1918) and of S. American ones by Janvier.

Opinions have differed as to whether the group should be treated as a single family or should be divided into a considerable number. There is little doubt that at the moment such division is impracticable if the fauna of the whole world is considered. Even the Ampulicinae which are unusually distinct seem to be only a specialized offshoot from the Sphecinae and show affinities with such genera as *Podium*.

FAM. SPHECIDAE.—The subfamily Astatinae includes a small number of species in most of the main regions; they rest in the soil and prey on immature Heteroptera. For the European species, see Verhoeff (1951). The Larrinae form a large, very widely distributed subfamily, most of whose species make small nests in the earth though in the large genus *Motes* (*Notogonia*) mud-cells are affixed to stones, etc. The majority of species prey on Orthoptera or Dictyoptera but *Miscophus* stores small spiders and some genera take Hemiptera. The subfamily Trypoxylinae is mainly made up of the two large genera *Trypoxylon* and *Pison*. Both build with mud—*Trypoxylon* sometimes subdividing natural crevices or, like *Pison*, building mud-cells on tree-trunks, leaves, etc. The prey is always Arachnida of which a considerable number is stored in each cell. There are three British species of *Trypoxylon* but the genus is universally distributed and there are more than 150 species in S. America. The Pemphredoninae includes a number of small black wasps, most of which prey on Homoptera though *Spilomena* takes Thysanopterous nymphs. Most of the nests are in wood or in hollow stems, only a few burrow in the soil. The S. American *Microstigmus* (Myers, 1934) is unique in making a nest of plant wool suspended on a long thread and in storing Collembola. There are about 30 British species of the subfamily. The extensive subfamily Sphecinae includes large but usually slender insects with the propodeum and often the petiole elongate (Fig. 542). The legs are adapted for digging and running and their methods of stinging are highly specialized. The best known genera are *Sphex* and *Ammophila*, which, as the Peckhams remark, include some of the most graceful and attractive of all wasps—not only on account of their form but also owing to their intelligence and individuality. The above-mentioned observers, and also Fabre, have studied their habits in detail and the records of their observations form some of the most remarkable chapters in insect biology. Stated very briefly,

the prey consists respectively of Orthoptera and Lepidopterous larvae which are stored in a single cell situated at the termination of a vertical tunnel in the ground. The method adopted by these insects in stinging their prey is the most complex known and has been observed by Fabre in the case of *A.* (*Podalonia*) *hirsuta* and by the Peckhams in *A. urnaria*. It is a multiple process but there is some variation with regard to the number of stings administered. In one instance Fabre mentions that stinging took place at twelve different points, beginning between the 1st and 2nd segments and progressing backwards. In his second example, the 3rd, 2nd and 1st segments were stung in the order given and thereafter the remaining segments up to the 9th. In other cases he noted that usually all the segments were stung. After stinging had been accomplished the prey, in some instances, was subjected to a further process known as malaxation, which consists in repeatedly compressing the neck of the victim with the mandibles. The Peckhams' observations largely confirm those of Fabre with the exception that the middle segments of the prey, upon which the egg is deposited, were never touched, while in Fabre's observations they invariably were. They also noted that malaxation was most severe in the case of a caterpillar which was only stung once. It is evident from the various observations which have been recorded that the order in which the segments are stung, the number stung, and the subsequent malaxation which may occur are all somewhat inconstant. The poison introduced during stinging either paralyses or kills the prey and also acts as an antiseptic, keeping the tissues fresh for many weeks. As Wheeler observes, Fabre's and Bergson's contention that the insect is a clairvoyant surgeon, with an intuitive knowledge of the internal anatomy of its prey, may be dismissed as a myth. In 1941 Baerends published a remarkable account of *Ammophila pubescens*, well known in Britain under the name *A. campestris*. This species practises progressive provisioning and maintains two or three nests at once, each in a different state of development. *Sceliphron* includes the 'mud-daubers' whose nests are constructed of kneaded mud or clay and are composed of about 10 to 50 cells. These insects occur in most of the warmer regions of the globe and are very fond of building their nests in human habitations. Their prey consists of spiders and it appears to be a matter of indifference whether the latter be killed or only paralysed and either event may follow as the result of being stung. An examination made by the Peckhams of cells recently provisioned show that while most of the spiders were dead, many clearly exhibited indications of being still alive. The latter died off from day to day and the dead Arachnids remained in good condition for a period of ten or twelve days (cf. also Shafer, 1949).

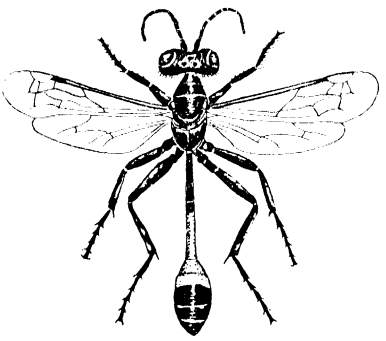


FIG. 542.—*Ammophila sabulosa*, female. × 2. Britain

The Podiini are mostly South American and nearly always prey on cockroaches. *Trigonopsis* constructs free mud-cells attached to the trunks or leaves. The Ampulicinae are rare in individuals and few in species. The prothorax is narrow and elongate and the base of the abdomen is constricted to form a short petiole. So far as known they are predacious upon Blattidae and Bingham mentions that in Burma they enter houses and search for their prey in likely situations. They do not form definite nests and, after having stung their prey into submission, the latter are dragged away and stored in any suitable hole or crevice (vide Williams, 1919). The family ranges into both hemispheres but is unrepresented in Britain. *Dolichurus* and *Ampulex* occur in France.

The subfamily Nyssoninae is large and very varied in habits and structure. The genus *Mellinus* includes a small number of species which prey on Diptera. The nest is a shallow burrow in the soil and *M. arvensis* is abundant in Britain in the late summer. *Alyson* and *Didineis* are small genera of which the species are rarely common. As far as is known, they nest in the soil and store up Homoptera. The genus *Nysson*, known by the projecting teeth on the propodeum, includes species which are parasites of allied genera. They enter the burrows of *Gorytes* (*s.l.*) and, without destroying the hosts' egg, deposit one of their own between the abdomen and the folded wings of one of the Homopterous prey (Reinhard, 1929). *Gorytes* and its allies nest in the soil and as far as is known prey on Homoptera. *G. mystaceus*,

a common British species, takes the nymphs of *Aphrophora spumaria*. *Sphecius* includes some very large species which prey upon Cicadas. *Stizus* preys on Orthoptera and the allied *Stizoides unicinctus* has become a parasite of *Sphex atratus* which has similar prey. *Bembix* and its allies are known by their elongate labrum and mouthparts. The genus itself is of world-wide distribution but there are numerous allied genera in the south-western United States. The species of *Bembix* are gregarious, a number of individuals occupying a limited area of ground but each one has a separate nest. Thus Wesenberg-Lund (1891) states that fifty *Bembix* will occupy an area about equal to that of an ordinary room. *Bembix* differs from almost all other solitary wasps in that the cells containing its larvae are left unsealed and the latter are fed from day to day. The difference in maternal care entails very great industry on the part of the parent wasps and results in a much less numerous progeny. The prey consists of Diptera and among the genera recorded as serving this purpose are such relatively large forms as *Echinomyia*, *Eristalis* and *Tabanus*. In *Bembix rostrata* a single female supports five or six larvae and each of the latter requires 50 to 80 flies during the fourteen or fifteen days spent in that stage. Parker (1917) discusses the biology of the family and believes that the parent wasps find their skilfully concealed burrows by olfactory sense. He mentions several instances in which the surface of the burrow was disturbed, and even water was poured over it, without causing the wasp to lose track of its nest. In addition to this work and that of Marchal the reader should also consult the writings of Fabre and G. W. & E. G. Peckham and the monograph by Nielsen (1945). The Philanthinae includes two tribes which may perhaps be less closely allied than the present classification indicates. *Philanthus* includes a large number of species which burrow in the ground and store bees. The victim is stung on or near the under surface of the mentum and death rapidly supervenes. *Philanthus triangulum* is the 'Bienenwolf' of the Germans, and is occasionally a serious enemy of the hive bee. According to Fabre, after the bee has been stung it is subjected to vigorous malaxation for the purpose of forcing out the contained honey. The latter is imbibed by the captor and its extraction is stated to be necessary before the bee can be safely used as food by the larval *Philanthus*. The species has also been the subject of a valuable study of orientation by Tinbergen (1932). In Britain, the species has been recorded at long intervals and probably becomes temporarily established after immigration from the continent. *Cerceris* (Fig. 543) is the largest genus of Sphecoids (Arnold) and includes more than 600 species. Like *Philanthus*, they make deep burrows in the ground and some of them prey on solitary bees in a way very similar to that genus. The majority, however, catch Coleoptera, especially weevils. The allied genus *Aphilanthops* stores queen ants (Wheeler, 1913). The principal genera of the Crabroninae are *Crabro* (*s.l.*) and *Oxybelus*. The former has now been split into many genera with very varied habits. They construct burrows either in the soil, or in rotten wood or in plant stems. The most usual prey is Diptera, but some of the species attack several other orders, such as Hymenoptera, adult Lepidoptera, Coleoptera or Ephemeroptera. Kohl's monograph of the European species (1915) is a classic and the biology of the British species, which number forty, has been summarized by Hamm & Richards (1926). *Oxybelus* is another large and widespread genus with characteristic spines on the postscutellum. The nest is a burrow in the soil and the prey are Diptera which are often brought in impaled upon the sting. There are three British species of which *O. uniglumis* is abundant.

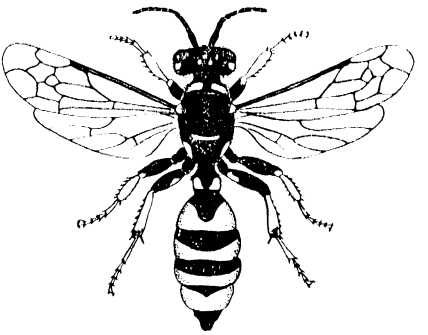


FIG. 543.—*Cerceris arenaria*, female. × 2·5. Britain

Superfamily **Apoidea**

Included in this superfamily are the social and solitary bees. The truly social species, which have evolved a worker caste, are confined to the families Halictidae and Apidae, the great majority of forms being solitary. The

adults are most important agents for pollinating flowers, the pollen adhering to the plumose body-hairs. The glossa is always well developed, generally pointed, and often exceedingly long. The food consists of nectar and pollen, the former supplying the carbohydrate ingredients and the latter the protein. The larvae are fed upon a similar diet, except that the nectar is regurgitated as honey before being served to them. These substances are stored in the cells, and the latter are never provisioned with animal food (but see *Melipona*). The females are provided with corbiculae consisting of special pollen-collecting hairs which are situated either on the abdominal sterna, or on the posterior tibiae and tarsi, or on the femora. Certain genera, however, notably *Nomada*, *Coelioxys* and *Psithyrus*, are inquilines in the nests of other species, and corbiculae are wanting in these instances. A useful account of the structure and biology of certain of the solitary bees is given by Semichon (1906). For the habits of these insects vide also Friese (1922–23), Malyshev (1936), Ferton, Fabre and the literature quoted under the different families. The classification adopted is that of Michener (1944).

Key to the families:

1. Antennal socket connected with fronto-clypeal suture by 2 sutures. Glossa acute, labial palpi with segments similar or the 1st alone, very rarely the 2nd also, elongate and flattened. Mid coxa at least externally much shorter than distance from its summit to posterior wing-base. Females and many males with a defined area on the last visible gastral tergite . . . . . ANDRENIDAE (p. 737)
–. Antennal socket connected with fronto-clypeal suture by a single suture, very rarely by 2 which then converge to enclose a triangle. Labial palpi variable but very rarely with the 1st segment alone elongate 2

2. Mentum and submentum virtually absent. Portion of galea before insertion of palp usually as long as distal part and evenly tapering proximally. Labial palpi usually with all segments similar. Fore wing with basal vein (1st sector of M) nearly always strongly curved. Prepectus usually defined. Postscutellum horizontal. Mid coxa externally much shorter than distance from its extremity to posterior wing-base . . . . . HALICTIDAE (p. 737)
–. Mentum and submentum present. Portion of galea before insertion of palp not longer and usually much shorter than distal part, not evenly tapering proximally. Fore wing with basal vein (1st sector of M) not curved 3

3. Glossa in females and in the majority of males rounded truncate, bilobed or bifid. Submentum elongate and rather broad, not V-shaped. Prepectus completely defined except in a few S. American and Australian genera. Mid coxa externally much shorter than distance from its summit to posterior wing-base COLLETIDAE (p. 737)
–. Glossa acute, often elongate. Submentum V-shaped. Prepectus rarely defined and, if so, only dorsally except in a few parasitic Apidae. Mid coxa externally two-thirds as long as distance from its summit to posterior wing-base, except in Melittidae and a few parasitic Apidae 4

4. Labial palpi with segments similar and cylindrical. Galea short. Mid coxa, except in *Macropis*, much shorter than distance from its summit to posterior wing-base. . . . . MELITTIDAE (p. 737)
–. Labial palpi with first 2 segments elongate and sheathing. Galea very elongate. Mid coxa, except in a few parasitic Apidae, two-thirds as long as distance from its summit to posterior wing-base 5

5. Labrum longer than broad and widened to broad articulation with clypeus. Suture connecting antennal socket to fronto-clypeal suture arising at outer margin of socket. 2 submarginal cells in fore wing, usually about equal in length. Last gastral tergite without a defined area except in *Lithurge*. Scopa, when present, on gastral sternites . . . . . MEGACHILIDAE (p. 737)
–. Labrum usually broader than long; if not, then narrowed basally to a short articulation with clypeus. Suture connecting antennal socket to fronto-clypeal suture

arising at inner margin of socket. Usually 3 submarginal cells in fore wing, rarely 1; if 2, the 2nd usually much shorter than 1st. Last gastral tergite often with a defined area. Scopa, when present, on the hind legs, rarely on gastral sternites also . . . . . APIDAE (p. 738)

FAM. COLLETIDAE.—The large genera *Prosopis* and *Colletes* are Holarctic and also more or less numerous in other regions. Nearly all the other genera are S. African, S. American and especially Australian. The group includes the most primitive Apoidea and the nests are relatively simple structures either in the soil, in hollow stems or in holes in wood. They are often lined with a salivary secretion which dries into a thin transparent pellicle.

FAM. HALICTIDAE.—This very large family of bees is, with the preceding, the only one to be well represented in Australia. *Halictus*, with 35 British species, is very widespread and the species numerous and often difficult to discriminate. The researches of Stöckhert (1923) and Noll (1931) have at last established that some species are social. In *H. malachurus*, for instance, only the fertilized female survives the winter. In the spring, she produces a brood of workers which greatly enlarge the subterranean nest, producing a comb-like structure by excavating soil surrounding the cells. Many such nests are illustrated by Claude-Joseph (1926). The old female now stays in the nest to lay eggs and to guard the entrance. The next brood consists of both sexes but, after mating, only the females seek winter quarters. The workers are smaller and slightly different structurally from the females and probably lay some of the unfertilized eggs from which the males develop. There seem to be a number of variants of this general cycle and many species are purely solitary without workers, but there is still need for much more investigation. The genus *Sphecodes* includes species which are usually red and black in colour and are very similar in structure but lack the scopa and live as parasites or inquilines in the nests of *Halictus* and *Andrena*. In warmer countries, *Halictus* is partly replaced by the genus *Nomia* which judging by the meagre records probably has a rather similar life-history. Also included in the family are such genera as *Dufourea* and *Systropha* which are much more oligolectic, i.e. visit only a few species of flowers.

FAM. ANDRENIDAE.—The principal genus in this family is *Andrena*, the characteristic solitary bee of the Holarctic region, poorly represented elsewhere. There are more than 60 British species (Perkins, 1919), but there are several hundred in the United States, each often gathering pollen and nectar from a very few species of flower. Though solitary bees, the nests are often in large, sometimes compact colonies; rarely (*A. bucephala*, etc.) several females use a common entrance gallery out of which it is presumed the individual burrows diverge. Many species act as hosts for particular species of the parasitic genus *Nomada* and they are also often attacked by Strepsiptera. The latter parasites may induce marked changes in the colour and structure of the host (p. 828). Another well-known genus in the family is *Panurgus*, which includes rather small black bees which visit yellow Compositae; two species are British. *Perdita* is a very large American genus, some of the species of which are minute in size.

FAM. MELITTIDAE.—A small and rather diverse family of bees which are usually markedly oligolectic. British genera include *Melitta*, much resembling *Andrena*, *Dasypoda*, with an enormous tibial scopa in the female, and *Macropis*. *M. labiata* obtains pollen almost exclusively from *Lysimachia vulgaris* and lines its small burrow with a paste made from the sap (Malyshev, 1929).

FAM. MEGACHILIDAE.—An enormous family of bees sometimes called 'gastrilegid' because of the ventral scopa of the female. This structure, however, is absent in the many parasitic species. *Megachile* includes the leaf-cutter bees, most of which construct cells either in rotten wood or in the soil out of cut fragments of green leaves; a few, however, build with mud, as does the allied genus *Chalicodoma*. Fabre's observations on *C. muraria*, the Mason bee, make up one of his most fascinating chapters. The bee is a densely hairy insect, rather larger than a hive bee, black in the female and brown in the male. The nest is built of exceptionally hard masonry constructed with soil particles mixed with salivary secretion and with many small pebbles included and cemented in position. It is attached to walls or to large stones. After eight or nine cells have been built, the whole is then plastered over with the same substance, and the completed nest assumes a dome-like form about the size of half an orange. Notwithstanding the great hardness of these nests, their inmates are very much subject to the attacks of such parasites as Bombyliids, *Leucospis* and *Stelis*. *Osmia* and its allies include a large number of species of Holarctic distribution and of very varied habits. They generally choose hollow places already existing whether

they be in wood, stones, mortar, in empty snail shells, Cynipid galls or elsewhere. Most of them build their cells with earth, but some use cow-dung, resin, or chewed-up leaves. Usually about 10–20 cells are found in a nest and each is stored with a mixture of pollen and honey. Smith recorded a nest (doubtless the combined nests of several females) attached beneath a large stone and composed of 230 cells. *O. tridentata* nests in bramble stems while the very common *O. rufa* will form its nest in almost any convenient hollow, whether it be in the ground or in wood, or it may take advantage of a key-hole, snail shell or other object (see summary by Poulton, 1916). In *Anthidium* (Fig. 544) the males are exceptional in being larger than the females, and like *Osmia* the species usually nest in ready-made cavities. Some of the species form a large mass of 'cotton wool' which they strip with their mandibles from the leaves of various plants. The single British species *A. manicatum*, chiefly occurs in the southern counties, and within the cottony mass the cells are made of a delicate membrane which serves to retain the pollen and nectar. Other species have been observed by Fabre to use resin in place of cotton for their nest material.

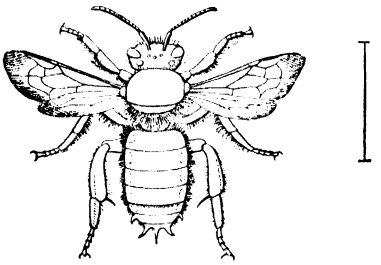


FIG. 544.—*Anthidium manicatum*, male. Britain

After F. Smith: reproduced by permission of the Trustees of the British Museum.

Parasitic genera in this family are *Coelioxys* parasite on *Megachile* and *Anthophora*, *Dioxys* on *Chalicodoma* and *Osmia*, and *Stelis* on *Osmia* and *Anthidium*.

FAM. APIDAE.—As at present constituted, the Apidae includes a vast range of solitary and parasitic bees and also the three principal groups of social species. Of the four subfamilies, the Fideliinae include a few anomalous African bees of doubtful affinities; the Anthophorinae are either soil-nesting, industrious bees or else parasites; the Xylocopinae are solitary bees nesting in plant-stems or in wood, and the Apinae are mostly social bees.

The very large genus *Anthophora* (with smaller, closely allied genera) includes stout, often very hairy bees which nest in the soil, sometimes in large colonies. The large black *A. acervorum* is common in Britain and is one of the earliest spring bees often visiting the flowers of crocus. *Eucera* and its allies are rather similar to *Anthophora* but are known by the elongate male antennae. *Hemisia* (*Centris*) is a large American genus of big, hairy, often banded bees which make very deep burrows in the soil. Of the numerous parasitic genera, the largest is probably *Nomada* which contains almost bare, usually black and yellow, wasp-like bees. They are mostly parasitic on different species of *Andrena*, but *Halictus*, *Panurgus* and *Eucera* are also attacked. *Melecta* includes black species often marked with patches of white tomentum and their hosts are species of *Anthophora*. *Epeolus* includes small black and reddish species with white, tomentose spots which parasitize *Colletes*. The British species of *Nomada* are described by Perkins (1919) and the interesting problem of the evolution of parasitic bees has been discussed by Wheeler (1919—parasitic Aculeates generally) and Grütte (1935). The genus *Xylocopa* or carpenter bees are large, almost humble bee-like, though the abdomen is usually bare dorsally. They excavate long galleries in timber or make nests in large plant stems. *X. violacea* extends as far north as Paris and its habits attracted the attention of Réaumur: both sexes hibernate and reappear in the following spring. According to Bingham *X. rufescens* is nocturnal and its loud buzzing may be heard throughout moonlit nights in Burma. In the tropical species of the subgenus *Mesotrichia* the propodeum and the first gastral tergite are each produced to form an almost closed cavity in which mites of the genus *Dinogamasus* live. The species of mite is specific to each species of bee (Perkins, 1899; LeVeque, 1928–31). The small, usually metallic bees of the genus *Ceratina* are almost bare except for the legs and nest in the pith of plant-stems. Though only *C. cyanea* is British, it is a very large genus with numerous species in Africa and elsewhere. *Allodape* is a somewhat similar genus with many species in warmer climates. Some S. African species exhibit a rudimentary form of social life (Brauns, 1926) and the closely allied genus *Eucondylops* has evolved from and is parasitic on *Allodape*. In the subfamily Apinae, the only solitary bees belong to the S. American *Euglossa* and its allies. These are moderate to very large bees, either bare and metallic or dark and densely hairy. The hind tibia is developed into a corbicle, much as in *Bombus*, and the nest is built either of mud or of resin. It is possible that some species are subsocial

but there is need for further study; at least two parasitic genera have evolved from this stock and are parasitic on *Euglossa*.

The Bombini (Bumble or Humble Bees) include some of the most familiar insects in temperate climates. They are abundant in the Holarctic region but generally confined to the mountains in tropical countries. They are absent from almost the whole of Africa, the plains of India and none are indigenous to Australia and New Zealand. The species of *Bombus* exhibit, in temperate regions, a social life which resembles that found in *Vespa* much more closely than that which obtains in the hive bee. The societies come to an end in autumn and a certain number of the females hibernate to reappear in spring when they form new colonies. The most abundant caste is that of the workers but the latter are not clearly distinguishable from the queens or females except by their smaller size. Soon after fertilization the females hibernate and this phase may be passed either in the ground, or in thatch, rubbish, moss, etc. In Britain the period of torpor lasts about nine months and according to Sladen (1912) it may commence as early as July, as is in the case of *Bombus pratorum*. The latter species is astir again in March or April while other species often wait

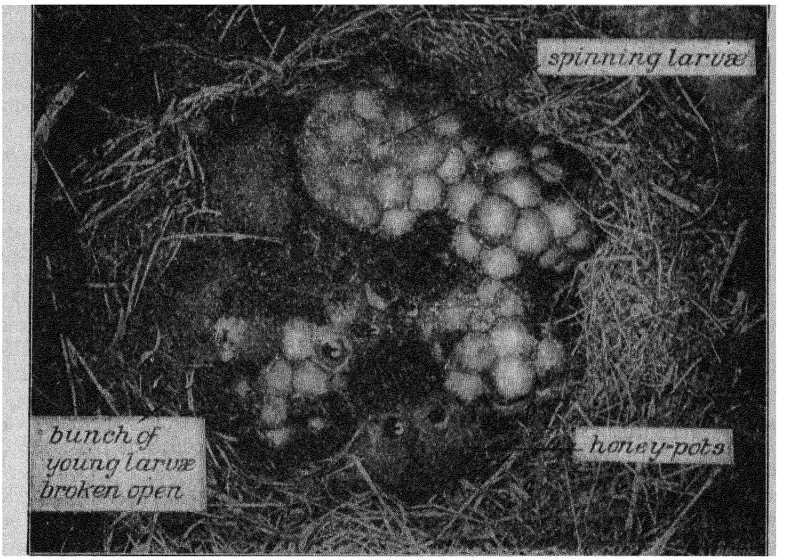


FIG. 545.—Nest of *Bombus lapidarius*
After Sladen.

until May or even June. Each queen seeks out a situation for her future nest: the latter may be underground and consists of fine grass or moss formed into a hollow ball (Fig. 545). Access to the nest is obtained by means of a tunnel which averages about two feet in length. Other Bombi, known as 'carder bees', form surface nests hidden away among grass, ivy or other herbage. They derive their name from their habit of collecting moss and other material used in nest formation and plaiting it with the aid of their legs and mandibles. Having formed the nest the next act of the queen is to collect a mass of pollen which is formed into a paste. Upon the top of this substance she constructs a circular wall of wax and, in the cell thus formed, she lays her first batch of eggs, capping the latter over with a covering of wax. She also constructs a waxen receptacle, or honey pot, which is filled with a store of honey for her own consumption. This store is drawn upon during inclement weather and while the queen is occupied in incubating her eggs. The larvae hatch in about four days and lie immersed in their food-bed of pollen: the queen further supplies them with regurgitated pollen and nectar which is passed to the brood through a hole which she forms in the upper part of the cell. About the 10th day the larvae spin tough pale yellow cocoons and on the 22nd or 23rd day after oviposition the first adults appear and are always workers. New cells are added to the nest as the season advances, and each cell contains on an average about a dozen eggs. The workers convert their old cocoons into honey pots and, in some species, additional waxen vessels are also

constructed. When sufficient workers have emerged, the work of pollen-collecting devolves upon them and the queen becomes restricted to the nest. After the queen has deposited about 200–400 worker eggs, according to the species, she lays other eggs which give rise to males and queens. Both Huber and Schmiedeknecht state that the male and queen cells are not provisioned before the eggs are laid in them, and those larvae destined to produce queens do not appear to receive any different diet from those which will give rise to males. The males and females do not appear until the end of the season. The survivors among these females form the next year's colonies: the males, on the other hand, are short-lived and having once left the nest do not return to it. The nest of *Bombus* usually presents an irregular appearance: the larvae, as they develop, increase in size, and their cell becomes distended, and has a mammilated appearance. The queen adds more wax to the covering so that the larvae always remain hidden, but much of the wax is removed after the cocoons are formed. The cells are only utilized once for rearing purposes and fresh cells are added above the old remains. The members of the genus *Psithyrus* are inquilines in nests of *Bombus*, each species generally sharing the food and shelter of a particular species of host. Furthermore, the colour and size resemblance of the inquiline to the *Bombus* with which it is commonly associated is especially striking. This is very evident in two abundant British Psithyri, i.e.: *P. rupestris* closely resembles *B. lapidarius* and *P. vestalis* likewise simulates *B. terrestris*. According to Sladen the above-mentioned species of *Psithyrus* sting the *Bombus* queens to death and usurp their places in the nests, the *Bombus* workers rearing the *Psithyrus* offspring; other workers, however, have found the two queens subsisting side by side. In such affected nests the population of the host species is naturally greatly reduced in numbers. From the nature of its life *Psithyrus* produces no workers and its males and females differ from those of *Bombus* in their more resistant and shinier integument which, in so far as the abdomen is concerned, is less densely clothed with hair. Owing to the absence of any polliniferous apparatus, the outer surface of the hind tibia of the female *Psithyrus* is convex and uniformly hairy, whereas in *Bombus* it is more or less concave, bare and shiny but marginally clothed with long hairs. In *Psithyrus* also, the female lacks both the comb at the apex of the hind tibia and the auricle at the base of the basitarsus.

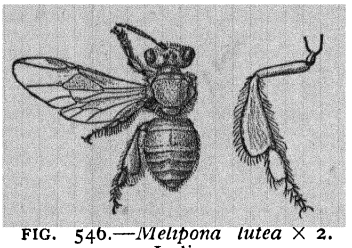


FIG. 546.—*Melipona lutea* × 2. India

After Bingham (F.B.I.).

There are 19 British species of *Bombus* and 6 of *Psithyrus* (Richards, 1927). The biology of these species is described in the well-illustrated manual of Sladen (1912): the works of Hoffer (1882) and Plath (1934) are also important.

The genera *Melipona* (Fig. 546) and *Trigona* (vide also p. 675) include about 250 species which are mainly neotropical with a certain number of members found in the tropics of the Old World. They nest in hollows in trees and rocks, or in walls, and their colonies include enormous numbers of often minute individuals (sometimes less than 3 mm. long) known as 'mosquito' or 'stingless' bees: the latter expression, however, is a misnomer, since a vestigial sting is present (von Ihering, 1904). The workers secrete wax which is produced between the abdominal terga: it is usually mixed with earth or resin forming a dark material called 'cerumen'. The nest consists of a part containing the brood which is separate from that devoted to storing honey and pollen. The entrance to the nest usually projects as a conspicuous funnel which is often guarded by workers during the day and closed with cerumen at night. For an account of the American species and of their habits see Schwarz (1932; 1948) and Salt (1929).

The best known member of the tribe Apini is the hive or honey bee, *Apis mellifera*. It has probably been more completely studied than any other species of insect, its habits having attracted attention from very early times. The structure and biology of this insect have been discussed in many volumes dating from the Renaissance onwards, and the details of its economy are so readily accessible that only the more important features will be referred to here. The insect is rarely, if ever, found wild in Britain, and has been introduced into almost every country of the globe. It is usually regarded as the highest member of the Apoidea, and differentiation into the three forms male, female and worker is more pronounced than among other bees. The male, or drone, is larger and stouter than the worker, and is readily distinguishable from the latter caste by the large holoptic eyes, whose great development is accompanied by a corresponding reduction of the frontal region of the head. The female, or queen, has

a particularly long abdomen extending some distance behind the closed wings. She performs none of the functions of nest building, food gathering, or brood care and lacks the special organs adapted for these purposes. Large prosperous colonies contain 50,000 to 80,000 workers, besides a queen and a variable number of males. The queen is able to survive for several seasons, but the males and workers are relatively short lived. Summer-hatched workers, owing to continuous toil, seldom appear to survive longer than six or seven weeks, but those hatched in autumn live to perform the labours of early spring. The colonies of this species are, therefore, not merely seasonal but are maintained from year to year, and are stored with provisions for winter consumption. When the population increases beyond the capacity of the hive, swarms are emitted which consist of the old queen and a number of workers. In this way the new community is fully prepared for both nest building and reproduction. The original colony is dominated by a new queen and, prior to her emergence, the old queen is prevented from destroying her by the workers. The latter, as far as possible, only allow new queens to develop when it is desirable to emit a swarm. The

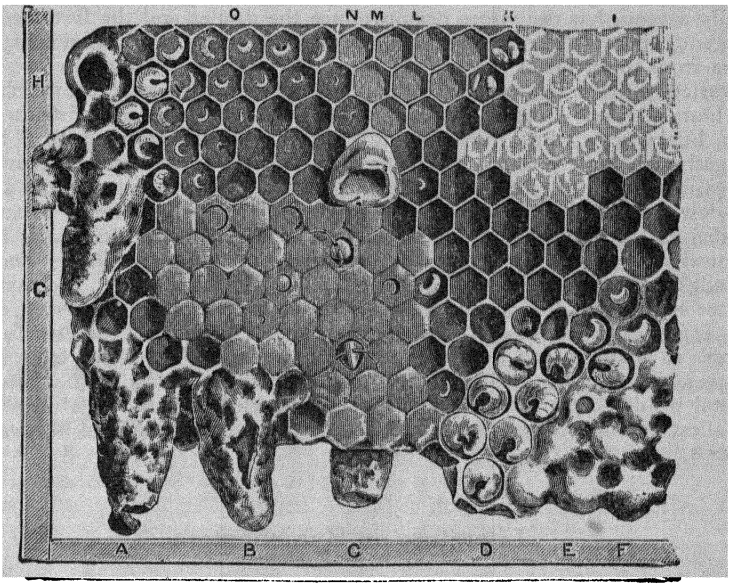


FIG. 547.—Comb of hive bee (natural size)

A, empty queen cell; *B*, do, torn open; *C*, do, cut down; *D*, drone larva; *E*, *F*, sealed drone cells; *G*, sealed worker cells; *H*, old queen cell; *I*, sealed honey; *K*, pollen masses; *L*, pollen cells; *M*, abortive queen cell; *N* emerging bee; *O*, eggs and larvae. *After* Cheshire.

virgin queen takes what is known as the marriage flight, and is followed by a number of males. Copulation occurs in mid-air and the fertilized queen then returns to the nest. If a second swarm be emitted the same season, a new virgin queen accompanies the workers and, as the swarm usually journeys further from the nest than the previous swarm, an opportunity is afforded for the queen to be fertilized by a male from another colony. At the end of the summer, the workers always eject the males from the hive, since they have no further part to play in the life of the community.

The honeycomb, or structural basis of the nest (Fig. 547), is composed of cells which are mostly hexagonal in form, and arranged in two series, placed back to back. The separate combs hang vertically downwards and the long axes of the cells are almost horizontal. The material used in construction is wax which is secreted by the younger workers. It is a product of hypodermal glands situated on the ventral aspect of the 4th to 7th abdominal sterna. The wax is secreted as a fluid and, according to Dreyling (1903), it is exuded through extremely fine cuticular pores, subsequently accumulating and hardening in the form of thin plates. The latter project from pockets situated between adjacent sterna, and the bee removes the wax plates by impaling them on the spines of the distal end of the first tarsal segment of the hind leg (Casteel, 1912). The leg is then flexed forwards, and the wax seized by the mandibles and kneaded into the required condition to form the cells. The cells in which workers

develop are smaller than those destined for rearing the males, while the royal cells in which the queens are produced are the largest of all and irregularly ovoid in form. Other of the cells are devoted to the storing of pollen and honey. In addition to wax, the workers also utilize a resinous substance which they collect from the buds and other portions of various trees. The material is termed propolis, and is used as a kind of glue to fasten loose portions of the comb and to fill up crevices, etc. The queen lays a single egg in each brood cell, and the incubation period is about three days. When the larvae are fully grown, the workers seal up the cells by means of a cover of wax and pollen: thus enclosed the larvae form the so-called cocoons in which pupation takes place. The complete development of the queen occupies approximately 15½ days, the worker three weeks, and the male 24 days. The young larvae are at first uniformly nourished on a diet rich in protein (40–43 per cent.) which is provided by the workers. This food is a secretion of the lateral pharyngeal glands. The larvae of the queens are fed upon this diet throughout life, while those destined to produce workers and males are nourished upon honey and digested pollen from the fourth day onwards. The subject of sex-determination is a highly complex one and it may be said that it is generally agreed that the virgin eggs produce the drones and the fertilized eggs the queens and workers. In rare cases, however, workers may produce queens and other workers from unfertilized eggs (Jack, 1917).

A variety of flowers is visited by bees in order to gather nectar, the most important being Dutch clover: heather, lime, other clovers, the blossoms of fruit trees and bushes, buckwheat, white mustard, etc., are also largely resorted to. The nectar, when gathered, largely consists of cane sugar which, in its conversion into honey, becomes inverted into glucose and laevulose. In addition to nectar, bees also utilize honey-dew and the juices of over-ripe or damaged fruits. In order to supplement the foregoing account the reader is referred to the work of Snodgrass (1925) for anatomical details, and for general information, including the theory and practice of apiculture, to the writings of Cheshire (1886), Ribbands (1953), and many others.

Other species of *Apis* are the three Indian representatives, *A. dorsata*, *indica* and *florea*. *Apis dorsata* constructs a single huge comb sometimes three or four feet in diameter. It is suspended quite exposed from rocks, branches, or from buildings. This species is easily irritated and readily attacks man or domestic animals, sometimes with fatal results. *Apis indica* is perhaps a subspecies of *mellifera* while *A. florea* is the smallest member of the genus and in some respects transitional between *dorsata* and *indica*.

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Order 28. **COLEOPTERA** (Beetles)

Minute to large insects whose fore wings are modified into horny or leathery-elytra which almost always meet to form a straight mid-dorsal suture: hind wings membranous, folded beneath the elytra, or often reduced or wanting. Mouthparts adapted for biting: ligula variably lobed. Prothorax large and mobile, mesothorax much reduced. Metamorphosis complete: larvae campodeiform or eruciform, seldom apodous: pupae adecticous and exarate.

The Coleoptera number approximately 220,000 described species (Schilder, 1949), and are consequently the largest order in the animal kingdom: about 3,700 species inhabit the British Isles. Although they are the predominant insects of the present epoch beetles do not meet the eye so frequently as members of other orders on account of their more concealed habits. Their adaptability and the structural modifications which they exhibit have evidently contributed much to their dominance, for the imagines of no other order of insects have invaded the land, air and water to the same proportional degree. The habits of beetles, therefore, are extremely varied: they are more especially insects of the ground and either inhabit the soil itself, or the various decaying animal and vegetable substances present in relation to that medium. Dung, carrion, refuse of all kinds, humus, rotting wood and fungi all support large associations of Coleoptera. The members of twelve families are true aquatic insects while many other families have aquatic or semiaquatic representatives. The Chrysomeloids and most Curculionoids are usually met with in association with herbaceous plants, bushes and trees. Representatives of the most diverse families, whether they be aquatic or terrestrial, possess ample wings and readily take to flight. Several species are littoral and are daily submerged by the tides. A considerable number of beetles occur in close relation with man since they are found in wool, furs, hides, furniture, museum specimens, and in dry stored foods and drugs. The great solidity of the integument exhibited in the majority of species has been an important factor in protecting them against enemies of various kinds. The various sclerites are fitted together with a precision that marks them out as truly marvellous pieces of natural mechanism.

Included in the order are some of the largest and also some of the most minute of living insects. Among the Scarabaeoids *Goliathus regius*, *Dynastes hercules* and *Megasoma elephas* attain a body-size not found outside the Coleoptera: *D. hercules* (including the cephalic horn) measures up to about 155 mm. long and the Cerambycid *Macrodontia cervicornis* (including the mandibles) attains approximately the same dimension. On the other hand, among the Corylophidae and Ptiliidae are insects so minute that they may reach a length of less than 0·5 mm.

The literature on Coleoptera has assumed enormous proportions. For a general introduction to the study of the order the student should consult the works of Fowler (1912), Jeannel & Paulian (1949) and Crowson (1950–54)

(revised edition, 1955). For the British species the monograph by Fowler (1887–1913) is indispensable: the works of Reitter (1908–16; 1909) and Kuhnt (1913) will also prove valuable for purposes of identification. The leading treatise on the European forms is that of Ganglbauer (1892–1904), but unfortunately it was never completed. The Palaearctic Coleoptera are catalogued by Winkler (1924–32) and the species of the world by Schenkling & Junk (1910–40): Leng (1920) has catalogued the N. American species and his volume contains a very full bibliography of the systematic literature on the order. The British species are listed by Kloet & Hincks (1945).

External Anatomy

The **Head** (Fig. 548).—The head is heavily sclerotized and there is probably no *epicranial suture*. A complete Y-shaped suture occurs, however, in some Hydrophilidae, but this may well be secondary (DuPorte, 1946; Snodgrass, 1947). In most of the Curculionoidea, and in a few isolated genera among other groups, the frons and vertex are prolonged anteriorly to form a *rostrum* (Fig. 551). The latter bears the mouthparts at its apex and the antennae are also carried forwards: as a rule the rostrum has a groove or *scrobe* on either side for the reception of the scape of the antenna. The *eyes* are very variable and may be totally wanting. Eyeless Coleoptera are met with among cavernicolous species and in certain subterranean forms, including those living beneath boulders. Eyes are similarly wanting in *Platypsyllus* and *Leptinus*. In the males of many of the Lampyridae the eyes are very large and contiguous, or nearly so, above and beneath: in the females they are often very small. Occasionally the eyes are partially or almost completely divided by a corneous ridge as in *Trixagus* and *Dorcus*: or they may be completely separated into an upper and a lower eye on each side as in *Gyrinus* and *Amphiops*. *Ocelli* are rarely present but a pair of these organs are found in certain Staphylinidae and in *Pteroloma* (Silphidae), while most Dermestids have a single central ocellus. The *clypeus* is divisible into *anteclypeus* and *postclypeus*. The latter sclerite is fused with the frons and the dividing suture is wanting: the anteclypeus is often infolded and not visible from above (Stickney, 1923). Among Curculionoidea the reduced fronto-clypeal region is often termed the *epistoma*. The *labrum* is very variably developed but is present in nearly all the families: it may, however, be concealed beneath the clypeus, or fused with it, as in the majority of the weevils. The floor of the head, in the median line, is formed by the *gula* and the latter sclerite is marked off from the genae, on either side, by the *gular sutures*. Among most Curculionoidea, and a few other beetles (*Necrophorus*, etc., Fig. 550), the gula is reduced or wanting and the genae meet in the mid-ventral line, and there is consequently only a single gular suture present.

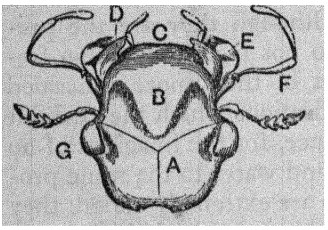


FIG. 548.—*Hydrophilus piceus*, dorsal view of head

A, vertex; *B*, clypeus; *C*, labrum; *D*, mandible; *E*, maxilla and *F*, its palp; *G*, antenna. Adapted from Newport.

The *antennae* exhibit a very wide range of variation and the usual number of segments is 11. They may, however, be 1-segmented, as in *Articerus*, or 2-segmented as in many Paussidae: on the other hand, they may consist of 27 segments or more in rare instances, and there are many transitions between these extremes.

The *mandibles* attain their extreme development in the males of many of the Lucanidae. In this family they often assume relatively enormous proportions and may be branched in an antler-like manner: in *Chiasognathus* their length exceeds that of the whole body (Fig. 549). In weevils of the genus *Balaninus* they have a vertical movement, side by side, instead of being horizontal and opposed, owing to the dorsal position of their condyles. In the Curculionid subfamilies Brachyderinae and Otiorrhynchinae each mandible often bears a round or oval area with a raised margin. These structures are the *mandibular scars* which served as supports for the deciduous *provisional mandibles* (Marshall, 1916). The latter organs apparently enable the newly emerged imago to cut its way through the cocoon but are cast off soon after the insect has freed itself. In a few genera, however, they are permanently retained. In *Passalus cornutus*, certain Staphylinidae, Meloidae, and other beetles a movable inner lobe or *prostheca* is present (Blackwelder, 1934).

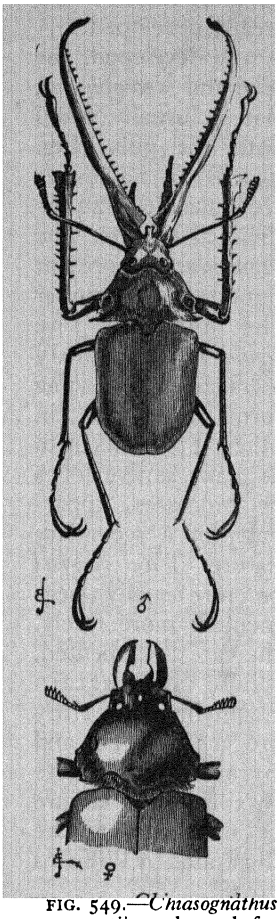


FIG. 549.—*Chiasognathus grantii*, male and female

After Darwin, *Descent of Man.*

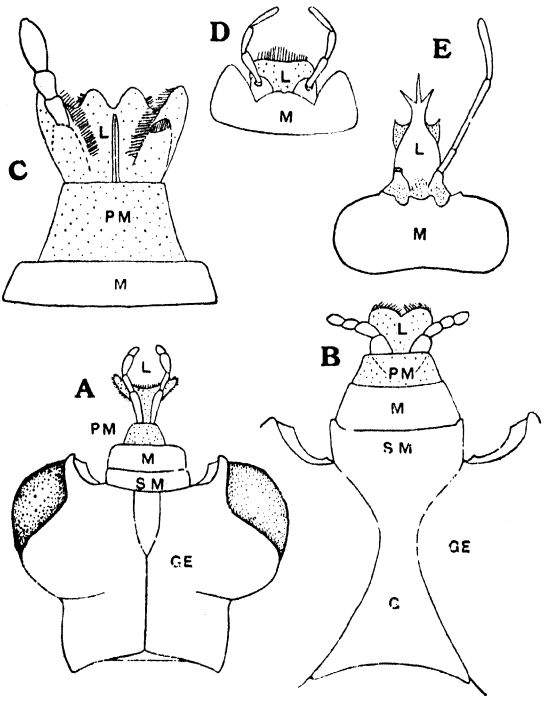


FIG. 550.—A, *Necrophorus interruptus*, ventral aspect of Head. B, *Xylodrepa quadripunctata*, median ventral region of head. C, *Ocypus olens*, labium. D, *Dytiscus marginalis*, labium. E, *Leistus spinibarbis*, labium

G, gula; *GE*, gena; *L*, ligula; *M*, mentum; *PM*, prementum; *SM*, submentum.

The *maxillae*, as a rule, are completely developed with the full number of elements present. In the Adephaga and Dytiscidae the *galea* is generally 2-segmented and palpiform. The *lacinia* is frequently large and blade-like and may carry an articulated process, well exhibited in the Cicindelidae where it is claw-like. Specialization by reduction is frequent: thus a single maxillary lobe or *mala* is present, for example, in the Corylophidae and most of the Nitidulidae as well as among

the Curculionoidea: in other members of the latter group the mala may be wanting. The *maxillary palpi* are generally 4-segmented, and more rarely 3-segmented, while in *Aleochara* they are composed of five segments: in the Pselaphidae and Hydrophilidae these organs are very greatly developed.

In the *labium* (Fig. 550) the *mentum* is large and well developed: the *submentum* is evident in some forms, including *Hydrophilus* and *Necrophorus*, but is usually fused with the gula (Fig. 550, B) or no longer recognizable as an individual sclerite. The *prementum* is present but often folded under the mentum. The *ligula* is extremely variable: in some forms it is entire, in others it presents up to as many as five lobes or processes, apparently of a secondary nature. The *labial palpi* are usually 3-segmented: more rarely, they are 2-segmented, while in certain Staphylinidae they are unjointed and bristle-like. The maxilla and labium of many genera are illustrated by Williams (1938).

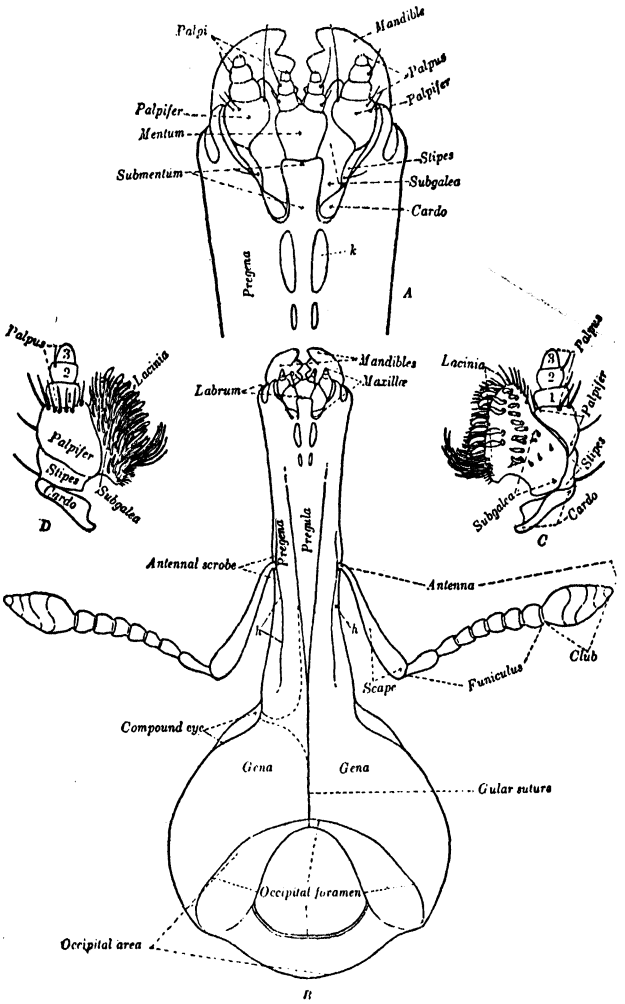


FIG. 551.—*Pissodes strobi*

A, ventral aspect of head; B, apex of rostrum, ventral; C, interno-lateral and D, externo-lateral aspects of maxilla. Adapted from Hopkins, *U.S. Dept. Agric. Entom. Tech. Ser.* 20, pt. 1.

The **Thorax.**—The *prothorax* is the largest of the thoracic segments and is usually freely movable, the latter feature being a marked characteristic of the order. The *pronotum* is composed of a single sclerite and is entirely visible from above. The *pleuron* is frequently undivided into sclerites, and the *notopleural* suture between that region and the pronotum, on either side, is absent in the Polyphaga: in the latter case a single cuticular shield covers the whole of the dorsal and lateral regions. The pleurosternal sutures are distinct except in the Curculionoidea in which group the whole of the prothoracic sclerites are fused into an undivided annular band. The anterior *coxal cavities* are either entire, when they are closed behind by the meeting of the prosternum and epimera, or by the meeting of the epimera alone: or they

may be open, when the space is only bridged over by the membrane. The *meso-* and *metathorax* are fused together: the former segment is considerably reduced while the latter, on the contrary, is largely developed, except in species in which the wings are absent or non-functional. The tergum of both segments is divisible into *prescutum*, *scutum* and *scutellum*. The latter sclerite is median in position and divides the scutum into two separated plates. The *metapostnotum* is generally distinct but, according to Snodgrass, the corresponding sclerite of the mesothorax is wanting. With the exception of the *mesoscutellum* the entire dorsal surface of both segments is usually covered by the elytra. In the metathorax, a furca is invaginated from the sternum and the details of its structure are of some importance in classification (Crowson, 1938, 1944). The arms of the furca provide attachments for the leg muscles and are best developed in species which actively use their legs.

The *legs* are generally adapted for walking or running, but in many of the Scarabaeids and certain of the Carabidae, they are also modified for fossorial purposes. In the Dytiscidae the hind pair are flattened and used for swimming, while in the Gyrinidae both the middle and hind pairs are thus modified. In the Halticinae the hind femora are greatly enlarged for saltatory purposes. The legs of Coleoptera consist of the usual number of parts and the form and disposition of the coxae are of great importance in classification. The tarsal segments are extremely variable in number and afford valuable family and superfamily characters. The primitive 5-segmented condition is characteristic of the Adephaga, the Scarabaeids and many other Polyphaga. Among the Heteromera the fore and middle tarsi are 5-segmented, and the hind pair 4-segmented. In the Chrysomeloidea and Curculionoidea the 4th and 5th segments are anchylosed, the former being very small. In the Staphylinoidea the segments are very variable in number. Among many of the males of this group, and the Adephaga, one or more of the segments of the anterior tarsi, and sometimes of the middle pair also, are dilated and different from their fellows: this feature attains a high degree of specialization among the Dytiscidae.

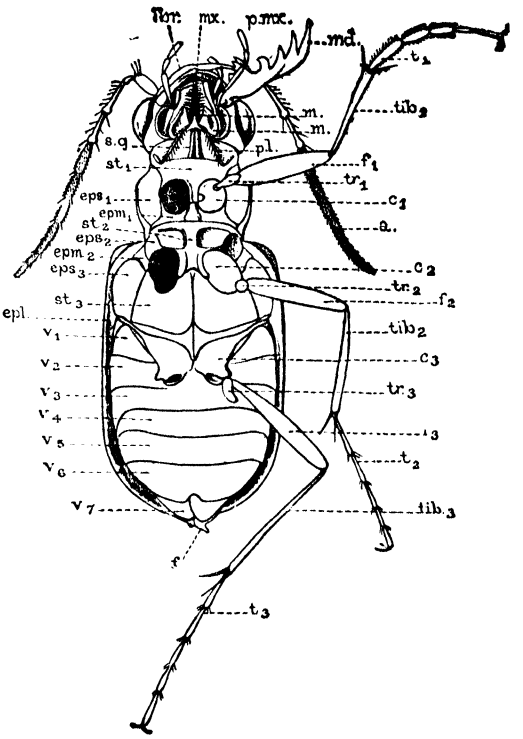


FIG. 552.—*Cicindela*, ventral aspect: male

lbr, anterior margin of labrum; *md*, mandible; *mx*, maxilla and *p.m.x*, palp; *m*, *m*, mentum; *p.l*, labial palp; *s.g*, gular sutures; st_1–st_3, thoracic sterna; eps_1–eps_3, episterna; epm_1–epm_2, epimera; *epl*, epipleuron; v_1–v_3, visible abdominal segments; *f*, aedeagus; c_1–c_3, coxae; tr_1–tr_3, trochanters; f_1–f_3, femora; tib_1–tib_3, tibiae; t_1–t_3, tarsi. From Fowler (F.B.I.), *after* Ganglbauer.

The *elytra* are the highly modified mesothoracic wings and arise

simultaneously with the hind wings: they develop in an exactly similar manner during the greater part of the larval life. In many Carabidae, Curculionidae and Ptinidae the hind wings are wanting and the elytra are often firmly united so as to be immovable. In some Dytiscidae, Jackson (1952) finds considerable variation; some species are winged but have no flight muscles, in others there is a more complete reduction in some or all individuals. In Coleoptera capable of flight the elytra are opened to form an angle with the body, and allow of freedom of motion of the wings, but play no direct part in flight. The sides of the elytra are often reflexed to form the *epipleura* (Fig. 552) which conceal the pleura and are well seen, for example, in the Gyrinidae.

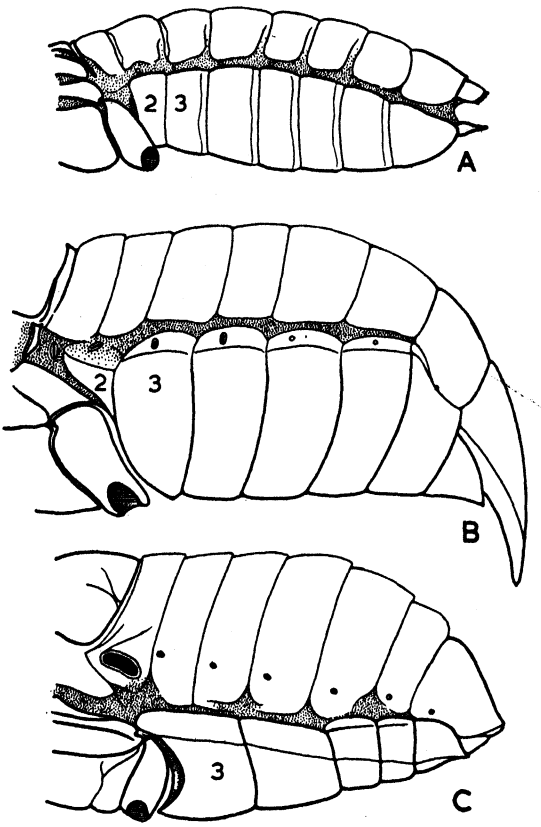


FIG. 553.—Three types of abdomen in Coleoptera. A. Hologastran (*Rhagonycha limbata*, Cantharidae). B. Haplogastran (*Melolontha melolontha*, Scarabaeidae). C. Cryptogastran (*Hylobius abietis*, Curculionidae)

2, 3: 2nd and 3rd abdominal sterna.

The hard texture of the elytra is due to the thickness of the lower layer of the cuticle, and also to the presence of pillars or trabeculae which connect the upper and lower elytral surfaces (Fig. 555). The cavity of the elytron is bounded by a thin hypodermis and contains blood, nerves and tracheae, often together with numerous groups of gland cells: sometimes small lobules of fat-body are also evident. Comstock states that there is a very close similarity between the tracheation of the elytra and the hind wings, but in no case yet examined do the principal tracheae retain the primitive type of branching. The venation of the hind wings has been studied by Kempers (1909), Kühne (1915), Orchymont (1920), Forbes (1922) and others. Three general types are recognizable (Figs. 556, 557). (*a*) *The Adephagid type.*—All the principal

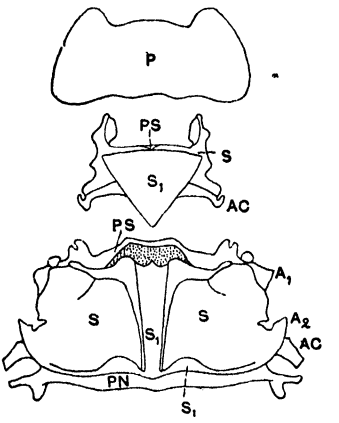


FIG. 554.—*Hydrophilus*, dorsal aspect of thorax with the segments disarticulated

A_1, anterior wing process; A_2, posterior do.; *AC*, axillary cord; *P*, pronotum; *PN*, postnotum; *PS*, prescutum; *S*, scutum; S_1, scutellum. Partly after Snodgrass, *Proc. U.S. nat. Mus.*, 36.

veins remain more or less completely developed and are usually joined by a greater number of cross-veins than occur in other Coleoptera. M_1 is connected with M_2 by means of one or two transverse veins: when two are present an oblong cell, the *oblongum*, is formed which is very characteristic

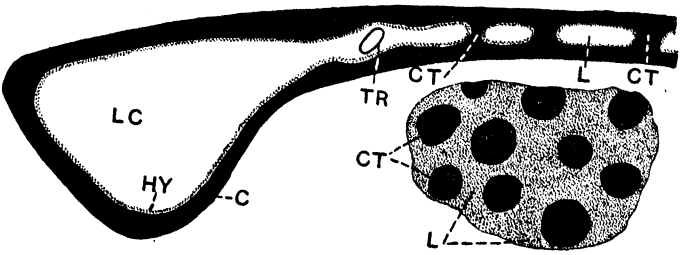


FIG. 555.—Transverse section of a portion of an elytron of *Dytiscus* passing through the outer margin: below, a small area of an elytron seen in surface view (diagrammatic)
C, cuticle; *CT*, trabeculae; *HY*, hypodermis; *L*, lacunae; *LC*, lateral blood channel; *TR*, trachea.

of the type. What appears to be the most generalized venation in the order is found in the Cupedidae. (*b*) *The Staphylinid type.*—Here the chief characteristic is exhibited in the disappearance of all the cross-veins, and the atrophy of the proximal portion of M, the remainder of that vein being isolated in the apical portion of the wing. (*c*) *The Cantharid type.*—In this type M and Cu often coalesce distally forming a very definite loop: at the

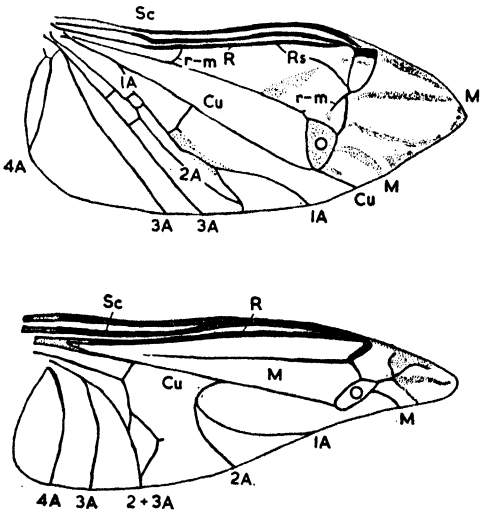


FIG. 556.—Adephagid type of wing. Above, Cupedidae (after Forbes). Below, Carabidae (original)
O = oblongum.

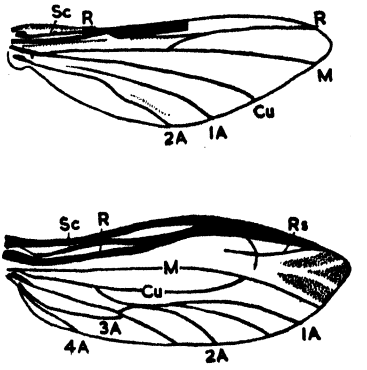


FIG. 557.—Two types of wing in the Polyphaga. Above, Staphylinid type (*Ocypus*). Below, Cantharid type (*Cantharis*)

point of junction a single vein (regarded as M) is continued to the wing-margin. R_2 frequently appears as a recurrent branch of the radius, and cross-veins are commonly present joining the cubital and anal veins. In some cases, the M loop is reduced to a mere hook, or may be absent (Passalidae and many Curculionoidea): when this type of modification occurs, and the cross-veins are atrophied, the Cantharid type is difficult to separate from the Staphylinid one.

The **Abdomen.**—The number of segments which enter into the composition of this region of the body is difficult to determine. As a rule the 1st tergum is membranous and one or more of the sterna from the 1st to the 3rd are aborted. The 1st sternite is never visible externally and is at most traceable in vestigial form at the back of the hind coxal cavities. Eight tergites are commonly visible externally, the 9th and 10th plates being invaginated. Five to seven sternites are visible externally and in this respect four types may be recognized:

(*a*) The Adephagid type. The hind coxae are immovably fused with the metathorax and completely divide the 1st visible abdominal sternite which is more or less fused with the next two, the sutures between them being partly obliterated (Fig. 552).

(*b*) The *haplogastrous type.* The 2nd abdominal segment exhibits a pleurite and a small lateral plate representing the sternite. Exceptionally, in some Staphylinidae, the 2nd sternite is complete (Fig. 553, B).

(*c*) The *cryptogastrous type.* The pleurite of the 2nd abdominal segment is fused to that of the 3rd and the sternite is membranous and nowhere visible externally (Fig. 553, C).

(*d*) The *hologastrous* type. In some Cantharoidea, the 2nd abdominal sternite is, perhaps secondarily, fully sclerotized and distinct from the 3rd (Fig. 553, A).

In many species the terminal abdominal segments of the female are retractile and tubular, thus functioning as an ovipositor, e.g. in the Cerambycidae. The 9th sternite is provided with paired structures to which the segmental appendages may contribute (Tanner, 1927). The male genitalia have been studied by Sharp & Muir (1912; 1918) and those of many species are also illustrated by Jeannel & Paulian (1949). The genitalia are withdrawn into the abdomen and concealed; they take the form of a tubular evagination; with certain associated sclerites, which arise between the 9th and 10th sternites. They have proved to have great value in classification.

Stridulating Organs.—In one form or another these organs are present in the imagines of a large number of families and have been studied by Darwin (*Descent of Man*), Gahan (1900), and Dudich (1920–21). As the latter author remarks, wherever any part of the exoskeleton is subjected to the friction of an adjoining part by the movements of the insect there, in some species or another, these organs are likely to be found. Their position is not constant, even in different genera of the same family, and they are often similar in structure and location in genera belonging to widely different families. They are most extensively developed in the Scarabaeoids where both the larvae and perfect insects are often capable of stridulation (vide Arrow, 1904). Gahan divides these organs among Coleoptera into four groups according to where they are located, but it is only possible here to refer to one or two examples. In certain Nitidulidae and Endomychidae there is a file-like area on the crown of the head which is rasped by the anterior margin of the prothorax. In other cases (certain Tenebrionidae, Scolytinae, etc.) there is a file-like area on the underside of the head, sound being produced by friction with a projecting ridge on the prosternum. Stridulating organs are found on the mandibles and maxillae in the larvae of various Scarabaeidae. They are so arranged that a series of teeth on the maxillae rasp against some granulations on the ventral side of the mandibles, when

the maxillae move forwards and backwards. Many of the Cerambycidae have stridulatory organs: in some cases the sound is produced by rubbing the hind margin of the prothorax over a striated area of the mesonotum: in others, it is produced by the friction of the hind femora against the edges of the elytra. The most remarkable stridulating organs are those met with in the larvae of the Lucanidae, Passalidae and of *Geotrupes* and its allies. They consist of a series of ridges or tubercles on the middle coxae, while the hind legs are modified in various ways as rasping organs. In certain of the Curculionidae there is a stridulating file on the underside of the elytra near their apices: the rasping is effected by a series of small tubercles situated on the dorsal side of the abdomen. In some cases the file is present on the abdomen in the females, and on the elytra in the males, and the rasping organs are similarly reversed.

Internal Anatomy

The **Digestive System.**—The digestive system of Coleoptera has been mainly studied by Dufour whose results have been published in a series of papers (1824–40) and Bounoure (1919). Beauregard (1890) and Mattingly (1938) have also studied the digestive organs in the Meloidae, Mingazzini (1889a) in the Scarabaeoids, Sedlaczek (1902) in the Scolytinae and Bordas (1903; 1904) in the Hydrophilidae and Silphidae. The mouth opens into the *pharynx* or widened commencement of the *oesophagus* and the latter region is a simple tube of variable length. At its hinder extremity the oesophagus expands to form the *crop* which is of very general occurrence although wanting according to Beauregard in pollen-eating beetles such as *Zonitis*, *Sitaris* and *Mylabris*: it is large and capacious in *Carabus* (Fig. 558) and other genera. The oesophagus or crop, as the case may be, is followed by the *gizzard* which is usually a small chamber lined by sclerotized ridges or folds, or with spines or denticles whose arrangement may be of generic importance (Balfour-Browne, 1934, 1935; Thiel, 1936): it is present in many carnivorous and wood-boring Coleoptera, notably in the Cicindelidae, Carabidae, Dytiscidae and Scolytinae. The *mid intestine* is very variable in form, and is often of a complex nature. Its most characteristic feature is the presence of large numbers of small enteric caeca which often vary in character in different portions of the stomach. In the Carabidae and Dytiscidae the latter region is a simple slightly tortuous tube provided with numerous closely packed caeca, but the latter are usually wanting from its posterior portion. In *Meloë* the mid intestine is large and sac-like, occupying the greater part of the abdominal cavity. In the Scarabaeoidea (Fig. 559) it is very long and convoluted while in *Copris lunaris* it is thrown into a series of numerous coils after the manner of a watch-spring. In the Scolytinae the mid intestine is divisible into three regions: a sac-like anterior region, a narrow tubular middle portion and a wider posterior which is partially or completely invested with small caeca. The hind intestine is always more or

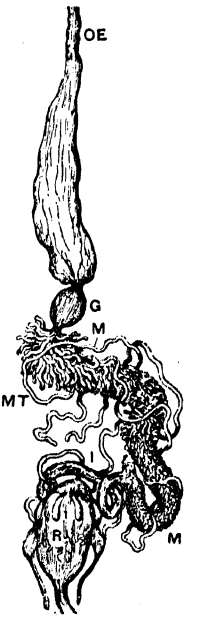


FIG. 558.—*Carabus monilis*, alimentary canal

OE, oesophagus; *G*, gizzard; *M*, mid intestine; *I*, ileum; *R*, rectum; *MT*, Malpighian tubes. *After* Newport.

less convoluted: it is relatively short in the Cicindelidae and Carabidae, but long in *Dytiscus* and many other genera. In the Dytiscidae (Fig. 560) it gives off a conspicuous *rectal pouch*, an organ which is characteristic of that family (Bordas, 1906). Although a relatively small sac in *Ilybius* it attains enormous dimensions in *Dytiscus* and bears an apical tubular appendix: a posterior caecum is also present in *Silpha* and *Necrophorus*. The *rectum*, when specially differentiated, is often a large chamber: *rectal papillae* are present in certain Passalidae and Silphidae, but as a rule they are wanting.

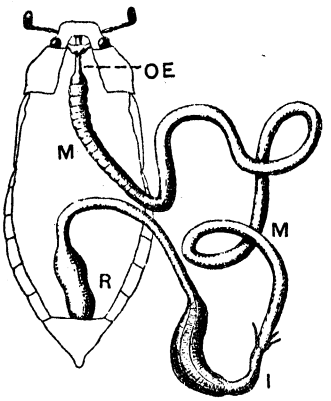


FIG. 559.—*Melolontha melolontha*, alimentary canal

Lettering as in Fig. 558. Adapted from Bounoure.

The *Malpighian tubes* are typically four or six in number and are of considerable importance in the classification of the families into major groups (Poll, 1932; Stammer, 1934). In the Lampyridae, where there are four of these vessels, the tubes of each pair unite distally, thus presenting the appearance of loops (Bugnion, 1920). A number of Coleoptera including *Donacia*, *Haltica*, *Cerambyx*, *Oedemera*, etc., exhibit the cryptonephric condition (Lison, 1937) in which the Malpighian tubes have two apparent terminations in the intestine owing to the fact that their distal extremities become applied to the walls of the colon or rectum, instead of remaining free as in most other insects. In no case, however, have any secondary openings into the hind intestine been discovered (Woods, 1916).

Gnathal glands have been little studied in Coleoptera and it is often stated that salivary glands are absent. Pradhan (1939) describes labial and maxillary glands in Coccinellids and Gupta (1937) records what appear to be labial glands in Tenebrionids. *Pygidial glands*, which are defensive in function, exist in many beetles and are very fully discussed by Berlese. They are paired organs secreting corrosive and pungent fluids which can sometimes be ejected to a distance of several inches. These glands open in close association with the anus and, among the Carabidae, they have been studied in detail by Dierckx (1899) and Bordas (1899). In *Feronia melanaria* (*vulgaris*), for example, each gland consists of spherical acini composed of

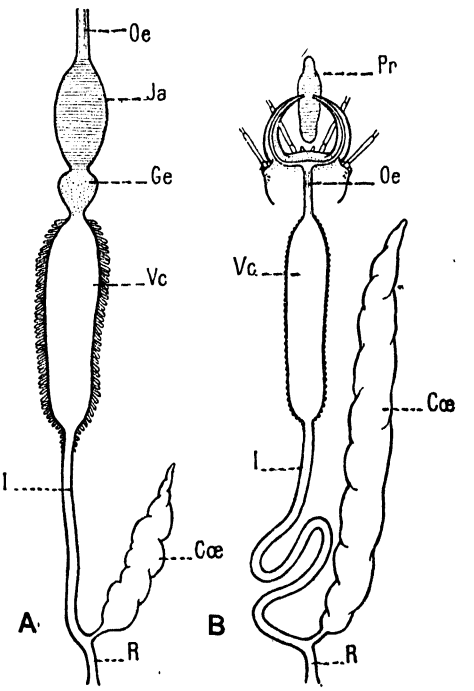


FIG. 560.—*Dytiscus marginalis*; alimentary canal of A, imago; and B, larva

Oe, oesophagus; *Ja*, crop; *Ge*, gizzard; *Vc*, mid intestine; *I*, hind intestine; *Coe*, caecum; *R*, rectum; *Pr*, prey. *After* Portier.

gland cells: each acinus opens by a separate duct into the common canal of its side. In *Carabus* and *Cychrus* the ejected fluid contains butyric acid and in *Mormolyce* it is stated to be capable of paralysing the fingers for twenty-four hours afterwards. In *Brachinus* and its allies, and also among the Paussidae, a volatile vapour is ejected with an audible sound: it is very corrosive and stains the fingers of those who handle these insects. In the Staphylinid genera *Staphylinus*, *Stenus*, etc., and also in *Blaps* eversible foetid anal glands are prevalent.

The **Nervous System.**—The most important differences in the nervous system are exhibited in the ventral cord (Brandt, 1879). As a rule the commissures retain their double nature, a feature which is well exhibited in the thorax of most beetles. The most generalized type of nervous system is found in the Cantharidae where, in addition to the supra- and infra-oesophageal centres, there are three thoracic ganglia and seven or eight abdominal ganglia. The latter number is maintained in *Dictyopterus* and seven abdominal ganglia are found in *Cantharis* and *Lampyris*. Reduction in the number of abdominal ganglia, unaccompanied by a similar specialization of the thoracic centres, may be traced through a number of genera. Thus, in *Cicindela* and *Tenebrio* there are six ganglia in the abdomen; in *Silpha*, *Mordella* and *Creophilus* there are five: in *Donacia*, *Meloë* and *Callidium* there are four: in *Cassida* there are three and in *Chrysolina* and *Coccinella 7-punctata* there are two. Among the Scarabaeids (*Geotrupes*, *Aphodius*, etc.) the abdominal ganglia are merged into the metathoracic ganglion to form a common centre. In a number of other Coleoptera the meso- and metathoracic ganglia are closely united or merged together owing to the disappearance of the connectives between them. This feature is characteristic of many other Scarabaeoids (*Melolontha*, *Passalus*, *Lachnosterna*, *Phyllopertha*, *Cetonia*) and the centre thus formed also includes the fused ganglia of the abdominal chain. In the Curculionidae there are usually two separate abdominal centres, in *Gyrinus* one, and in *Necrophorus* five. The maximum specialization is found in *Serica brunnea* and *Amphimallon solstitialis*. In the former insect all the thoracic and abdominal ganglia unite to form a single complex: in the latter species Brandt states that coalescence has proceeded still further, the infra-oesophageal ganglion being also involved in the fusion.

The **Circulatory System.**—The structure of the dorsal vessel has only been investigated in a few examples. The heart is divided into a variable number of chambers and is continued as the aorta through the thorax into the head where it becomes branched at its apex. In *Melolontha* Straus-Dürckheim found nine chambers with eight pairs of ostia. In *Lucanus* Newport described seven chambers and a similar number of pairs of alary muscles.

The **Respiratory System.**—The tracheal system attains its highest degree of differentiation among the actively flying members of the Scarabaeoidea, particularly in *Geotrupes* and *Melolontha*. Its trunks are greatly ramified and in many species there is an elaborate system of air-sacs. The latter structures do not attain a great size, their chief characteristic being the large numbers present. In *Melolontha* they occur throughout the body, even penetrating into the recesses of the head (Straus-Dürckheim). In *Lucanus* (male) the large massive head and mandibles are filled with air-sacs, especially the mandibles. Newport states that the air sacs are developed in rows from long tracheae which penetrate the jaws, and the latter apparently unwieldy structures are thus rendered extremely light.

As a rule ten pairs of spiracles are present: the first is situated between

the pro- and mesothorax and the remaining pairs are metathoracic and abdominal in position. Among the Scarabaeids and certain Curculionids and other Coleoptera, the eighth pair of abdominal spiracles is either absent or vestigial and non-functional. In the Scolytinae the number of functional abdominal spiracles varies from five to seven. Special modifications in aquatic species are mentioned under the families concerned.

The **Reproductive System.**—The *male reproductive organs* have been investigated by Dufour (1825), Escherich (1894), Bordas (1900), Williams (1945) and others. They consist of the testes, the vasa deferentia, one or more pairs of accessory glands and a median ejaculatory duct. Vesiculae seminales

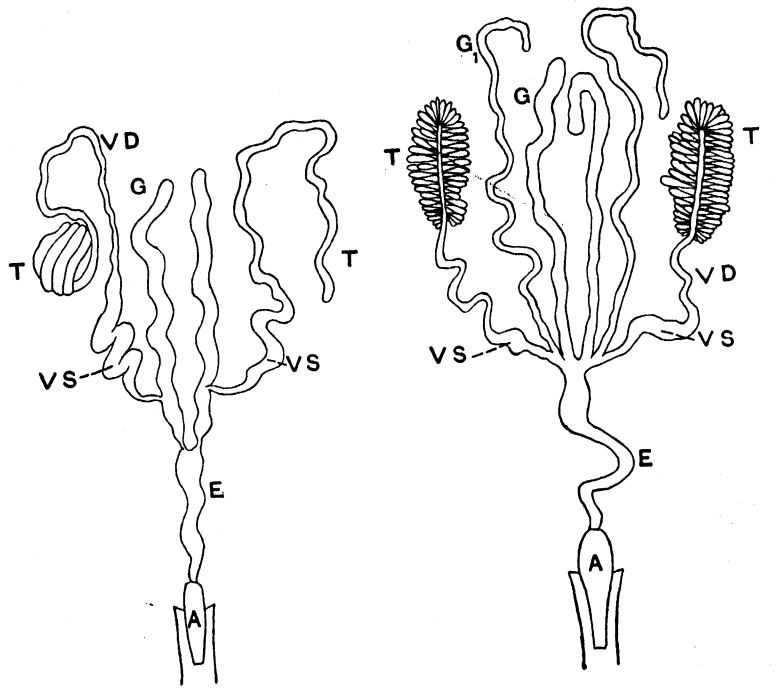


FIG. 561.—Male reproductive organs of—left, Adephaga; right, Polyphaga. The right testis in the Adephaga is represented uncoiled

A, aedeagus; *E*, ejaculatory duct; *G*, accessory gland (ectadenes); G_1, accessory gland (mesadenes); *T*, testis; *VD*, vas deferens; *VS*, vesicula seminalis. Adapted from Bordas.

are often present as dilatations of the vasa deferentia. Two general types of reproductive organs are recognized by Bordas and are based upon characters afforded by the testes (Fig. 561). In the Adephaga, these organs are simple and tubular and more or less closely coiled, each being enclosed in a membrane. In the second type the testes are compound and divided into a number of separate follicles. The latter may be rounded capsules, each communicating with the vas deferens by means of a separate duct, as in the Chrysomelids, Curculionids, and Scarabaeids. Or, the testicular follicles may be composed of aggregations of small rounded or oval sessile sacs which open directly into the vas deferens (most other Polyphaga).

The accessory glands exhibit many differences with regard to their position, number and mode of origin. Escherich (1894) has divided them into ectadenia and mesadenia: the former are believed to arise as ectodermal invaginations of the ejaculatory duct, while the latter are stated to be of

mesodermal origin, since they are formed as outgrowths of the vasa deferentia. Definite ontogenetic evidence is needed, however, to substantiate these conclusions.

The *female reproductive organs* (Stein, 1847; Williams, 1945) may likewise be divided into two types, according to whether the ovarioles are polytrophic or acrotrophic in character. The former type is characteristic of the Adephaga and the latter type is found, so far as known, throughout the Polyphaga. The ovarioles vary greatly in number: thus in *Ips typographus*, *Hylobius abietis* and *Sitona lineatus* there are two ovarioles to each ovary: in *Ocypus olens* there are three, in certain Elateridae four, in *Dorcus* and *Saperda carcharias* twelve, in *Byrrhus pilula* there are about twenty, and in the Meloidae they are extremely short and much more numerous. In some Coleoptera (*Dytiscus*) a colleterial gland is present in association with each oviduct. A *spermatheca* is generally present and opens, by a slender and often exceedingly long duct, either into the vagina or the bursa copulatrix. An accessory gland, of variable character, is generally found in connexion with the spermatheca. In many Coleoptera a second passage or 'canal of fecundation' leads from the spermatheca or its duct and opens into the vagina near the point of union of the two oviducts (Fig. 562). This canal is believed to allow of the direct passage of the spermatozoa from the spermatheca to the eggs. A *bursa copulatrix* is present as a diverticulum of the wall of the vagina. It is believed that the spermatozoa are received into this sac during copulation and subsequently make their way into the spermatheca. A *spermatophore* is found in some species but not in others (Khalifa, 1949). The process of fecundation in Coleoptera, however, is very little understood and the significance of the frequently great length of the spermathecal duct is unknown.

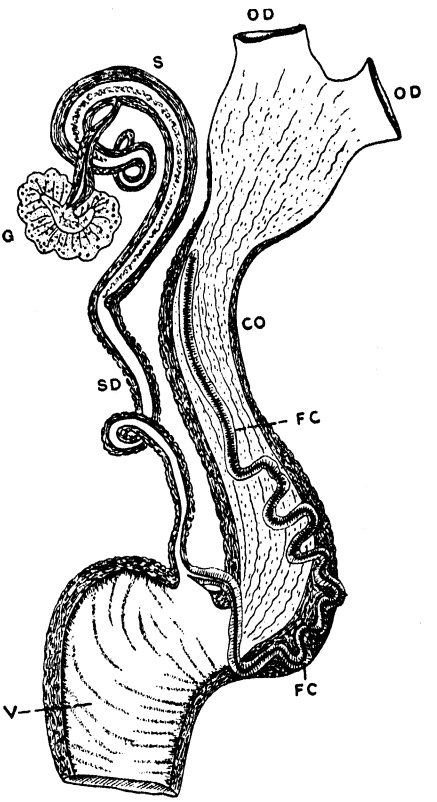


FIG. 562.—*Oodes helopioides* (Carabidae), proximal portion of female reproductive organs

OD, paired oviduct; *CO*, common oviduct; *S*, spermatheca with *SD* duct and *G* gland; *FC*, fecundation canal; *V*, vagina. *After* Stein.

Metamorphoses

The **Egg.**—The eggs of Coleoptera are usually ovoid in form and rarely exhibit any marked diversity of form of structure as is seen, for example, in the Hemiptera and Lepidoptera. In *Ocypus* they are of unusually large size and few in number, while in the Meloidae they are small and the number

laid by a single female may run into several thousand. Many Coccinellidae lay their eggs in batches on leaves, the Hydrophilidae enclose them in cocoons, while among the Cassidinae they are protected in highly specialized oothecae. In the Curculionidae they are frequently deposited in deep holes drilled by the rostum of those beetles in the food-plant. In the Scolytinae the females have the habit of entering into the trunk or plant within which the eggs are laid.

In several genera—*Necrophorus* (Pukowski, 1933), *Platystethus* (Hinton,

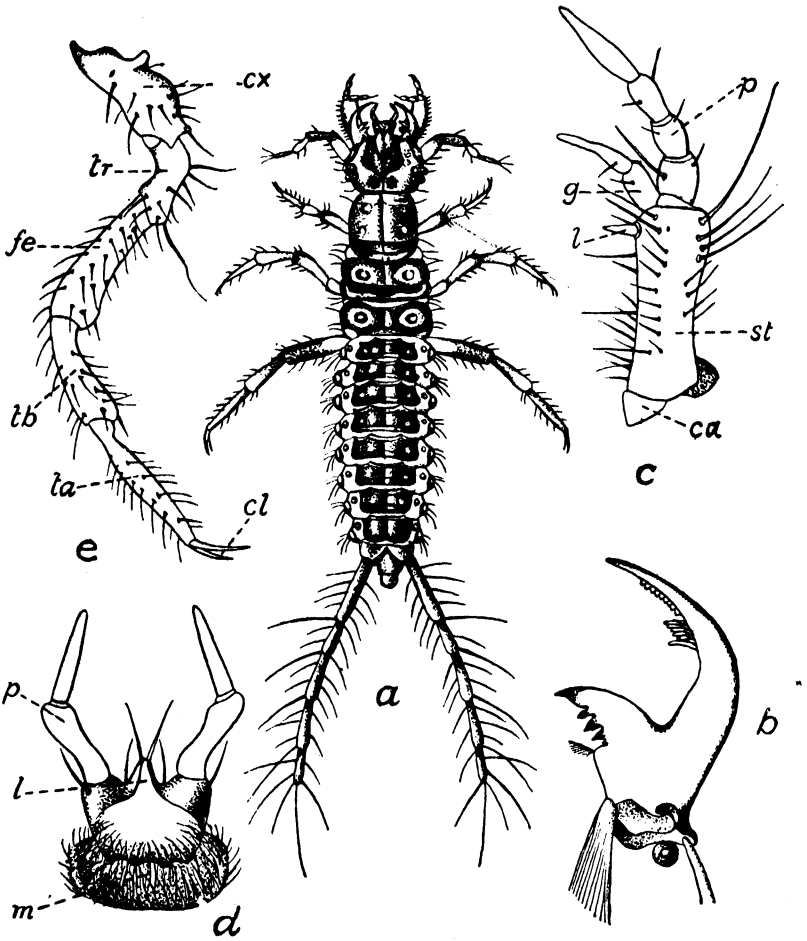


FIG. 563.—*a*, Larva of a Carabid (*Loricera*) × 8. *b*, Mandible × 60; *c*, Maxilla of *Nebria* larva; *d*, Labium × 32; *e*, Leg of *Nebria* larva × 24

From Carpenter *after* Schiödte.

1944), some Scolytinae—the females exhibit maternal care, protecting and sometimes feeding the young larvae (von Lengerken, 1954).

The **Larva.**—In Coleopterous larvae the head is well developed, the mouthparts are adapted for biting and do not differ in their essential features from those of the adults (Böving, 1936; Anderson, 1936). Such larvae never possess abdominal feet, but they are generally provided with thoracic legs: cerci (or urogomphi) may be present or absent. The tracheal system is generally peripneustic with usually nine pairs of spiracles: the first pair is located,

as a rule, between the pro- and mesothorax, and the remaining pairs are situated on the first eight abdominal segments. There is, in many cases, a marked similarity among larvae of the same family. This is well exhibited for example in the Carabidae, Buprestidae and Curculionidae. On the other hand, the larval differences found among the Chrysomelidae are scarcely paralleled in any other family of insects. Some of the most remarkable forms occur in the aquatic families Haliplidae, Gyrinidae and Hydrophilidae with their special adaptations to life in the water. Among terrestrial larvae, those of the Dermestidae, with their dense clothing of tufted hairs, are totally different in appearance from all other Coleoptera.

The primitive campodeiform larva (Fig. 563) is characteristic of the Adephaga, many of the Staphylinoidea, and of the first instar in the Meloidae and Rhipiphoridae. Among other of the Staphylinoidea and the vast majority of the Cucujoidea, the larvae are more highly modified and, although they incline to the campodeiform type, they are transitional between the latter and the eruciform type (Fig. 564). Among the Chrysomeloidea, Curculionoidea and Scarabaeoidea the eruciform larva is prevalent. The extreme apodous type is characteristic of the great majority of the Curculionoidea. It is also met with in certain of the Cerambycidae and Buprestidae, in the dung-feeding larva of *Cercyon*, and in the Eucnemidae, while an apodous stage occurs in the ontogeny of members of the Meloidae and Bruchidae. It is a comparatively easy matter, therefore, to arrange a graduated series of larval Coleoptera. At the head of such a series is the active, armoured campodeiform type, with well-developed antennae and mouthparts, completely formed legs with tarsi and paired claws, and movable jointed cerci: larvae of this nature are well exhibited in the Carabidae. At the other extreme are the soft apodous maggots of the Curculionidae, with their vestigial antennae, reduced mouthparts and no cerci. The mode of life is the primary modifying factor in the development of larval types and, in the absence of an exposed or predatory life, structural changes sooner or later supervene and attain their culminating point in the degenerate internal-feeding larvae that live surrounded by an abundance of nutriment. Hypermetamorphosis is known to occur in a few Coleoptera. It is well exemplified in the Meloidae whose first instar is a campodeiform larva, and in the later development modified campodeiform, eruciform and apodous stages may be passed through in the ontogeny of an individual species (Fig. 194). Hypermetamorphosis similarly prevails in the Rhipiphoridae, Micromalthidae, in *Lebia scapularis* and in the parasitic Staphylinids *Aleochara bilineata* and *algarum*.

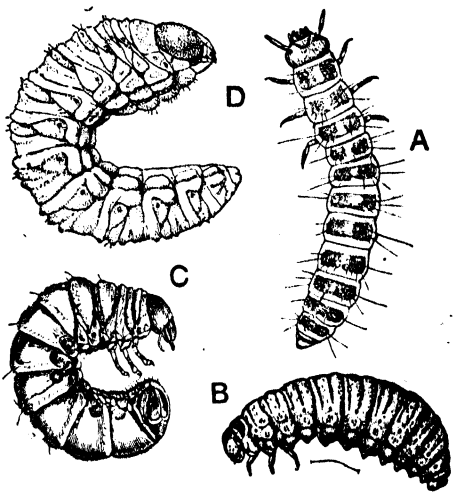


FIG. 564.—Coleopterous larvae

A, campodeiform (Cucujidae); *after* Chittenden, *U.S. ent. Bull.*, 4 n.s. B, eruciform (Chrysomelidae); *after* Chittenden, *U.S. Dept. Agric. Year Book*, 1896. C, scarabaeiform (Scarabaeidae), *after* Riley. D, eruciform and apodous (Curculionidae), *after* Chittenden, *U.S. ent. Bull.*, 23 n.s.

The head bears a variable number of ocelli: thus there may be six of

these organs on either side as in the Carabidae and Hydrophilidae, four in the Cicindelidae, or they may be reduced to a single one, and even the latter may degenerate into a mere pigment spot. In many larvae which are internal feeders ocelli are totally wanting. Antennae are well developed in campodeiform larvae, and are very long in those of the Helodidae: almost every stage in reduction may be traced until they are represented by papilla-like vestiges as in the Curculionidae. The mandibles are large and exserted in predacious forms, and in the Dytiscidae they are specially modified for suctorial purposes. In larvae which live internally in wood, and other plant-tissues, they are short and stout. Structures resembling superlinguae are comparatively well developed in the Dascillidae, and vestigial structures of a similar nature occur in the Scarabaeidae (Carpenter & MacDowell, 1912): rudiments have also been found by Mangan in the Dytiscidae. The maxillae (Figs. 563, 565) are always well developed: their palpi are variable being long in *Gyrinus* and *Stenus*, while in eruciform larvae they are often reduced to the condition of 2-segmented papillae. In the majority of Coleopterous larvae there is a single lobe or mala which is often composed of two segments. Separately differentiated galeae and laciniae are evident, however, in a number of cases and are present, for example, in *Agriotes*, the Byrrhidae, certain Silphidae and in the Scarabaeids. The labium is characterized by the absence of paraglossae: the palpi are commonly 2-segmented but in the Curculionidae they are represented by unjointed tubercles. The glossa is frequently present, but is very variable, and in many genera it is not separately distinguishable. In *Silpha* the ligula is represented by a pair of rounded lobes which are perhaps to be regarded as being those of a divided glossa. The legs exhibit different degrees of development: among the Adephaga they are undoubtedly primitive and are characterized by the presence of a distinct tarsus and paired claws. These features are lost in the Polyphaga, where the tarsus is not separately differentiated, and the claws are single. Exceptions are extremely few, but in the first instar of the Micromalthidae and Meloidae a tarsus is present and the claws are paired. The abdomen is 10-segmented and, among the Carabidae and Staphylinidae, the anal segment is often tubular and functions as a pseudopod. Cerci are well developed jointed appendages in many campodeiform larvae: in other cases they may be fixed and unjointed (*urogomphi*). The morphology of the rigid horny anal processes of many larvae is not understood: they have the appearance of being non-appendicular outgrowths of the body-wall, but when their development is studied they may prove, in some cases, to be highly modified cerci.

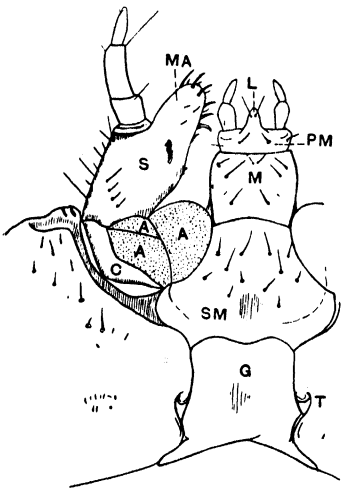


FIG. 565.—Gula, labium and right maxilla of a Tenebrionid larva (*Embaphion*)

AA, articulating areas; *C*, cardo; *G*, gula; *L*, ligula; *M*, mentum; *MA*, mala; *PM*, prementum; *S*, stipes; *SM*, submentum; *T*, tentorial pit. Adapted from Böving, *J. agric. Res.*, 22, 1921.

The respiratory system is subject to comparatively few modifications. The position of the first pair of spiracles is somewhat variable: although commonly intersegmental, they may as in *Cantharis* (*Telephorus*) be located

on the mesothorax. Well-developed metathoracic spiracles have been observed in the Lycidae but in other families they are absent or vestigial. The most striking variations occur in aquatic larvae (Hinton, 1947): *Peltodytes* and *Gyrinus* are apneustic, and respire by means of filamentous processes of the body-wall, while certain of the Hydrophilidae are metapneustic.

Information on the internal anatomy of Coleopterous larvae is fragmentary and very scattered. The alimentary canal has been studied by Portier (1911) in the Dytiscidae and Hydrophilidae, by Payne (1916) in *Cantharis*, by Woods (1916; 1918) in *Haltica*, and by Mingazzini (1889) in the Scarabaeids. In the latter group and also in *Cantharis* and *Calosoma* it pursues a straight course from the mouth to the anus, the hind intestine in these instances being short (Fig. 566). In the Dytiscidae and Scolytinae the gut is convoluted owing to the increase in length of the hind intestine. A well-developed crop is present, for example, in *Calandra* but in *Cantharis*, *Haltica* and *Dendroctonus* it is represented by a small distal enlargement of the oesophagus. A gizzard is present in the latter genus, while both crop and gizzard are wanting in the Dytiscidae and Hydrophilidae. The mid intestine is very variable, but always forms a large portion of the gut, and frequently exhibits differentiation into several distinct regions. In *Cantharis* it is a large simple sac, but in many larvae it is coiled and tubular, as for example, in the Dytiscidae, Hydrophilidae, and also in *Haltica* and *Dentroctonus*. Differentiation into separate regions is evidenced by change of calibre, by the histological structure, and the presence or absence of enteric caeca. In *Oryctes*, and other Scarabaeids, the latter structures are very large and are restricted to three annular bands (Fig. 567): in *Calandra* they are represented by numerous papilla-like outgrowths. An extensive caecum is sometimes present in relation with the hind intestine. In *Dytiscus* it occupies a considerable part of the body cavity and a large caecum is also present in many Scarabaeids. In the Coprinae the larvae have a characteristic dorsal hump which serves for the accommodation of this organ. The Malpighian tubes, as a rule, are similar in number and character to those of the imagines. The nervous system generally consists of three thoracic and seven or eight abdominal ganglia. In *Coccinella 7-punctata* the abdominal ganglia are concentrated in the anterior segments of the hind body, the intervening commissures being very much abbreviated. In *Melolontha*, and other Scarabaeids, the whole of the ventral ganglia are concentrated in the thorax.

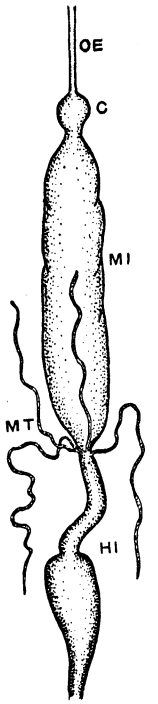


FIG. 566. — *Cantharis*, alimentary canal of larva

OE, oesophagus; *C*, crop; *MI*, mid intestine; *MT*, Malpighian tubes; *HI*, hind intestine.



FIG. 567.—*Oryctes nasicornis*, alimentary canal of larva

OE, oesophagus; $C_1C_2C_3$ enteric caeca; *MI*, mid intestine; *S*, sac of hind intestine; *R*, rectum. *After* Mingazzini.

The heart has been observed by Payne in *Cantharis*. It is of an extremely

narrow calibre and apparently exhibits no division into chambers: nine pairs of alary muscles are present. Segmental glands have been described in a few cases: a pair is present on each of the thoracic and abdominal segments in *Ocypus* (Georgevitsch, 1898), *Chrysomela* (Berlese), and *Cantharis* (Payne).

The **Pupa.**—The pupae in this order are of the exarate type, pale-coloured, and are invested by a thin, soft cuticle. In some of the Staphylinidae they are obtect (Hinton, 1946: 318), being covered by an exudation that solders the appendages down to the body and forms a hardened coat. In the Coccinellidae the pupae likewise have a hardened integument and are, moreover, often conspicuously coloured. A large number of Coleoptera pupate in earthen cells below ground: many others pupate within the food plant. A cocoon is frequently present, but the nature and origin of the substance by means of which it is produced needs investigation. In certain of the Curculionidae the cocoon is formed by a product of the Malpighian tubes, while among several of the Scarabaeids it is described as being formed from the contents of the posterior caecum. Many of the Cerambycidae construct pupal cells largely impregnated with carbonate of lime. The naked exposed pupae of the Coccinellidae are often protected by the persistent remains of the last larval skin (cf. Hinton, 1946a).

Literature on the Metamorphoses.—The most important publications on the life-histories of these insects are those of Schiödte (1862–81), which are written in Latin and have excellent illustrations, and of Böving & Craighead (1931). The complete literature on the transformations of European Coleoptera, up to 1894, has been collated and arranged by Rupertsberger, while Beutenmüller (1891) has catalogued the references to those of the American species. A series of papers by van Emden (1939–49) provides keys for the identification of the British species and gives many references to the literature.

Classification of Coleoptera

Most recent classifications of the beetles derive from that of Ganglbauer (1903) which has been expounded in more detail in relation to previous systems by Gahan (1911), Fowler (1912) and Leng (1920). The suborder Archostemmata has been more recently added (Kolbe, 1908; Böving & Craighead, 1931). Further valuable discussions of the subject have been published by Peyerimhoff (1933) and Meixner (1935). A series of papers by Crowson (1950–54) (revised 1955) has been much used in the account which follows. This author, however, treats the Strepsiptera (p. 825) as a superfamily of the beetles and in 1955 erects a fourth suborder, the MYXOPHAGA, for the families CALYPTOMERIDAE (hitherto part of the Clambidae, p. 779), LEPICERIDAE (with one or two Central American species), SPHAERIIDAE (p. 779), and HYDROSCAPHIDAE (p. 779). These forms are stated to have notopleural sutures, a more or less distinct oblongum, but Rs reduced. The insects are all small and seem to require further study.

Suborders

1. Hind coxae immovably fixed to the metasternum, completely dividing the 1st visible abdominal sternite which is more or less fused with the 2nd and 3rd. Notopleural suture present in prothorax. Wings usually with 2 *m-cu* cross-veins defining an oblongum. 4 simple Malpighian tubules, testes tubular, coiled inside a membranous sheath, only 1 pair of male accessory glands, ovarioles polytrophic. Larva with a tarsus and 2 (rarely 1) claws developed in the legs, mandibles without a molar area . . . . . **Adephaga** (p. 769)

–. Hind coxae not immovably fixed to the metasternum and not completely dividing the 1st visible abdominal sternite 2

2. Wings with the distal part spirally coiled in repose, usually with an oblongum. Notopleural suture present in the prothorax. Larval legs with a tarsus and claws, at least in the first stage; cerci absent; mandibles with a molar area **Archostemmata** (p. 774)

–. Wings with distal part not spirally coiled, never with 2 *m-cu* cross-veins. Notopleural suture absent or incomplete. Malpighian tubules of various types, testes not tubular and coiled, ovarioles acrotrophic. Larval legs without a distinct tarsus and nearly always with 1 claw . . . . . **Polyphaga** (p. 774)

Suborder **ADEPHAGA**

This includes a single superfamily, the Caraboidea. In many respects, such as the larval structure, the group retains a primitive character. In other ways, however, for instance in the structure of the hind legs, the Adephaga are probably specialized for an active predatory life which was not pursued by their ancestors. A few only of the Carabidae have become secondarily vegetarian. Crowson (1955) has recognized one more family, the Trachypachidae, with a few European and American species, which run to couplet 5, but otherwise have the appearance of Carabids.

Table of families:

1. Terrestrial insects with the hind coxae not extending to the elytra, so that the metapleura and the 1st visible abdominal segment are in contact. First 2–4 antennal segments without pubescence 2

–. Aquatic insects with the hind coxae extending to the elytra and dividing the metapleura from the 1st visible abdominal segment. All antennal segments with similar surface ornamentation 5

2. Metasternum without transverse groove in front of hind coxae which are well separated. 1st visible abdominal sternite exposed between hind coxae, 2nd and 3rd fused. Head and prothorax with deep longitudinal grooves. Hind wing without oblongum . . . . . RHYSODIDAE (p. 770)

–. Metasternum with no transverse groove in front of hind coxae which are almost or quite contiguous. 1st visible abdominal sternite not or hardly exposed between hind coxae 3

3. Clypeus extending laterally in front of antennal insertions. Lacinia of maxilla usually with a hook articulated at apex. Elytra not regularly striate. Hind wing usually without oblongum . . . . . CICINDELIDAE (p. 770)

–. Clypeus not extending laterally in front of antennal insertions. Lacinia of maxilla very rarely with such a hook 4

4. Front tibia with both spurs terminal. Front coxal cavities closed behind. Elytra with a notch or fold at sides posteriorly . . . PAUSSIDAE (p. 771)

–. If both front tibial spurs are terminal the fore coxal cavities are open behind. Elytra without this notch or fold . . . . . CARABIDAE (p. 770)

5. Hind coxae produced into large plates, covering first 2 or 3 abdominal sternites HALIPLIDAE (p. 772)

–. Hind coxae not produced into such plates 6

6. Metasternum with a distinct transverse suture in front of hind coxae . . 7

–. Metasternum without such suture 8

7. Front coxae conical, projecting, their cavities closed behind. Tibiae and tarsi fringed with long swimming hairs . . . . HYGROBIIDAE (p. 772)

–. Front coxae spherical, their cavities open behind. Legs not adapted for swimming . . . . . AMPHIZOIDAE (p. 772)

8. Eyes not completely divided. Antennae filiform. Mid and hind legs not very short and broad . . . . . DYTISCIDAE (p. 772)

–. Eyes completely divided into dorsal and ventral parts. Antennae short and thick, 2nd segment with a process. Mid and hind legs forming short, broad paddles GYRINIDAE (p. 773)

FAM. RHYSODIDAE.—The members of this small family (Arrow, 1942) are readily distinguished from other Adephaga by their stout and conspicuously moniliform antennae (Fig. 568). There are rather more than 100 species, mostly tropical, but with a few extending into southern Europe. All stages live in rotten wood and the larvae are of a reduced type without cerci.



FIG. 568.—*Rhysodes boysi*

FAM. CICINDELIDAE (Tiger Beetles).—The members of this family are among the most voracious and fierce of all insects, particularly in the larval stages and, on account of these habits, they have earned the popular designation of tiger beetles. The differences from the Carabidae are not very striking and apart from convenience the group might well be placed as a subfamily of the Carabids. They are characterized by the markedly prominent eyes, the large and acutely toothed mandibles, and by the lacinia usually terminating in an articulated hook. The legs are long or very long, and there are generally six ventral abdominal segments visible in the female and seven in the male (Fig. 552). The family comprises about 2,000 species (cf. Horn, 1938), the majority being denizens of tropical and subtropical lands. About half its members belong to the genus *Cicindela* and to the latter are assigned the four British representatives of the family. Tiger beetles are often brightly coloured, although they seldom appear conspicuous in their natural surroundings. Their movements are very active, they run with extreme rapidity and many quickly take to the wing. Although their flights are of short duration, their darting movements render it extremely difficult to follow their course with the eye. A large number of the species are most active in hot sunshine but others, including apterous forms, are nocturnal. The species of *Cicindela* chiefly affect open sandy localities, either inland and away from water, or on the seashore or along the margins of rivers: *Collyris*, *Tricondyla* and their allies are largely arboreal.

The larvae of species of *Cicindela* are described and figured by Schiödte, by V. E. Shelford and by van Emden (1935). They are characterized by the head and prothorax being larger and broader than the rest of the body. The mandibles are large and there are six ocelli (two vestigial) on each side. The legs are rather long and slender, the tarsi bear paired claws and there are no anal cerci. The most characteristic organ consists of a pair of hooks arising from a swollen base on the dorsal side of the 5th abdominal segment. These larvae are ground dwellers, living in burrows which may extend for a foot or more in the earth. The broadened head and prothorax occupy the entrance to the burrow, and its curiously bent body enables the larva to maintain a firm contact with the sides of its abode. This is mainly achieved by the dorsal hooks already mentioned, and the legs also assist in this respect. The food consists of other insects that may wander near the mouth of the burrow and, when the prey is sufficiently near, the larva suddenly throws back its head, seizes the victim with its long sharp jaws, and draws it within the retreat where it is devoured. According to V. E. Shelford the larva of *Cicindela purpurea* requires twelve or thirteen months for its growth and during that time it passes through three ecdyses. The larva of *Neocollyris* has been described by R. Shelford (1907) and by Docters van Leeuwen (1910). It is of the typical Cicindelid form but there is only a single pair of ocelli on each side of the head. In the place of the pair of dorsal abdominal hooks there is a series of three smaller hooks on either side of the same segment. This larva bores into the shoots of tea and coffee plants and, according to van Leeuwen, that of *Tricondyla* is very similar in structure and habits.

FAM. CARABIDAE.—This important family comprises about 20,000 described species and is distributed throughout the world. In temperate regions its members are almost entirely ground beetles occurring in the soil, under stones, in moss and rotting wood, under bark, etc. The elytra in many species are firmly soldered together and the wings are often atrophied. In the tropics there are numerous arboreal genera, with well-developed wings and considerable powers of flight. Carabidae are closely allied to the preceding family but are readily distinguished by the form of the clypeus, and the absence of the terminal hook on the lacinia of the maxilla. In many genera the legs are slender, and adapted for running; in others (*Clivina*, *Dyschirius*, etc.) they are shorter, and are used for digging. Although a considerable number of the species is metallic or otherwise brightly coloured, the majority have the sombre dark coloration of ground insects. Many Carabidae, in their general configuration,

bear a resemblance to the Tenebrionidae, but may be easily separated upon tarsal characters. Although both the larvae and adults are essentially carnivorous a few have been recorded as devouring cereals and the seeds of plants, the habit being noted in species of *Ophonus*, *Zabrus*, *Omophron* and *Amara*. *Ophonus rufipes* sometimes causes damage to strawberries. *Calosoma* largely preys upon Lepidopterous larvae and *C. sycophanta* has been imported in large numbers from Europe into N. America, in order that its predacious habit may be utilized in destroying the larvae of the gipsy and brown-tail moths (Burgess, 1911). Species of *Anophthalmus*, and other genera, are devoid of eyes and live in caverns or beneath huge boulders deeply embedded in the earth. Members of the tribe Brachinina have the property of secreting an evil-smelling defensive fluid from the anal end of the body. In the case of the Bombardier beetles (*Brachinus*), this fluid rapidly volatilizes into a gas which appears like a minute jet of smoke when it comes into contact with the air, and its discharge is accompanied

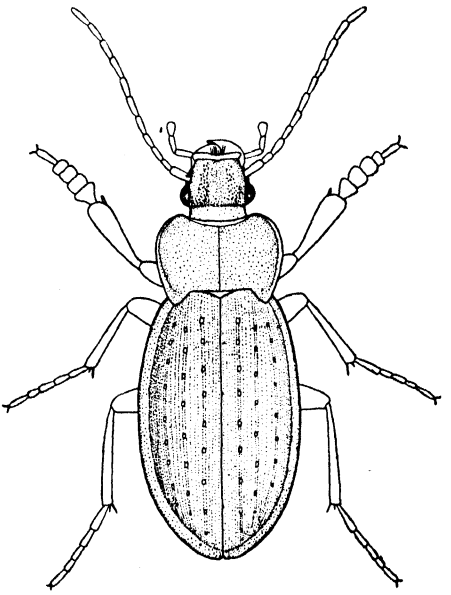


FIG. 569.—*Carabus nemoralis* × $\frac{5}{2}$. Europe

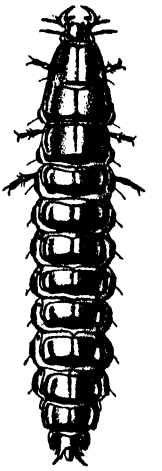


FIG. 570.—*Carabus cancellatus* larva × $\frac{7}{4}$

From Fowler (F.B.I.) *after* Schiödte.

by a distinctly audible sound. The fluid which is said to contain oxides of nitrogen possesses caustic properties producing an effect upon the skin resembling that of nitric acid.

Carabid larvae (Fig. 570) are very active, linear or elongate in form, with ten abdominal segments, and the legs are terminated by a pair of claws. The head carries a pair of sharp caliper-like mandibles and there are six ocelli on either side. The 9th abdominal segment carries a pair of cerci of variable length and the 10th segment is tubular in form, and generally provided with a pair of protrusible vesicles (Kemner, 1912–13). In addition to the writings of Schiödte and Xambeu, a number of Carabid larvae are described by Böving (1910; 1911), Dimmock & Knab (1904), Kemner (1912; 1913), and van Emden (1942) provides a key to the genera.

The Carabidae are divided into many subfamilies, the largest being the Pterostichinae with over 5,000 species. The Carabinae comprise many of the larger and more striking forms (Fig. 569), and the Thyreopterinae includes the arboreal Malayan genus *Mormolyce*, in which the lateral borders of the elytra are produced into broad leaf-like expansions. The Pseudomorphinae are likewise an aberrant group, and have the head grooved on either side for the reception of the antennae.

FAM. PAUSSIDAE.—The Paussidae as here defined include the Ozaeninae which are usually placed in the Carabidae. There is much to be said for Darlington's (1950) view that the Paussids should also be treated as a subfamily of the Carabids. There are about 400 species, all tropical or subtropical and, except the Ozaeninae, probably all associating with ants. They differ from the usual Adephagid type in

possessing fewer than six visible abdominal sternites, but the researches of Escherich, Wasmann and others show that they resemble Carabidae in certain features of their internal anatomy. Most of the peculiarities which distinguish the Paussidae from other families are adaptations to a myrmecophilous life, and are most strikingly exhibited in the antennae (Fig. 571). In *Protopaussus* these appendages retain the simple 11-segmented Carabid type; in *Cerapterus* and other genera they are 10-segmented and exceedingly broad and compressed; in *Pleuropterus* most of the segments are soldered together and in *Paussus* and many other genera they are apparently 2-segmented. The 2nd segment is greatly enlarged to form a club, which assumes the most bizarre shapes, and is probably developed as the result of the consolidation of an originally multi-articulate flagellum. According to Wasmann (1910) the antennal development is correlated with the growth of a glandular exudatory tissue which produces an aromatic secretion. This tissue is found not only in the enlarged antennal segments but also beneath the body-wall of the head, prothorax and apex of the abdomen. Its positions are indicated by the presence of tufts of yellow hairs or groups of cuticular pores which facilitate the diffusion of its secretion. The latter is eagerly licked by the ants off the bodies of their Paussid inquilines, who are thus enabled to make a return for the hospitality they receive (cf. p. 728). The metamorphoses of the family have received very little attention: the larva of *Paussus* is of a modified carabid type (Böving, 1907; van Emden, 1936).

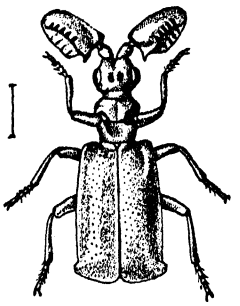


FIG. 571.—*Paussus testaceus*, Tenasserim
After Fowler (F.B.I.).

FAM. AMPHIZOIDAE.—A very small family (Edwards, 1950) consisting of four species which are indigenous to N. America and one to Tibet. They frequent cold, rapid streams where they cling to stones and timber, but are not adapted for swimming. They feed on drowned insects. The larva of *Amphizoa* is described by Hubbard (1892): it is likewise aquatic, the side margins of the segments are extended into lamellate prolongations and the larva bears a close resemblance to that of a Silphid. Six ocelli are present on either side, the tarsal claws are paired, and there are eight abdominal segments terminated by a pair of short spine-like cerci. The only pair of functional spiracles is terminal, the remaining pairs being obsolete.

FAM. HYGROBIIDAE.—Like the Amphizoidae this is a very small family with a remarkably discontinuous geographical range, its single genus *Hygrobia* occurring in Britain and S. Europe, central Asia and Australia. The species are aquatic but, unlike those of *Amphizoa*, the legs are adapted for swimming. *Hygrobia hermanni* is capable of loud stridulation which is produced by rubbing the apex of the abdomen against a file on the inner aspect of the elytra. The larva of this species is figured by Schiödte; the spiracles are minute and functionless, and it respires by means of a series of ventral branchiae. The body has a club-shaped appearance owing to the greatly enlarged head and prothorax and the narrow linear abdomen. The latter is terminated by two very long cerci and a median process of very similar proportions. For an account of the biology of this species vide Balfour-Browne (1922).

FAM. HALIPLIDAE.—A family of about 200 small aquatic beetles of very wide geographical range. They and their larvae feed upon algae in both running and standing water, where they are found among aquatic vegetation or under stones. Three genera and rather more than a dozen species are British. Their larvae are very peculiar and quite distinct from those of any other family of Coleoptera. The whole body is invested by segmentally arranged groups of fleshy process, which are long and thread-like in *Peltodytes*, and shorter in *Haliplus*. In the latter genus there are eight pairs of abdominal spiracles, but in *Peltodytes* spiracles are wanting and the processes of the body-wall function as tracheal gills (Bertrand, 1928).

FAM. DYTISCIDAE (True Water Beetles).—Although this family occurs all over the world it is more especially characteristic of the Palaearctic region: about 4,000 species are known, over 100 being British (Balfour-Browne, 1940–50). Its members frequent both running and standing water, one or two species inhabit thermal springs, while others occur in brackish or more or less salt water. The remarkable eyeless genus *Siettitia* has been found in subterranean waters in France. The structure and classification of the family form the subject of a comprehensive memoir by Sharp (1882) and this authority points out that, although the Dytiscidae are aquatic in their larval and imaginal instars, they are to be regarded as modified terrestrial Adephaga.

In this connexion it may be noted that (1) in their general structure and venation they resemble the Carabidae, the main differences being in the form of the metasternum, the hind coxae, and natatorial legs; (2) they drown more quickly than many land beetles do, the imagines can exist perfectly well on land, and are capable of prolonged flight; (3) the pupae, so far as is known, are terrestrial. These insects may be readily distinguished from the Hydrophilidae, which they resemble in general shape, by their filiform antennae: Dytiscidae are, furthermore, exclusively carnivorous both as larvae and adults. The hind legs function as swimming organs, and are greatly flattened, widely separated and fringed with long hairs. In the males of certain genera the first three segments of the fore tarsi are dilated to form highly efficient adhesive pads which are provided beneath with cup-like suckers. The latter are moistened with a glutinous secretion and, according to Blunck (1912), this product indirectly aids adhesion after the manner of grease in an air-pump and, directly, by increasing the adhesive force. The male, by the aid of these sucker-pads, is enabled to retain hold of the female for many hours continuously. The best known member of the family is *Dytiscus marginalis*, a species which has been more fully studied from every aspect than any other example of the Coleoptera. The eggs of this insect are laid singly, each in an incision made by the ovipositor in the stem of a water-plant. The larva is extremely voracious and preys upon various aquatic animals including molluscs, worms, insects, tadpoles and even small fishes. The victim is pierced by the long sickle-shaped mandibles which, as Meinert and others have shown, are traversed internally by a fine, almost closed in, groove. The latter communicates at the base of the mandible with a transverse conduit which, along with its fellow of the opposite side, opens into the cibarium. A secretion of the mid gut is injected through the channelled mandibles into the prey and digestion of the tissues of the latter takes place externally. By means of the pumping action exerted by the pharynx the liquefied food is imbibed through the mandibular canals and thence into the gut. For details concerning the structure of the mouthparts and the physiological questions involved vide Portier (1911). In the imago, on the other hand, the mandibles are masticatory and digestion takes place wholly internally. The larva swims with the aid of its legs which are fringed with hairs and are efficient oars: it is also capable of making sudden movements by throwing its body into serpent-like curves. The last two abdominal segments and the small pair of terminal lobes are fringed with hairs, which enable the larva to hang head downwards, suspended from the surface film. In this position it is able to take in air by the caudal pair of spiracles: the remaining seven pairs of the latter organs are rudimentary and closed. When fully fed, the larva makes its way to the moist earth near the water, and there constructs a cell in which pupation takes place. In the adult beetle the last two pairs of spiracles are markedly larger than those preceding. When the insect comes to the surface to breathe the caudal extremity rises above the water, thus placing the enlarged spiracles in communication with the atmosphere. A supply of air, furthermore, is retained beneath the elytra and clings to the felted hairs covering the abdominal terga. This is utilized during submergence and is renewed when the beetle comes to the surface, the elytra being slightly elevated to allow of the free entry of air beneath them.

The literature on *Dytiscus* is very extensive: for further details concerning its structure and biology reference should be made to the great monographic work edited by Korschelt (1923). The larvae of Dytiscidae and of the two preceding families are described by Bertrand (1928).

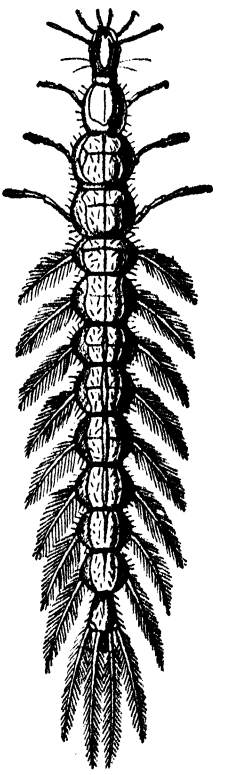


FIG. 572.—*Gyrinus marinus*, Larva × 6

From Fowler (F.B.I. *after* Schiödte.

FAM. GYRINIDAE (Whirligig Beetles).—Included in this family are about 700 species which are surface swimmers. They are mostly gregarious and sometimes occur in large congregations. Individuals are seen constantly darting in graceful curves around one another with an agility that renders their movements difficult to follow with the eye. The various species are very uniform in appearance, being ovoid or elliptical, more or less flattened, and of a steely-black or

bronze lustre. The antennae are very different from the prevalent Adephagid type, being extremely short and stout, auriculate basally, and inserted beneath the front. The eyes are divided into upper and lower organs, and it has been suggested that the former are adapted for aerial vision and the latter for use beneath the water. The fore legs are long and prehensile: in the male the tarsi are often dilated and provided with suckers. The hind legs are broad, greatly flattened, and highly adapted for swimming, while the middle pair are similarly modified, but in a lesser degree. *Gyrinus* is chiefly carnivorous and its eggs are laid end to end in rows upon submerged water plants. The larva (Fig. 572) is elongate with deeply constricted segments, the mandibles are pointed and perforated by a sucking canal, and the legs long with paired claws. Each of the first eight abdominal segments bears a pair of plumose tracheal gills, and two pairs of similar organs are carried on the 9th segment. Pupation takes place in a cocoon which is attached to water plants. *Orectochilus*, the only other common British genus, is mainly nocturnal in habits.



FIG. 573. — *Cupes latreillei* *After* Lameere.

Suborder ARCHOSTEMMATA

This includes with certainty only the family **CUPEDIDAE**, but Crowson (1950) has suggested that the **MICROMALTHIDAE** (with one or two Central American species) may also find a place here. The Cupedidae with about 20 species are found in both hemispheres, including Australia. Mesozoic fossils are not uncommon in British rocks. The structure of the adult shows several affinities with the Adephaga but its internal anatomy is unknown. The larva, however, is a specialized wood-feeder (Snyder, 1913; Fukuda, 1938). The body widens somewhat posteriorly and terminates in a stout anal spine; there are no cerci and the legs are short and single-clawed. The Micromalthidae has one species *Micromalthus debilis*, of the U.S.A., since introduced into Hawaii and S. Africa. The larva develops in timber, especially in mines, and undergoes the most complex developmental cycle of any beetle (Barber, 1913; Pringle, 1938; Scott, 1941), including four larval forms (cf. p. 191).

Suborder POLYPHAGA

This suborder includes the majority of beetles and their grouping into superfamilies is a matter of great difficulty. There is a number of exceptional genera which are difficult to fit into the system or which still need further study. The following key, based on that of Crowson (1950), must be used with care.

Superfamilies of the Polyphaga

1. Pleural sclerites of the true 2nd abdominal sternite distinct from those of 3rd, sternite itself represented by small lateral plates (Fig. 553, B), rarely fully developed when the elytra are much shorter than the abdomen. Tarsi usually with 5 segments, fore tibia often spinose or toothed. Antennae filiform or clubbed, club often made up of last 5 segments (**Haplogastra**) 2

–. Pleural sclerite of the true 2nd abdominal sternite almost always fused to that of 3rd, sternite itself usually entirely membranous (Fig. 553, C), more rarely fully sclerotized. Antennal club, if developed, not usually made up of the last 5 segments (**Cryptogastra**) 5

2. Antennae usually 10-segmented, with 3–7 apical segments produced on one side to form a lamellate club. Species usually stout **Scarabaeoidea** (p. 782)

–. Antennae never with a club of this type. Species usually less stout. Wing-venation of Staphylinid type (Fig. 469) 3

3. Maxillary palpus nearly always longer than the antenna of which the first 3–5 segments are glabrous, the next segment cup-like, and the last ones form a strong pubescent club. Head usually with a Y-shaped impressed line on the front. Wings usually with Cantharid venation (Fig. 469). Habits mostly aquatic **Hydrophilóidea** (p. 776)

–. Antennae not so constructed and not shorter than the maxillary palpi. Head without a Y-shaped impressed line. Habits rarely aquatic . . . 4

4. Antennae with last 3 segments rarely forming a compact club; if they do, 1st segment not elongate. Exoskeleton rarely very hard and shining, elytra truncate and usually leaving more than 2 abdominal segments exposed **Staphylinoidea** (p. 778)

–. Antenna geniculate with last 3 segments forming a compact club. Exoskeleton hard, black, shining, elytra truncate and leaving 1 or 2 abdominal segments exposed . . . . . **Histeroidea** (p. 777)

5. Hind coxa almost always with a vertical posterior surface and with the postero-ventral edge produced into a plate which partly covers the retracted femur. Antennae filiform, serrate or pectinate, very rarely the last 1–4 segments sharply differentiated from the rest. Tarsi nearly always 5-segmented, rarely with the 4th reduced and enclosed in the lobes of the 3rd 6

–. Hind coxa rarely with a vertical posterior surface and the postero-ventral edge produced into plates; if so, the antennae has the last 3 segments very long or forming a club 12

6. Mid coxae widely separated, hind coxae close together with broad femoral plates, fore coxae transverse with exposed trochantins. Tarsi with 5 segments, none lobed below, last not longer than the others together. Head with no distinct fronto-clypeal suture. . . . . **Byrrhoidea** (p. 787)

–. If the mid coxae are widely separated, the hind coxae are also widely separated or the tarsi have 1 or more segments lobed beneath, or the head has a distinct fronto-clypeal suture 7

7. Fore coxa more or less projecting, hind coxa with a femoral plate. Tarsi 5-segmented, usually at least the 4th with adhesive lobes beneath, last not longer than the others together, empodium if present small and bisetose. Head with fronto-clypeal suture nearly always distinct. Normally 5 visible abdominal sternites. Antennae filiform to pectinate. Pronotal hind margin not crenulate **Dascilloidea** (p. 786)

–. If the fore coxa projects, the hind coxa has incomplete femoral plates and there are more than 5 visible abdominal sternites 8

8. Fronto-clypeal suture distinct. Tarsi with segments rarely lobed beneath, if so the hind margin of the pronotum is crenulate; last segment of tarsus often as long as the others together . . . . . **Dryopoidea** (p. 787)

–. Fronto-clypeal suture not distinctly developed. Last segment of tarsi not as long as rest together. Hind margin of pronotum not crenulate . . . 9

9. Fore coxa projecting with large exposed trochantin, hind coxa with large femoral plate, empodium large and plurisetose. Antennae pectinate or flabellate. 1st visible abdominal sternite nearly always in same plane as metasternum **Rhipiceroidea** (p. 789)

–. If fore coxa projects the femoral plates of hind coxa are incomplete or absent, empodium absent or small and bisetose 10

10. Metasternum with well-marked transverse suture. Suture between first two visible abdominal sternites more or less obliterated. Abdominal tergites all well sclerotized. Prothorax normally immovable on mesothorax, prosternal intercoxal process received into a deep mesosternal cavity. Antennae short, serrate. Fore coxa small, rounded. Tarsi with ventral adhesive lobes at least on segments 2–4 . . . . . **Buprestoidea** (p. 789)

—. Metasternum without a transverse suture. First 2 visible abdominal sternites as clearly separated as the 2nd and 3rd. Abdominal tergites weakly sclerotized. Prothorax more or less movable on the mesothorax. Tarsi rarely with more than 1 segment with adhesive lobes beneath. 11

11. Hind coxa almost always with complete femoral plates, fore coxa nearly always rounded, trochantins hidden. Prothorax nearly always with acute hind angles, prosternal intercoxal process movable in mesosternal recess. Normally 5 visible abdominal sternites, 1st in same plane as metasternum **Elateroidea** (p. 790)

—. Hind coxa with femoral plates very narrow, incomplete, or absent, fore coxa large, projecting. Prothorax usually with obtuse hind angles, prosternal intercoxal process not or scarcely received into mesosternum. 6 or 7 visible abdominal sternites, 1st not in same plane as metasternum . . **Cantharoidea** (p. 793)

12. Fore coxa usually somewhat projecting, hind coxa often with a more or less distinct femoral plate. Tarsi of 5 segments, 1st sometimes very small. Antennae nearly always with last 3 segments differentiated from rest. 5 visible abdominal sternites 13

—. If fore coxa is projecting, tarsi are usually heteromerous or apparently with 4 segments, hind coxa without femoral plate. Ocelli absent . . . 14

13. Prothorax not hood-like. Tarsi never with 1st segment very small, trochanters normal, their junction with femora very oblique. 1 or 2 ocelli often present. Antennae not filiform, rarely serrate, last 3 segments not greatly elongate **Dermestoidea** (p. 794)

—. Prothorax nearly always produced over the head like a hood. Tarsi with 1st segment very small or trochanters elongate and joined to femur by a transverse suture. Ocelli absent. . . . . **Bostrychoidea** (p. 795)

14. Tarsi 5-segmented but 4th segment very small and concealed by the lobes of the 3rd, 1st to 3rd with adhesive lobes beneath. Transverse suture of metasternum usually distinct laterally 15

—. If tarsi are 5-segmented with the 4th segment very small, the antennae have a marked 3-segmented club, the head is not rostrate and the gular sutures are distinct. Transverse suture of metathorax not distinct laterally . . 16

15. Head not rostrate, or if slightly so, gular sutures distinct and separate. Antenna without a 3-segmented club, not received into a groove **Chrysomeloidea** (p. 808)

—. Head more or less produced into a rostrum, gular sutures nearly always confluent. Antenna usually geniculate and clubbed, 1st segment retractable into a groove (scrobe) . . . . . **Curculionoidea** (p. 811)

16. Tarsi 5-segmented. Fore coxa projecting, or transverse and empodium conspicuous and bisetose. Abdomen with 5 or 6 visible sternites **Cleroidea** (p. 797)

—. If tarsi are all 5-segmented, fore coxa is rounded or transverse. Empodium small or absent 17

17. Tarsi 5-segmented, filiform. All coxae more or less projecting. Antennae short, more or less serrate. Abdomen with 6 or 7 visible sternites **Lymexyloidea** (p. 798)

—. If the fore coxa projects, the tarsi are heteromerous. Antennae filiform or clubbed, rarely serrate. Abdomen normally with 5 visible sternites, if with 6 or 7, tarsi nearly always heteromerous . . . . . **Cucujoidea** (p. 799)

Superfamily 1. **Hydrophiloidea**

The adults of this group are known by the elongate maxillary palpi which seem to have taken on the tactile functions of the antennae as the latter became involved in respiration. They have six simple Malpighian tubes and the larval maxilla has separate galea and lacinia. Although the majority of species are aquatic, they are less fully adapted for such a life than the Dytiscidae. The group is sometimes divided into four families but this is perhaps unnecessary.

FAM. HYDROPHILIDAE.—A large family comprising about 2,000 species which are especially numerous in the tropics. The adults live upon decomposing vegetable matter and, in many cases, the larvae have a similar habit but those of *Hydrophilus* and its allies are predacious. A large number of the species have elongate maxillary palpi (Fig. 548) and, on this account, the family has often been termed the Palpicornia: this character, however, is not always very evident. The long palpi perform the functions of antennae, the latter being used in respiration by the submerged insect. Although a large number of the Hydrophilidae are truly aquatic, the family name is inappropriate as a considerable number are land insects. The latter are met with in damp or marshy places or among vegetable refuse, while *Cercyon* and *Sphaeridium* are common in dung. Species of *Helophorus* sometimes caused damage to root-crops. One of the best known members of the family is *Hydrophilus piceus* which is almost the largest British Coleopteron. It is less perfectly adapted for

swimming than *Dytiscus* and does not have the agility that characterizes predacious insects. Much has been written on this species, especially with reference to its peculiar mode of respiration. A dorsal air-reservoir is present beneath the elytra and there are ventral hairy tracts which also serve to retain an air-film. On either side of the thorax and abdomen there is a longitudinal tract of delicate pubescence bounded above by the overhanging edges of the prothorax and elytra. The spiracles open into these linear tracts, and the latter also communicate with the dorsal air-reservoir. When the insect rises to renew its air supply the body is slightly inclined to one side so as to bring the angle between the head and prothorax, on one side of the body, to the surface. The hairy antennal club plays an important part in breaking the surface film, and facilitating the entry of air into the cleft already mentioned, and its passage into the lateral tracts. The complete details of the respiratory process are too lengthy for discussion here and the student is referred to the works of Miall (1912), Portier (1911), and Hrbáček (1950).

Hydraena, *Octhebius* and their allies occupy an anomalous position and could almost as well be placed in the Staphylinoidea. Many of them are not fully aquatic in their early stages which feed on filamentous algae.

The eggs of *Hydrophilus*, *Hydrochara*, *Hydrobius* and other genera are enclosed in cocoons of a remarkable construction (vide Portier): the latter are usually attached to grass or floating objects, but *Helochares* and *Spercheus* fasten them to their own bodies. The larvae of the family do not admit of any general description on account of their great diversity of form and structure: those of a number of forms have been studied by d'Orchymont (1913) and Böving & Henriksen (1938). Several of the aquatic genera, including *Hydrophilus*, are metapneustic and the spiracles are placed on the last body segment in a kind of atrium. *Hydrocharis* and *Berosus* have long fringed gill-like structures on the first seven abdominal segments: in *Helophorus aquaticus* the larva is strongly sclerotized, the thoracic terga are entire, and each of the first eight abdominal segments is protected by four transverse plates. The larvae of *Cercyon* and *Sphaeridium* are degenerate and grub-like with the legs atrophied or vestigial. In the majority of the larvae of this family cerci are present and sometimes elongate.

Superfamily 2. **Histeroidea**

This group consists of one large family and two very small ones. The latter are little known and their larvae have not been described. The Histeridae have six Malpighian tubules and the predatory larva has falcate mandibles and a maxilla with no lacinia but with a small galea borne on an elongate palpiger.

Table of families:

1. Anterior tibia with external spines but not dentate. Antennae not geniculate, club 3-segmented. Fore coxa transverse, trochantin exposed . SPHAERITIDAE
–. Anterior tibia externally dentate. Antenna geniculate. Fore trochantin concealed 2

2. Fore coxa more or less projecting, all coxae approximated to mid-line. Antennal club 3-segmented. Head with gular sutures separate. 1 abdominal tergite not covered by elytra. Empodium distinct, bisetose . . . SYNTELIIDAE
–. Fore coxa not projecting, all coxae widely separated. Antennal club usually not distinctly segmented. Gular sutures usually confluent posteriorly. 2 abdominal tergites exposed. Empodium absent . . . . . HISTERIDAE

FAM. SPHAERITIDAE.—The single genus *Sphaerites* contains three species. *S. glabratus* is found in coniferous woods in Scotland, probably associating with fungus. The discovery of the larva would probably make the systematic position of the group more certain.

FAM. SYNTELIIDAE.—The genus *Syntelia* has a few species in Mexico and the Orient where it has been found at sap exuding from wounded trees.

FAM. HISTERIDAE.—The Histeridae are a large family (ca. 2,500 species, Wenzel, 1944) of compact hard, shining beetles with geniculate and strongly clubbed antennae. The elytra are truncated behind leaving the two apical segments exposed. For the most part they are black or brown insects, but in some cases the elytra are

marked with red, and a few species are metallic. When alarmed they simulate death and closely retract the antennae and legs beneath the body. *Hister* (Fig. 575) frequents dung and carrion: *Hololepta* and *Platysoma* live beneath bark and are greatly flattened: others are cylindrical and live in the burrows of wood-boring insects. Several genera are found in ants' nests and others in those of termites. The larvae have a soft and often much wrinkled in tegument, very short legs and no ocelli or labrum. The mandibles and palpi are prominent, while the broad 9th abdominal segment bears short 2-segmented cerci. So far as known they are carnivorous; the larva of *Saprinus virescens* preys upon that of *Phaedon*, *Hister pustulosus* attacks Agrotid larvae, while the dung-feeding and lignicolous forms probably prey upon Dipterous and other larvae.



FIG. 574.—*Syntelia indica*
After Fowler (F.B.I.).

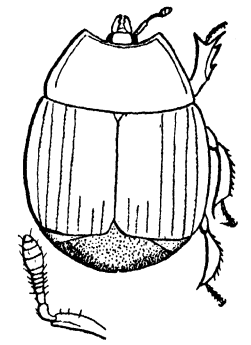


FIG. 575.—*Hister unicolor*. Europe

The genus *Niponius* is chiefly characterized by the very large head and slender tarsi: its larva frequents the burrows of Scolytinae and probably preys upon the immature stages of the latter. *Niponius* (Gardner, 1935) occurs in Japan, the Himalayas and Borneo: for its larva, see Gardner (1930).

Superfamily 3. **Staphylinoidea**

In this very large group, the elytra are usually short, leaving at least some abdominal tergites exposed; the venation is of a special type (Fig. 469) in which veins M and Cu are not connected, and there are four Malpighian tubules. In the larva the galea and lacinia of the maxilla are more or less fused and the palpiger is not elongate. In habits, the species are mould-eaters or predatory, very rarely phytophagous (some Silphidae). Very few of them are found in dry situations.

Table of families:

1. Hind coxa with femoral plate extending for at least half their length. Antennae 8–11-segmented with a club of 1–3 segments. Tarsi 3–4-segmented. Elytra usually without epipleura 2
–. Hind coxa without or with much shorter femoral plate, or if it is well developed, antennae 11-segmented and filiform or with a club of more than 3 segments. 6

2. Abdomen with 3 visible sternites. Antennae 11-segmented with a 3-segmented club. Tarsi 3-segmented, claws very unequal . . SPHAERIIDAE (p. 779)
–. Abdomen with 5–6 visible sternites. Claws equal 3

3. Hind coxae contiguous. Tarsi 4-segmented. Elytra covering abdomen, head and prothorax large, insect capable of rolling itself into a ball. CLAMBIDAE (p. 779)
–. Hind coxae more or less separated. Tarsi normally 3-segmented. Insect not capable of rolling itself into a ball 4

4. Prosternal intercoxal process broad, projecting back over the mesosternum. Eyes absent. Antennae short, retractile into grooves beneath the head. Myrmecophilous . . . . . LIMULODIDAE (p. 779)
–. Prosternal intercoxal process narrow, not so projecting back. Antennae not retractile into grooves 5

5. Antennae 11-segmented, club of 2–3 loose segments. Femoral plates developed only on inner half of hind coxa. Tarsi of 3 segments, first 2 together not one-third as long as 3rd. Last abdominal sternite without spinous processes. Insects terrestrial . . . . . PTILIIDAE (p. 780)

–. Antennae of 8 segments, last large. Femoral plate of hind coxa complete. Tarsi with first 2 segments together at least half as long as 3rd. Last abdominal sternite with 2 projecting spinous processes. Insects aquatic
HYDROSCAPHIDAE (p. 779)

6 Abdomen not unusually mobile, with at least 3, usually 4 or more, of anterior tergites membranous. Elytra not leaving more than two, usually no, abdominal segments exposed. Antennal club usually 5-segmented 7
–. Abdomen usually very mobile, with not more than 3 anterior tergites membranous. Elytra usually leaving at least 3 segments exposed. Antennae not clubbed, or with a club of, usually, 3 segments 11

7. Fore coxa small, rounded. Eyes absent. Antennae filiform or all segments after 2 forming a club, segment not or scarcely smaller than 7 or 9. Vertex of head with a keel which overlaps pronotum. Tarsi 5-segmented, front ones not widened in male . . . . . LEPTINIDAE (p. 780)
–. Fore coxa larger, transverse or conically projecting. Antennae usually with a 5-segmented club and with segment 8 smaller than 7 or 9. (Some Hydrophilidae, *Hydraena* etc., p. 776, might run down here) 8

8. Fore coxal cavities closed behind, hind coxae usually contiguous. Elytra almost always covering the abdomen. Male fore tarsi nearly always dilated
ANISOTOMIDAE (p. 780)
–. Fore coxal cavities open behind. Elytra often truncate. Antennae with segment 8 scarcely smaller than 7 or 9, or else hardly clubbed 9

9. Fore coxa with trochantin exposed, hind coxae almost or quite contiguous. 6 visible abdominal sternites. Antennae inserted widely apart under sides of front. (The Sphaeritidae (p. 777) might run down here but have a 3-segmented antennal club) . . . . . SILPHIDAE (p. 780)
–. Fore coxa with trochantin hidden, hind coxae more or less widely separated. Species often very small or antennal insertions approximated. . . 10

10. 1st visible abdominal sternite as long as next 3 together. Elytra truncate, first 3 abdominal tergites membranous. Maxillary palpi normal. Species glabrous, very shining . . . . . SCAPHIDIIDAE (p. 781)
—. 1st visible abdominal sternite hardly longer than 2nd. Elytra covering abdomen of which at least 4 tergites are membranous. Maxillary palpi with penultimate segment very large, last small. Species pubescent, not very shining
SCYDMAENIDAE (p. 781)

11. Abdomen not dorso-ventrally flexible. Tarsi normally with 3 (very rarely 2) segments; claws 1 or 2 and very unequal. Maxillary palpi with last segment very large, often much modified, labial palpi with 1–2 segments. Exoskeleton usually with deep foveae . . . . . PSELAPHIDAE (p. 781)
—. Abdomen more or less dorso-ventrally flexible. Tarsi nearly always with 2 equal claws. Last segment of maxillary palpi rarely large, labial palpi usually with 3 segments . . . . . STAPHYLINIDAE (p. 781)

For the first two and the fourth families see p. 768.

FAM. SPHAERIIDAE.—The genus *Sphaerius* is widespread but with very few species. *S. acaroides* occurs in the fens in England. The genus needs much more study to determine its affinities.

FAM. CLAMBIDAE.—There are about 40 species found in most regions of the globe, with 5 in Britain. The adults are found in decaying vegetable matter but the metamorphoses are not well known. The power of rolling into a ball is also possessed by *Agathidium* (Anisotomidae). In his later work, Crowson (1955) places this family in the Dascilloidea.

FAM. LIMULODIDAE.—Five genera and about 27 species of myrmecophilous beetles are placed in this family (Seevers & Dybas, 1943). They are mostly American, with one genus in Australia.

FAM. HYDROSCAPHIDAE.—The genus *Hydroscapha* has species in the warmer parts of the Holarctic region, including France. They might be described as aquatic Ptiliidae but the larva (Böving, 1914) resembles that of *Hydraena* in its mouthparts. It is apneustic with balloon-like respiratory processes on the pro- and metathorax and on the 8th abdominal segment.

FAM. PTILIIDAE.—The 350 members of this family are very minute: the Neotropical *Nanosella fungi* is stated to be the smallest known Coleopteran and measures 0·25 mm. long, while the maximum size in any species is only about 2 mm. The elytra are variable in length and the wings very narrow, with a marginal fringe of exceptionally long setae. These insects occur in all kinds of decaying vegetable matter, in fungi, and under bark. The larvae (Perris, 1876) have 3-segmented antennae, peripneustic respiration, and articulated urogomphi. About 60 British species are now recognized (cf. Matthews, 1872).

FAM. LEPTINIDAE.—*Leptinus testaceus* is not very rare in Britain on small rodents or in their burrows. It is also sometimes found elsewhere, e.g. in nests of *Bombus* and the larva has been described by Reid (1942). *Silphopsyllus* is found in Russia on the Desman and is more strictly confined to its host, apparently by its adaptation to a certain temperature. *Platypsyllus castoris*, found on the beaver in Europe and N. America, is much more modified in adult structure, though the larva (Bugnion & du Buysson, 1924) is much less aberrant. The head of the adult is provided with a comb-like row of spines near the hind margin, the mandibles are vestigial, and the elytra are short, leaving six abdominal segments exposed. The wings are absent.

FAM. ANISOTOMIDAE.—Formerly placed in the Silphidae, these bettles may be distinguished by the form of the antennae. According to Crowson, some of the club segments contain peculiar sensory vesicles, best developed in genera like *Liodes* which breed in subterranean fungi. *Catops* and its allies comprise about 800 species found in various types of decaying vegetable matter. Many are found in caves and some of these, such as *Leptodirus*, are extraordinarily modified—blind, with narrow head and thorax, globose elytra and long appendages. Others again are found in the nests of mammals or, more rarely, insects. The Coloninae with 100 species and the Anisotominae with about 400 species mostly breed in subterranean Ascomycetes and the adults are often nocturnal. *Scotocryptus* lives in the nests of *Melipona*.

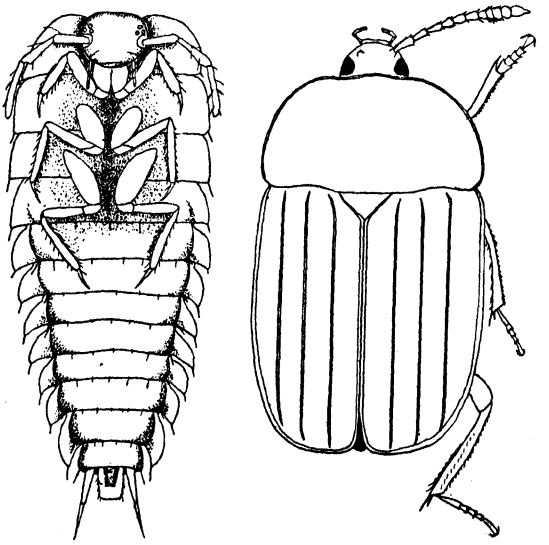


FIG. 576.—*Silpha tristis*, larva and imago

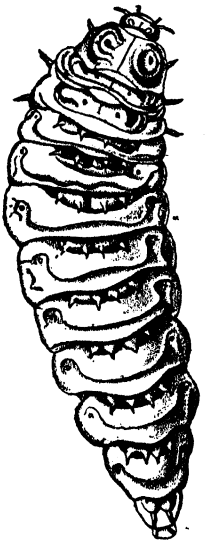


FIG. 577.—*Necrophorus vespillo*, larva × 3

From Fowler (F.B.I.) *after* Schiödte.

FAM. SILPHIDAE.—The members of this family are mostly rather large and are commonest in the Holarctic region. There are about 230 species. Nearly all the species feed on carrion and *Silpha* comprises the roving carrion-beetles (Fig. 576). The larvae of some species wander in search of decomposing vegetable matter, those of *Phosphuga atrata* are predacious upon snails and that of *Xylodrepa 4-punctata* upon Lepidopterous larvae. On the other hand, the species of *Aclypea* are vegetarian and often damage beet and other root-crops. *Necrophorus* includes the well-known

burying beetles which bury the bodies of small vertebrates by excavating beneath them. The eggs are laid in a gallery leading from the buried corpse and the larvae (Fig. 577) in their earlier instars are fed by the female (Pukowski, 1933).

FAM. SCYDMAENIDAE.—The members of this family are almost all very small insects: they are very widely distributed and more than 1,200 species are known, about two dozen being British. They mostly occur in moss, under bark, etc., or in ants' nests, often in company with Pselaphidae. Although related to the latter family, their 5-segmented tarsi, and longer elytra, afford a ready means of separation. They are more closely allied to the Silphidae and chiefly differ from the latter in the coarser eye-facets and the separated hind coxae. The larva of *Scydmaenus tarsatus* is figured by Meinert (1888): it is flattened and onisciform in general shape with laterally expanded margins to the segments. Scarcely anything appears to be known of the biology of the family.

FAM. SCAPHIDIIDAE.—The members of this family are fungivorous or occur in rotting wood both as larvae and adults. They are small, oval, convex and very shining insects with filiform or slightly clavate antennae. Their affinities have been much disputed, but they are probably allied to the Staphylinidae. Only about 250 species are known, and the few British representatives belong to the genera *Scaphium*, *Scaphidium* and *Scaphisoma*. The larva of the last-mentioned genus is described by Perris: it is of a modified campodeiform type with elongate hairs along the sides, rather long antennae, and greatly reduced cerci.

FAM. PSELAPHIDAE.—A large family (ca. 3,500 species) of very small reddish or yellow beetles bearing a resemblance to ants. Although worldwide in distribution it attains its greatest development in the tropics. The species mostly live in ants' nests; they present great diversity of form, the antennae and maxillary palpi being especially remarkable. The Pselaphinae usually have 11-segmented antennae and greatly developed maxillary palpi, notably in the males of certain genera. The members of this subfamily are less highly modified than the Clavigerinae; some are known to be myrmecophilous, while others occur under bark, among moss, etc. The Clavigerinae are sometimes regarded as a separate family, and are true symphiles. The antennae are composed of one to six segments and rival those of the Paussidae in their specialization: the maxillary palpi are greatly reduced or rudimentary and are evidently no longer needed in species which are fed by their hosts. At the base of the abdomen there is an extensive hollow which is surrounded by tufts of golden-yellow hair diffusing a substance that the ants are fond of. The European *Claviger testaceus* is well known and lives in the nests of *Lasius*: the ants feed it with regurgitated food and individuals have been kept under observation by Janet for over four years. The chief authority on the Pselaphidae is Raffray and some of the more remarkable forms are figured in his monograph (1908): rather more than 30 species are British. The larva of *Chennium* resembles the Staphylinid type and is described by Xambeu (1889).

FAM. STAPHYLINIDAE (Rove Beetles: Fig. 578).—The principal feature of this family is seen in the very short elytra, hence the older name of Brachelytra for the group. Notwithstanding the small size of these organs, they conceal large well-developed wings, which are complexly folded away beneath them. On the other hand the unfolding of the wings can take place with great rapidity, thus allowing the insect to resort to almost instantaneous flight. In a few genera (*Olophrum*, *Lathrimaeum*, etc.) the elytra are larger than usual, leaving only the apex of the abdomen uncovered. The head is very variable in form and size and frequently differs in the sexes: the antennae are 10- or 11-segmented and either filiform or more or less clubbed. The eyes are very variable in development though rarely wanting and, in a few cases, a single ocellus or a pair of these organs is also present. The number of segments to the tarsi is inconstant and the latter are sometimes heteromerous (see Blackwelder, 1936). The abdomen is frequently terminated by a pair of styliform appendages, and certain species exhibit the curious habit of curling the distal portion of the hind body over the back in a threatening manner. The Staphylinidae include quite 20,000 species of which over 800 inhabit the British Isles. The majority of species are small and inconspicuous, but a few are brightly coloured and the largest British species, *Ocypus olens* (Fig. 578), attains the exceptional length of 28 mm. Members of the family abound where there is decaying organic matter, including dung and dead animals, while many are predacious. *Stenus* with its protrusible labium (Schmitz, 1943) attacks such insects as Collembola. More than 300 species are known to be myrmecophilous (vide p. 727): thus *Myrmedonia* includes synechthrans preying upon dead or disabled ants, while other genera live as tolerated guests of Doryline ants and exhibit a remarkable mimetic resemblance to the latter. *Dinarda* is a synoekete in the

nests of certain species of *Formica* and the Aleocharine genera *Lomechusa* and *Atemeles* are highly evolved symphiles which are assiduously tended by ants. Numerous termitophilous genera have been brought to light by Silvestri, Trägårdh and Seevers. Certain of these are viviparous, and *Corotoca*, *Spirachtha*, *Termitomimus* and other genera are physogastric, the abdomen assuming bizarre forms.

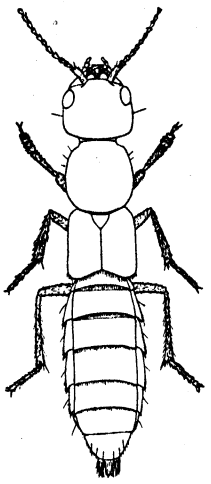


FIG. 578. — *Ocypus olens*, male × 2. Europe

Staphylinid larvae (Fig. 193) are typically campodeiform and often closely resemble those of the Carabidae. There is no distinct labrum, the body is protected by sclerotized segmental scuta and the terminal segment is tubular. The legs have only one claw and cerci are present. The larvae of certain species are definitely known to be carnivorous and predacious, a habit which is apparently very general. The larvae of *Aleochara bilineata* and *A. algarum* are pupal parasites of cyclorrhaphous Diptera. The life-history of the former species has been followed by Wadsworth (1915). The newly hatched larva is campodeiform and gnaws its way into the puparium of its host. It subsequently undergoes hypermetamorphosis, becoming eruciform, with obvious degeneration in adaptation to a parasitic life. There is, furthermore, strong presumptive evidence that members of other genera are similarly parasites, and they are likely to afford a considerable field for investigation. The degenerate eruciform type of larva also occurs in *Lomechusa* as an adaptation to myrmecophilous habits. The larvae of *Syntomium* and *Micropeplus* are aberrant, being short and broad and markedly onisciform. A considerable number of Staphylinid larvae has been described by Paulian (1941): for a generic synopsis of the family vide Eichelbaum (1909).

Superfamily 4. **Scarabaeoidea**

This is one of the most distinct sections of the Coleoptera and the species, besides the characters given in the key have the following features in common: four Malpighian tubules, dentate fore tibia with one apical spur, 8th abdominal tergite forming an exposed pygidium, larva without tergal plates or cerci and almost always with cribriform spiracles. Many modern authors recognize a considerable number of families but the classification adopted below is conservative. The species are primarily fossorial, and the burrowing habit persists to a greater or less degree in the majority of the species. In form they are compact and very stoutly built; they are endowed with remarkable muscular powers but they walk without much agility, and in an ungainly fashion. Nearly all species, however, are active fliers: apterous forms are relatively few and, although most frequent in the female, they may occur in both sexes. In some members of the group the colours are bright and striking, and the head and thorax are often ornamented with remarkable cuticular outgrowths, producing some of the most bizarre forms in the insect world. Sexual dimorphism is a very characteristic phenomenon, the differences affect almost every part of the body and, in many cases, the males and females of a species are so unlike that they have been relegated to different genera (Fig. 549) (Arrow, 1944). Scarabaeoids are also remarkable for the variety of their stridulating organs, not only in the imagines, but more particularly among the larvae: the sound produced is usually very highly pitched, and often inaudible to the human ear, if the insect be held more than a few inches distant. The eggs are large and few in number: they are noteworthy from the fact that they have been observed to change considerably their form and size during growth after deposition. During the larval stage these insects feed upon dead vegetable or animal matter, roots, or dung and occur in the ground, in the decaying

parts of trees, or in debris, etc. The larvae are described by Schiödte, Perris and others. They are easily recognized and exhibit great similarity. They are broad and fleshy, whitish or greyish white and the body is curved in the form of a letter C; the legs are well developed, but are rarely used for locomotion. The majority of species lie upon the back or side and are surrounded by sufficient food to render active movement unnecessary. The head is large and downwardly inclined and strongly sclerotized; the three thoracic segments are short, bringing the legs closely together, and the last two to four abdominal segments have a somewhat inflated appearance being much larger than those preceding. Eyes are seldom present, but the antennae are well developed and 2- to 5-segmented. The mandibles are powerful and exposed, and the maxillae terminate either in one or two lobes. The prothorax and first eight abdominal segments each bear a pair of spiracles. A general account of the group is given by Arrow (1910).

Table of families:

1. Abdomen with 5 visible sternites which are usually sharply set off from their pleurites, abdominal spiracles all in the pleural membrane, tergites all covered by the elytra. Antennae 10-segmented 2
–. Abdomen with 6 visible sternites, pleurites rarely sharply set off. . . . 5
2. Antennal club often of more than 3 segments which are never closely co-adapted. Empodium well developed. Mandibles large and projecting. Species usually elongate and parallel-sided 3
–. Antennal club with 3 closely co-adapted lamellae. Empodium small or absent. Mandibles small, not much projecting 4
3. Antennae more or less geniculate, club loose. Prementum entire, ligula inserted dorsally . . . . . LUCANIDAE (p. 784)
–. Antennae not geniculate, club segments capable of closer application to one another. Prementum emarginate, ligula inserted at apex . PASSALIDAE (p. 783)
4. Body not capable of rolling into a ball. Upper surface dull, scaly or setose TROGIDAE (p. 784)
–. Body capable of being rolled into a ball. Upper surface polished, glabrous ACANTHOCERIDAE (p. 784)
5. Antennae with 11 segments. Mandibles and labrum freely exposed. Mid coxae almost contiguous, hind tibia with 2 spurs. Abdominal spiracles all in the pleural membrane, elytra completely covering the abdomen GEOTRUPIDAE (p. 784)
–. Antenna with 8–10 segments. Some abdominal spiracles often lying in the sternites SCARABAEIDAE (p. 784)

FAM. PASSALIDAE.—The members of this family are somewhat flattened, black or dark brown insects. The elytra (Fig. 579*a*) cover the abdomen and are deeply longitudinally striated, and the mandibles are not specially developed in the male. About 800 species have been described and they inhabit decaying wood in the moist warm forests of the world. None are European, and only a single species occurs in America north of Mexico. Ohaus has claimed that the two parent beetles are accompanied by several larvae which they tend throughout life until maturity is attained, but this observation has not been confirmed. The adults disintegrate the wood and chew it into a condition suitable for consumption by their progeny. The larvae (Gravely, 1916) are more elongate and less markedly crescentic than those of most Scarabaeids (Fig. 581). They are, furthermore, active and have the first two pairs of legs relatively long: the third pair are greatly modified, each leg being reduced to a very short coxa and a more elongate trochanter. The latter is adapted to form an organ which works across a striated area on the mesocoxa, thus producing a squeaking noise. Stridulation is effected in the adults by friction between the wings and the upper surface of the abdomen.

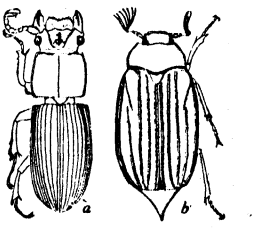


FIG. 579.—*a*, *Passalus interruptus*. Paraguay; *b*, *Melolontha melolontha*. Britain

FAM. LUCANIDAE (Stag Beetles).—In these insects the abdomen is covered by the elytra but the latter are almost always devoid of longitudinal striae. Stag beetles are familiar on account of the great development of the mandibles in the males which in some cases attain a length equal to that of the rest of the body (Fig. 580). The significance of these enormous mandibles is not clear: notwithstanding their formidable appearance in *Lucanus cervus*, for example, they are not as strong, or as capable of inflicting as severe a bite, as the short stout mandibles of the female. The male insects are usually much larger than those of the other sex and they exhibit great variation in size among individuals of the same species. These variations are coupled with striking differences in the development of the head and mandibles and it is often possible to distinguish large (teleodont), small (priodont) and intermediate (mesodont) forms. In other cases there are no intermediates known between the extremes and species, like *Odontolabis sinensis*, consequently exhibit what has been termed high and low dimorphism. Lucanid larvae (van Emden, 1935a) inhabit the rotting wood of trees or their roots. They possess well-developed antennae and legs, the maxillae are single-lobed and they differ from many Scarabaeid larvae in that the segments are not raised into three folds. The larva of *Lucanus cervus* stridulates by rubbing certain hard ridges on the third pair of legs over a rugose area at the base of the second pair: the third pair, however, is not specially modified or reduced in size as in the Passalidae and *Geotrupes*. The duration of larval existence in this family does not appear to have been definitely ascertained: in *L. cervus* it lasts about four years, while certain other species are stated to require six years to complete their development. Pupation takes place in a cell formed of gnawed wood fragments. The Holarctic genus *Sinodendron* is of an aberrant character, the species being completely cylindrical and instead of the mandibles differing in the male, the latter sex carries a cephalic horn. The thorax is very truncated in front and the antennae are short and non-geniculate. The larva occurs in rotting wood of ash, etc.: it is more slender than the usual type and gradually narrowed posteriorly. About 900 species of Lucanidae are known but only three genera, each with a single species, occur in the British Isles.

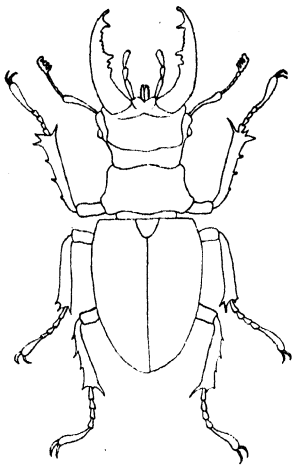


FIG. 580. — *Lucanus cervus*, male, natural size. Europe

FAM. TROGIDAE.—The 150 described species are widely distributed and mostly fall within the genus *Trox* of which there are two British species. The species are often found in dry places and feed on carrion or dung. The larva is without stridulatory files and the claws are unusually long and acute.

FAM. ACANTHOCERIDAE.—This includes about 100 tropical species, mostly associated with rotten wood. The larvae differ from those of the Trogidae in having 4- not 3-segmented antennae and normal claws.

FAM. GEOTRUPIDAE.—The 'dor' beetles are large convex insects mostly of coprophilous habits. *Lethrus*, however, is apterous and the larval burrow is stored with green plant material, so that they may be injurious to crops. *Geotrupes* with six British species is a very familiar insect. It is the 'shard-borne beetle' of Shakespeare and the beetle which 'wheels his droning flight' of Gray's Elegy. *Geotrupes* constructs burrows about 18 inches deep in the earth, below a patch of dung, and portions of the latter are carried down to serve as food for the larvae. Each burrow is filled at its blind end with a plug of dung in which a single egg is deposited. The larvae stridulate very much after the manner of Passalids, but the hind legs have suffered less reduction and the positions of the file and rasping organ are reversed. The adults stridulate by rubbing together a file on the hind coxae and the sharp edge of the coxal cavity. About 300 species have been described.

FAM. SCARABAEIDAE (Chafers, etc.).—A very large family of more or less convex insects, with the mandibles not specially developed in the males, and with the elytra not usually completely covering the abdomen. Over 19,000 species are known and about 90 occur in the British Isles. A classification of this extensive group, with a table of subfamilies, is given by Arrow; many of his groups are now commonly given family rank. A key to a number of the larvae is provided by Perris.

The Cetoniinae are typically represented in England by the 'rose chafer'—*Cetonia*

aurata. They are exceedingly brilliantly coloured, mostly diurnal insects, especially found in the tropics, and number about 2,500 species. Their mouthparts are adapted for dealing with soft or liquid food and the labrum is membranous and concealed; the mandibles, with few exceptions, are thin and incapable of biting, and the maxillae are invested with long hairs. The larvae are generally found among roots, in decaying wood, accumulations of dead leaves and other plant refuse. The life-histories of *Cetonia*, *Oxythyrea* and *Potosia* have been followed by Fabre (1905). The larvae of *P. cuprea*, and other species, inhabit the nests of *Formica* where they have been found consuming the woody material of which these habitations are composed. The Cremastochilini are exceptional in being mostly sombre-coloured nocturnal insects, living as larvae and adults in the nests of ants and termites.

The Dynastinae include some of the largest and most striking of all Coleoptera.

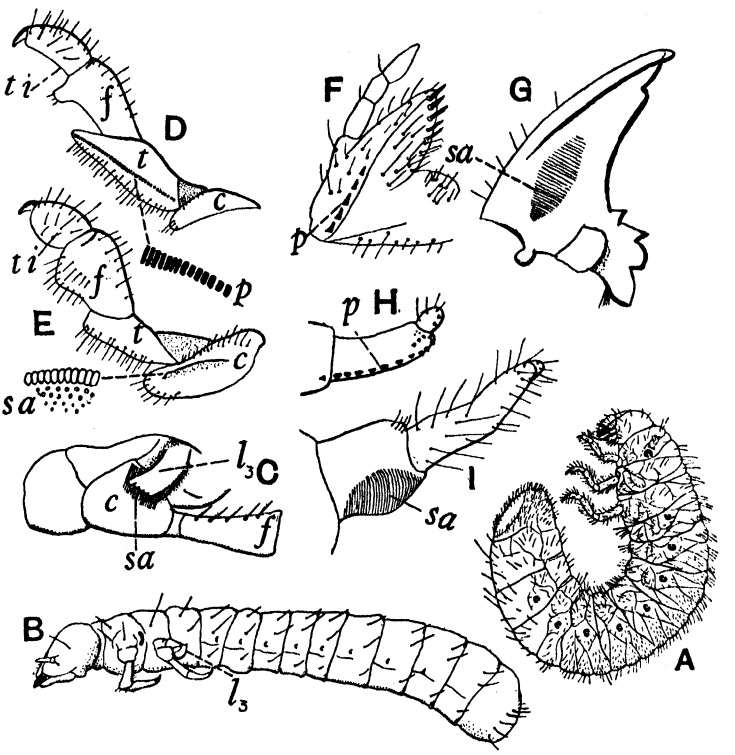


FIG. 581.—Scarabaeoid larvae and stridulatory organs

A, larva of *Anomala polita* (Scarabaeidae: *after* Gardner). B, larva of *Passalus* with C enlarged detail of part of 2nd leg and reduced 3rd leg. D, *Lucanus cervus*, 3rd leg and E, 2nd leg. F, *Phyllopertha horticola* left maxilla and G right mandible. H, *Geotrupes* 3rd leg and I 2nd leg. *c*, coxa; *f*, femur; l_3, reduced 3rd leg; *p*, plectrum; *sa*, stridulatory area; *t*, trochanter; *ti*, tibia.

The majority of these species are black and, being nocturnal or crepuscular in habits, they are not very often seen at large. They are chiefly remarkable on account of the extreme development of sexual dimorphism which is exemplified in the presence of large horny processes in the males. On the head there is usually a slender, recurved, and sometimes toothed or bifurcated frontal horn: on the prothorax there are commonly one or more processes which often arise from the margins of a dorsal cavity. In a few cases, e.g. *Oryctes rhinoceros*, both sexes are horned. Many species possess stridulating organs consisting of a file-like area on the penultimate tergum which is rasped by the apices of the elytra. The Dynastinae are almost all tropical, and more especially Neotropical. Very little is known of their biology, but their larvae have been found in tree-trunks and in compost while the adults sometimes feed on palm-leaves. Several species are injurious, their larvae attacking the roots of sugarcane and rice. *O. rhinoceros* is a great pest of coconut plantations, destroying the tissue at the leaf-bases and providing for the onset of decay. Banks (1906) states that it will also develop freely

in vegetable refuse and in soil. *O. nasicornis* is often found in decomposing bark refuse of tanneries in S. Europe.

The Melolonthinae include the 'cockchafers' and the common European *Melolontha melolontha* (Fig. 519) formed the subject of the classical anatomical memoir by Straus-Dürckheim. They differ from the two preceding groups in the presence of an evident sclerotized labrum. The larvae feed among decaying vegetable matter or among the roots of plants and are, in some cases, exceedingly injurious. In the case of *M. melolontha* the eggs are laid in several batches of fifteen or more during early summer which are deposited to a depth of 6 to 8 inches in the ground. The larvae hatch after an interval of about three weeks, and the insect remains in this stage for three years in England, and for a longer or shorter period in other countries according to climatic conditions. During the cold months the larvae descend into the ground but, for the rest of the year, they come nearer the surface and devour the roots of corn, grass, etc., sometimes causing great injury. At the end of the third summer, they form oval pupal cells at a depth of two feet or more in the soil. The adults emerge about October but do not leave the ground until about the following May, when they are common about oak and other trees upon whose foliage they feed.

The Rutelinae are likewise an extensive subfamily and many of the species are brightly coloured. In general facies they resemble the Melolonthinae but are usually separable on account of the mobile claws which are of unequal size. They are represented in Britain by *Phyllopertha horticola*, whose imagines often devour the leaves and blossoms of roses and fruit trees, and *Anomala aenea*. Species of *Lachnosterna* are very destructive, as larvae, in N. America.

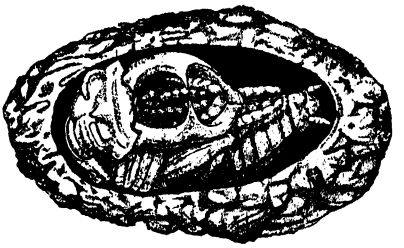


FIG. 582.—*Lucanus cervus*, male pupa in its cell

After Roesel.

The Aphodiinae are more or less oblong convex species of small size with concealed labrum and mandibles. They are often found abundantly in dung (Madle, 1934; Schmidt, 1935). The extensive genus *Aphodius* is represented in Britain by about 40 species.

The Coprinae are round or oval and often very convex beetles living almost entirely in dung. Their mandibles are membranous and incapable of biting. Much of our knowledge of their biology is due to Fabre, and the curious ball-rolling habit of the sacred *Scarabaeus* of the ancient Egyptians has attracted attention from very early times. Similar habits are met with among the close allies of this insect living in S. Europe, Asia and Africa. The ball is composed of dung which, in this form, is transported to a suitable retreat as food for the beetle itself. The mass of dung which contains the egg is pyriform and it is constructed in a separate underground chamber of material brought there for the purpose. In *Copris* this chamber is very large and is the combined work of the male and female. It contains two to seven pyriform cells of dung, each containing a single egg, and the 'nest' is guarded and tended by the female. In some of the Indian species of *Heliocopris* and *Cartharsius* the egg balls are very large and coated with clay. When first discovered they were thought to be ancient stone cannon balls, and Lefroy mentions one being found 8 feet below ground. In certain species, including *Copris hispanus*, the female, instead of dying after oviposition, tends her brood to maturity and then produces a second generation, but the number of eggs laid in each case does not appear to exceed four. Several genera are myrmecophilous and have the usual secretory glands and hair tufts indicative of symphiles. The subfamily is represented in Britain by *Copris lunaris* and several species of *Onthophagus*. The larvae of British Scarabaeids have been tabulated by van Emden (1941).

Superfamily 5. **Dascilloidea**

The principal characters of this group are in the adult, the filiform or slightly serrate antennae; the more or less conically projecting fore coxae whose cavities are completely open behind; the hind coxae excavated to receive the femora; the side margins of the pronotum complete and the hind margin never crenulate; six simple Malpighian tubules. In the larva, the

labrum is free, the mandible has a distinct mola and a ventral tubercle, maxillary galea and lacinia distinct, legs well developed, tergites more or less corneous, cerci absent.

Table of families:

1. Maxillary palpi normal, segment 2 not slender, much shorter than the next two together. 5 (rarely 6) visible abdominal sternites 2
–. Maxillary palpi with segment 2 usually very slender and as long as the next two together. Often 6 or 7 visible abdominal sternites. . PSEPHENIDAE (p. 788)

2. Head incapable of apposition against prosternum. Postgena not keeled. Fore coxa small, not oblique, trochantin exposed. Tarsi with ventral membranous lobes at least on segments 2–4 . . . . . DASCILLIDAE (p. 787)
–. Head capable of apposition against prosternum. Fore coxa large, oblique, trochantin concealed. Tarsi without membranous lobes beneath 3

3. Hind coxae narrower than metasternum, their front margins slightly oblique. Postgena keeled. 4th tarsal segment bilobed . . . HELODIDAE (p. 787)
–. Hind coxae very large, wider than metasternum, their front margins strongly oblique. Postgena not keeled. All tarsal segments simple EUCINETIDAE (p. 787)

FAM. DASCILLIDAE.—About 200 species, mostly of moderate size, are usually found on flowers in the adult stage. The larva (Gahan, 1908) feeds on grass-roots, sometimes to an injurious extent, and resembles a Scarabaeid. The ocelli are absent and its spiracles are cribriform.

FAM. HELODIDAE.—These small insects have a thin and very loosely articulated exoskeleton. They are found near water in which the larvae live. The latter are provided with rectal tracheal gills (Beier, 1949; Bernet Kempers, 1944) and are unique in having multiarticulate antennae. *Scirtes* is notable for its power of jumping (Lombardi, 1928). There are about 340 species of which 13 are British.

FAM. EUCINETIDAE.—About 25 species, mostly in the genus *Eucinetes*, are widely distributed and found in rotten wood. The adults are long, narrow and boat-shaped.

Superfamily 6. **Byrrhoidea**

With the elimination of several dubious elements, this group is reduced to the single well-defined family, the Byrrhidae. In the adult, the head is deflexed with no visible clypeus, the fore coxa is large with an exposed trochantin, the broad prosternal intercoxal process is received into an emargination of the flat mesosternum, and there are six simple Malpighian tubules. The larvae are relatively stout, sometimes capable of rolling up, and without cerci or gills.

FAM. BYRRHIDAE.—There are about 270 species which mostly occur on the ground beneath stones, at roots of grasses or in moss. Their most striking feature is the power these beetles have of withdrawing their appendages in close contact with the body and remaining motionless: in this attitude they are hard to detect and often closely resemble their surroundings. The best known British species of the family is *Byrrhus pilula*, which is often found on paths in spring. Its life-history is in need of investigation and, according to Chapuis and Candèze, the larva is cylindrical and fleshy and may be recognized by the large size and breadth of the prothorax and the last two abdominal segments. The head is short and broad, the antennae very short and there is a pair of ocelli on either side. The pronotum is markedly sclerotized and sculptured, and the last abdominal segment carries a pair of retractile locomotory processes. The larvae occurs beneath turf or moss and is about 18 mm. long.

The family **Georyssidae** has often been associated with the Byrrhids though the characters of the adult agree better with the Hydrophilidae (apart from the maxillary palpi) (cf. Crowson, 1955). About 30 species are placed in a single widely distributed genus of subaquatic habits.

Superfamily 7. **Dryopoidea**

The beetles of this group (Hinton, 1939), are mostly subaquatic but except in some Elmids which exhibit plastron respiration (p. 146) they show

few special adaptations. The larvae, however, often have rectal or abdominal tracheal gills and a mobile operculum by which the 10th abdominal segment can be tightly connected within the 9th. The adult may have four or six Malpighian tubules which are cryptonephric in the Dryopidae.

Table of families:

1. Fore coxa more or less projecting or hind margin of pronotum crenulate. Antennae long, filiform, serrate, pectinate or flabellate 2
–. Fore coxa transverse or rounded. Antennae filiform or more or less short and thick 5

2. Maxillary palpi exserted laterally, segment 2 usually as long as next two together. Head somewhat rostrate, clypeus prolonged between the antennal sockets, labrum deflexed, transverse occipital keel absent. Hind margin of pronotum often crenulate. Tarsi simple . . . . . PSEPHENIDAE (p. 788)
–. Maxillary palpi not so constructed. Head not rostrate, with an occipital keel if the hind margin of the pronotum is crenulate. Tarsi usually with segment 4 small and 3 bilobed 3

3. Hind margin of pronotum not crenulate. Head without a transverse occipital keel. Tarsi simple . . . . . EURYPOGONIDAE (p. 789)
–. Hind margin of pronotum crenulate. Occipital keel usually present . . 4

4. Antennae not fitting into prosternal grooves, their sockets not approximated. Mid coxae closely approximated . . . . . PTILODACTYLIDAE (p. 789)
–. Antennae fitting into prosternal grooves, their sockets approximated. Mid coxae widely separated. Legs retractile into grooves . CHELONARIIDAE (p. 789)

5. Tarsi 4-segmented, last segment not longer than the rest together, claws slender. Fore and mid tibiae broad and spinose. Antennae short and thick HETEROCERIDAE (p. 789)
–. Tarsi nearly always 5-segmented, with the last segment usually as long as the rest together. Fore and mid tibiae narrow, not spinose. Antennae often filiform. 6

6. Mid coxae widely separated, hind coxae nearly or quite contiguous. Antennae filiform or somewhat distally thickened. Last segment of tarsi shorter than the rest together . . . . . LIMNICHIDAE (p. 789)
–. If the mid coxae are separated, the hind coxae are equally so. Last segment of tarsi usually longer than the rest together, claws large 7

7. Antennae very short, 6 more apical segments forming a pectinate club DRYOPIDAE (p. 789)
–. Antennae usually slender, never with such a club . . ELMIDAE (p. 789)

FAM. PSEPHENIDAE.—This family with a few species in India and America is interesting on account of its remarkable larvae (Fig. 583) (Böving, 1926). The latter

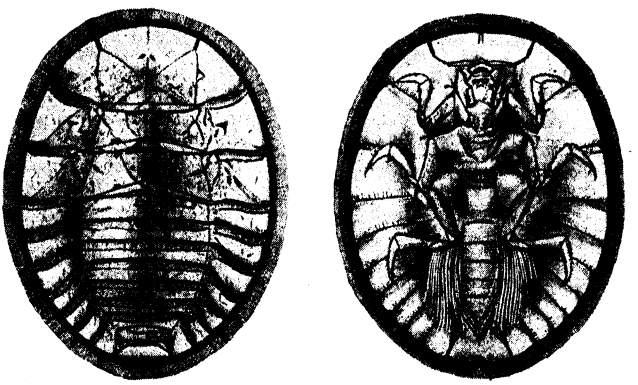


FIG. 583.—A Psephenid larva, Himalaya. A, dorsal; B, ventral. × 15

occur in swift rivers and in waterfalls, *Psephenus* being especially abundant in the rapids of Niagara, while larvae of this and other genera are also plentiful in the

Himalayan rivers. They are flattened, rounded or ovoid and almost scale-like in form: the margins of the body are greatly expanded and consequently the appendages are not visible from above. They cling with great tenacity to stones, etc., and the whole body appears to act in a suckerlike fashion rendering these larvae difficult to remove. Respiration takes place either by means of abdominal gills, or by the aid of a retractile tuft of anal filaments which is only visible in the undisturbed living larva. The pupae in *Psephenoides* are submerged and soldered down to the stones upon which the larval life was passed: they closely resemble the larvae when viewed from above, but are armed with tufts of long filamentous gills (Hinton, 1947). The British species, *Eubria palustris*, is now referred to this family.

FAM. EURYPOGONIDAE.—A few species in N. Asia and in N. America constitute this family which is placed here primarily because of the structure of their larvae.

FAM. PTILODACTYLIDAE.—A little-known family of about 200 tropical species. Some are Elaterid-like, and the males have enlarged eyes and flabellate antennae. The larvae are either aquatic or live in rotten wood.

FAM. CHELONARIIDAE.—While the adult beetles of this family resemble Byrrhids, the larvae resemble those of Dryopids or Elmids. There are about 50 species in the tropics of Asia and especially of America.

FAM. HETEROCERIDAE.—These small beetles are densely pubescent and live in galleries which they excavate in the mud bordering pools and streams. Their larvae inhabit the same situations and may be recognized by the prominent mandibles, the very broad thoracic segments and the much narrower abdomen: the whole body is strongly setose. The family is very widely distributed and about 500 species are known, several being indigenous to the British Isles.

FAM. LIMNICHIDAE.—The adult beetles resemble the Byrrhidae except in the presence of a fronto-clypeal suture, but Hinton (1938) has shown that there is a close relationship to the next family. There are a few, principally Palaearctic, species of which one is British.

FAM. DRYOPIDAE.—As now defined, this family is not very extensive but widely distributed. They show all transitions from a terrestrial to a purely aquatic life. Such British forms as *Dryops* occupy an intermediate position. Their larvae live in damp earth beneath stones or feed on waterlogged wood and somewhat resemble those of Elateridae.

FAM. ELMIDAE.—Several hundred species of this widely distributed family are known and all stages may be found together in the weeds in running water. As in the previous family all stages in adaptation to aquatic respiration are found. The larvae are typically onisciform and cling to weeds or stones (cf. Hinton, 1940).

Superfamily 8. **Rhipiceroidea**

The adults of this group are known by their strongly flabellate antennae and by the nose-like projection which replaces a free labrum. There are two families, the **Rhipiceridae** (Sandalidae) with membranous processes beneath the first four tarsal segments and the **Callirhipidae** in which these processes are absent. There are about 180 species, found in most regions, and one N. American *Sandalus* is a parasite of immature Cicadas.

Superfamily 9. **Buprestoidea**

The single family **Buprestidae** has often been placed near the Elaterids, but amongst other differences the adults have a scutellary stria on the elytra, a well-marked transverse suture on the metasternum and six cryptonephric Malpighian tubules, while the larva has a free labrum.

It is an essentially tropical family comprising over 15,000 species; relatively few are European and only five genera with twelve species occur in Britain. They are among the most brilliantly coloured of all insects and some species, owing to the splendour of their metallic lustre, are used in embroidery and in jewellery (Fig. 584). They are typically inhabitants of hot moist forests and are exceedingly active on the wing, often taking flight at the least alarm. The larvae (Xambeu, 1892–93) are distinct from

those of other Coleoptera, and characterized by the great expansion of the prothorax and the slender hind body which imparts to them a clubbed appearance (Fig. 585). The head is small and almost entirely withdrawn into the thorax, the antennae extremely short, and there are no ocelli. The legs are vestigial or absent, the abdominal segments are nine in number and there are no anal processes except sometimes in *Agrilus*. There are nine pairs of spiracles, the first pair being situated between the

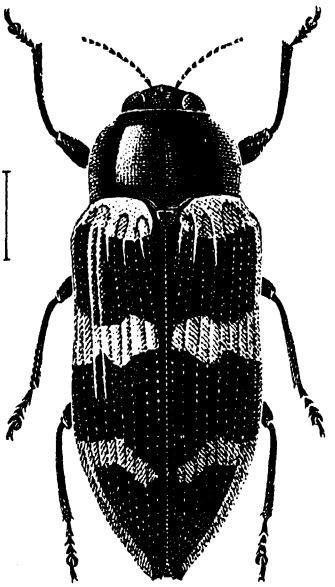


FIG. 584.—*Stigmadera interstitialis*. Australia
After Carter.

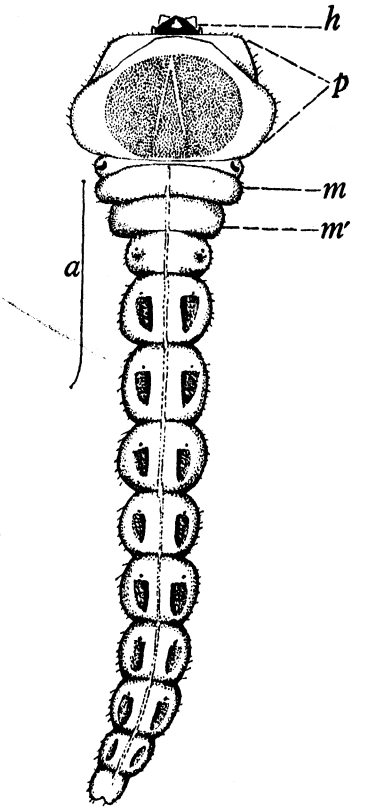


FIG. 585. — *Chrysobothris*, larva
a, actual length; *h*, head; *p*, prothorax; *m*, mesothorax; *m'*, metathorax.

pro- and mesothorax or on the latter segment. The larvae mostly gnaw rather broad flattened galleries in or beneath the bark of trees or in roots: some are found in the stems of herbaceous plants and one or two mine leaves. Some of the genera of this family are exceedingly large: *Agrilus* comprises nearly 700 species while *Sphenoptera* and *Chrysobothris* each include about 300. For further information on the family reference should be made to the work of Kerremans (1906–14) and Théry (1942).

Superfamily 10. **Elateroidea**

In this superfamily, the adults have small fore coxae with concealed trochantins, hind angles of pronotum acutely projecting, no transverse metasternal suture, hind coxae contiguous and freely ending (normally four) Malpighian tubules. The larvae have no free labrum, no channel along the mandibles and no median epicranial suture. The majority of species fall in the familiar family, the Elateridae.

Table of families:

1. Hind coxa flat with no femoral plates, trochanters very elongate. Labrum concealed . . . . . CEROPHYTIDAE (p. 792)
–. Hind coxa with well-developed femoral plates, trochanters shorter. Labrum often free 2

2. Labrum concealed. Antennal sockets distant from eyes. All 5 visible abdominal sternites more or less fused 3
–. Labrum free. Antennal sockets usually close to eyes. First 3 or 4 visible abdominal sternites connate, last one free 4

3. Abdomen with 5th visible sternite movable. Mandibles slender, prominent. Tarsal claws pectinate. 3 N. American species . . . PEROTHOPIDAE
–. All 5 visible abdominal sternites more or less connate. Mandibles stout, not prominent. Tarsal claws simple . . . . . EUCNEMIDAE (p. 792)

4. No transverse ridge above antennal sockets in front of which the clypeus does not extend laterally. Mandibles sharply bent, very prominent. Prosternum without an anterior process ('chin-piece'). First visible abdominal sternite without a clearly marked keel between the hind coxae. . . . CEBRIONIDAE (p. 791)
–. Head with a transverse ridge above antennal sockets or the clypeus extending laterally in front of them. Mandibles less prominent. Prosternum usually with a chin-piece. First visible abdominal sternite with a distinct keel between the hind coxae 5

5. Femoral plate of hind coxa much narrowed outwardly. Prosternal intercoxal process usually narrow and bent downwards towards its apex. Mid coxae approximated. Antennal sockets close to eyes, front usually transversely keeled above them . . . . . ELATERIDAE (p. 791)
–. Femoral plate of hind coxa broad throughout. Prosternal intercoxal process rather broad and flat. Mid coxae separated by a distance at least equal to the width of one of them. Antennal sockets less close to eyes, front narrowed between these and not transversely ridged above them . . . . TRIXAGIDAE (p. 792)

FAM. CEBRIONIDAE.—About 200 of these rather large beetles are found mostly in regions with a Mediterranean climate. The larva is not unlike a large 'wireworm' but with a large gula and an eversible ventral cervical membrane. The female is often wingless and does not leave the subterranean burrow where she is sought out by the active male.

FAM. ELATERIDAE.—A large family of some 7,000 species, found in all the main regions. The adults possess the power of leaping when lying on their back. The mechanism of this act is not entirely clear, but the existence of the saltatory power is connected with the mobility of the articulation between the pro- and mesothorax. As a preliminary, the apex of the prosternal process catches against the edge of the mesosternal cavity. When, however, the process slips over the catch it is driven with considerable force into the mesosternal cavity accompanied by a clicking sound. The force imparted by this jerking movement causes the insect to pivot on its elytra and to spring into the air. The elasticity of its skeleton also seems to assist in bringing about the leap (Fig. 587).

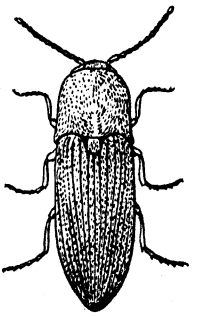


FIG. 586.—*Agriotes obscurus*, Europe. × 4

(Reproduced by permission of the Ministry of Agriculture.)

The Elaterinae have the antennae inserted near the eyes. They are mostly sombre coloured elongate insects, but a few are red or have metallic colours. The most remarkable species are the 'fire-flies' (*Pyrophorus*) which are mainly Neotropical. *P. noctilucus* emits an exceptionally bright light from a rounded yellow area on either side of the thorax and, when on the wing, an additional source of light is revealed at the base of the ventral surface of the abdomen. The eggs and larvae are also luminous. In the young larva the photogenic organ is situated at the junction of the head and thorax: in older larvae there are numerous small lateral organs in addition. The photogenic organs are very similar in structure to those of the Lampyrinae and are dealt with on p. 119. The larvae of

the Elaterinae are elongate and cylindrical and very tough-skinned (Fig. 588). The head is corneous and flattened, the antennae very short and 3-segmented, eyes are present, the labrum is not defined, and the trunk-segments are very alike. The whole body is usually reddish-brown or yellow, owing to the strong sclerotization of all the segments, and the legs are short. The prothorax is the largest, and the 9th segment is specially differentiated and exceedingly variable, thus affording important generic and specific characters. It is often corneous and margined with teeth and may terminate in single or paired processes which, in their turn, may be simple, bifid or denticulate. In *Agriotes* this segment is relatively simple and bears a pair of dark-coloured pits possibly sensory in function. The larva of *Cardiophorus* is very different from the prevailing Elaterid type, being extremely long and vermiform, owing to the great development of the inter-segments of the abdomen. The 9th segment of the latter region bears a pair of recurved hooks and a terminal fasicule of setae. Larvae of certain genera are exceedingly injurious to agriculture and are known as 'wireworms': under this category are species of *Agriotes* (Fig. 588), *Limonius*, *Athous* and others. The 'wireworm' group of larvae are root-feeders and are extremely destructive to pastures, cereals, root-crops, etc.: no effectual method of control has yet been devised. Other larvae are lignicolous and xylophagous (*Melanotus*, etc.), or possibly carnivorous (e.g. *Athous rhombeus*). Exact observations regarding the length of the larval stages are greatly needed: in the case of *Agriotes obscurus*, which is probably the commonest English wireworm, Rymer Roberts considers that the early estimate of five years is approximately correct. This species constructs an earthen pupal cell, and the pupal instar only occupies about

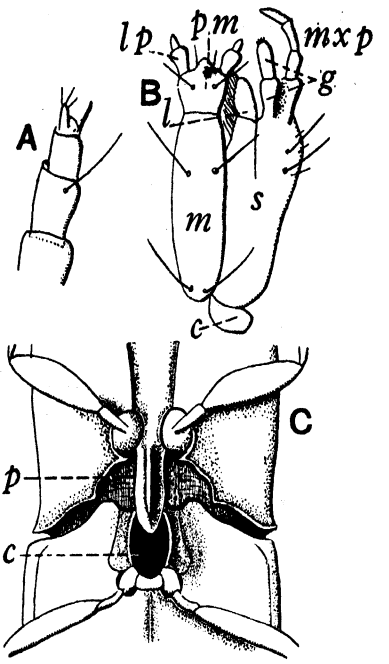


FIG. 587.—Elateridae

A, right antenna. B, labium and left maxilla of *Agriotes* larva. C, base of pro- and meso-sternum of *Athous* (adult) showing process *p* and cavity *c* of leaping apparatus; *g*, galea; *l*, lacinia; *lp*, labial palp; *m*, mentum; *mxp*, maxillary palp; *pm*, prementum; *s*, stipes.

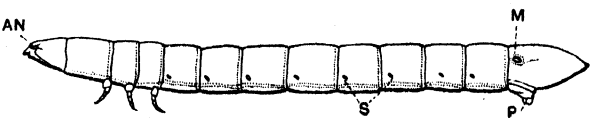


FIG. 588.—Larva of *Agriotes obscurus*. × 5

AN, antenna; *M*, margin of pit: *P*, anal pseudopod; *S*, spiracles.

three weeks. A large number of Elaterid larvae have been described by Beling (1883), Henriksen (1911), Hyslop (1917), Guéniat (1935) and van Emden (1945): for the metamorphosis of *Agriotes obscurus* vide Ford (1917) and Rymer Roberts (1919–22).

FAM. TRIXAGIDAE (Throscidae).—There are rather more than 200 of these small Elaterid-like beetles of which six are British. The larvae live in decaying vegetable matter.

FAM. CEROPHYTIDAE.—About a dozen species found in Europe and America. All stages are found in hollow trees.

FAM. EUCNEMIDAE.—Small Elaterid-like beetles, commonest in warm climates and attached to rotten wood. Of the 1,000 known species, three are British, the commonest being *Melasis buprestoides*. The larval head is greatly reduced, the legs are absent, and there are horny posterior processes.

Superfamily 11. **Cantharoidea**

It is not easy to find diagnostic characters for all the adults of this group. This integument is usually soft and the parts loosely articulated; there are usually four Malpighian tubules which are never cryptonephric. The larval cuticle is usually soft and pubescent and the mandibles are internally channelled or perforated in connexion with their predatory mode of life.

Table of families:

1. Fore coxae somewhat transverse, prosternum with an anterior lobe ('chin-piece') and with a well-developed intercoxal process received by the mesosternum. 4th tarsal segment not lobed. A few species in Asia and California BRACHYPSECTRIDAE
–. Fore coxae projecting, prosternum without chin-piece and with no or with a very narrow intercoxal process. 4th tarsal segment usually lobed 2

2. Prosternal intercoxal process complete though narrow, received by the mesosternum. Prosternum long in front of fore coxae and trochanters elongate. A few species in the Mediterranean region . . . . . HOMALISIDAE
–. Prosternum with no intercoxal process and not long in front of fore coxae unless the trochanters are short 3

3. Head very broad in front, constricted at neck, antennal sockets widely separated. Prosternum long in front of fore coxae. 4th tarsal segment not lobed. A few species (♂ only) in Persia and S. America . . . . KARUMIIDAE
–. Head not so constructed or prosternum short in front of coxae. 4th tarsal segment lobed below 4

4. Prosternum more or less long in front of fore coxae, antennal sockets lateral. Female usually apterous . . . . . DRILIDAE (p. 793)
–. Prosternum short in front of fore coxae 5

5. Antennal sockets more or less widely separated, under sides of front. ♂ antennae 12-segmented, segment 3 short. ♂ elytra usually not fully covering the abdomen, ♀ usually apterous . . . . . PHENGODIDAE (p. 793)
–. Antennal sockets more or less approximated or facing dorsally. If antennae are 12-segmented, segment 3 is long 6

6. Luminous organs usually present, at least in one sex, sexual dimorphism often marked. Elytra usually with epipleura anteriorly broad. Trochanters short, hind coxa in ♂ with femoral plates . . . . . LAMPYRIDAE (p. 793)
–. Luminous organs absent, sexes usually similar. Elytra with narrow or no epipleura. Trochanters often long, hind coxa without femoral plates 7

7. Trochanters short, very obliquely joined to femora. Ventral lobe of 4th tarsal segment bilobed. Antennal sockets less approximated, facing more or less dorsally . . . . . CANTHARIDAE (p. 794)
–. Trochanters long, transversely joined to femora. Ventral lobe of 4th tarsal segment entire. Antennal sockets closely approximated, facing antero-laterally LYCIDAE (p. 794)

FAM. DRILIDAE.—About 80 species, mainly European, of which *Drilus flavescens* is British. The larva preys on snails (Crawshay, 1903).

FAM. PHENGODIDAE.—An American family of about 50 species in which luminous organs producing light of more than one colour may be present in both the adult and larva. The eggs and pupae may also be luminous to some extent.

FAM. LAMPYRIDAE.—There are about 1,100 species of 'glow-worms' and 'fire-flies' and two are British. They differ from the Lycidae in having the middle coxae contiguous, whereas, in the latter group, they are spaced apart. They are nocturnal insects, and most of the members are provided with photogenic organs which emit a more or less bright light usually, although not invariably, strongest in the female. These organs are borne on certain of the hind segments of the abdomen—often the 6th and 7th in the male, and the latter segment in the female. The eggs, larvae and pupae are also luminous to a variable degree. There is an extensive literature on the structure and physiology of the photogenic organs (vide p. 119): as a rule the light is pale yellowish green. The function of this luminescence is difficult to conceive

with reference to the immature stages but, in the adults, it serves in most cases to bring the sexes together. In many forms the male is winged with greatly developed eyes, and the female devoid of both elytra and wings (vide Fig. 589), being larviform with the eyes small. This dimorphism is well exhibited in the common European 'glow-worm' *Lampyris noctiluca*. The biology of this insect has been studied by Newport (1837), Fabre, and others, and its larva by Vogel (1915). The adult insect takes little or no food, but the larvae (Fig. 590) are carnivorous, feeding upon snails and slugs, which they seize with their sharp sickle-like mandibles. The latter are each traversed by a fine canal through which a dark-coloured secretion is injected into the tissues of the prey. As there are no salivary glands, the secretion is apparently produced by a pair of acinose glands near the anterior end of the mid gut which probably open at the base of the mandibles. The secretion has the property of breaking down the tissues of the mollusc, and digestion is largely external, the larva imbibing its prepared meal by means of the pumping action of its cibarium. Unlike the *Dytiscus* larva, the food appears to be taken in through the mouth which is guarded by a mass of hairs precluding the entry of anything excepting small particles. The larvae of *Photinus* and *Photuris* have been studied by Williams (1917) and their photogenic organs are situated on the 8th abdominal segment. They persist in the pupa but are replaced in the imago by structures located on the 6th and 7th segments. In the Mediterranean 'fire-flies' (*Luciola*) both sexes are winged. They are gregarious, but the females are more imperfect than the males and are rarely seen. The function of the light is obscure, and it is most brilliant in the males.

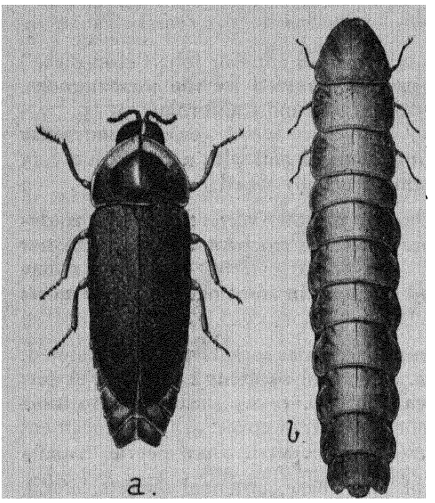


FIG. 589.—*Lamprophorus tardus*, India. *a*, male × 2: *b*, female, nat. size

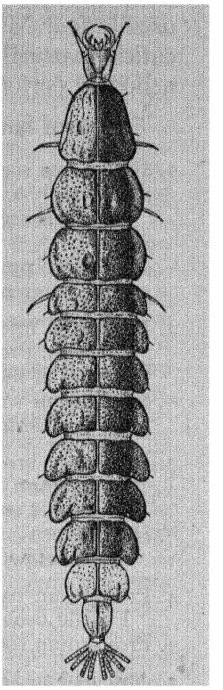


FIG. 590.—*Luciola lusitanica*, larva × 8. France
After Bugnion.

FAM. CANTHARIDAE.—This large family includes 3,500 species (41 British) which are active and probably always predacious both in the larval and adult stage. Some of the best known members are species of *Cantharis* and *Rhagonycha*, often called 'soldier beetles' which frequent flowers and herbage. Their somewhat flattened larvae are found in the soil or among moss, etc. They have a velvety appearance due to a covering of fine hairs (Payne, 1916). The head is flat, the antennae short, and there is a single ocellus behind each: the anal segment has a ventral pseudopod but there are no cerci.

FAM. LYCIDAE.—The adults of this large family (2,800 species) are diurnal and are found on leaves and flowers or under bark: the 4 British members are rare and local. The group is chiefly tropical and the species are often brightly coloured and conspicuous and are said to be distasteful to birds, etc. *Duliticola* of the E. Indies has a normal male but a larviform female—the so-called 'trilobite' larva (Mjöberg, 1925).

Superfamily 12. **Dermestoidea**

The four families grouped here by Crowson (1950) have often been much more widely separated in the system and no doubt the question needs more study. In the adult there seem to be usually six cryptonephric Malpighian

tubules and in the larva some of the tergites are setose or spinose. Some of the adults have dorsal ocelli which very rarely occur in the order.

Table of families:

1. Fore coxal cavities closed behind. Head with 2 ocelli. Hind coxa extending laterally beyond the outer edge of the metepisternum. 12 Holarctic species DERODONTIDAE
–. Fore coxal cavities apparently widely open behind. Hind coxa rarely extending laterally as far as the outer edge of the metepisternum 2

2. Fore coxae transverse. Mid coxae widely separated, hind coxae almost contiguous. Head without ocelli and not reflexible on prosternum NOSODENDRIDAE (p. 795)
–. Fore coxae more or less projecting. If mid coxae are separated, the hind coxae are equally so. Head often with 1 ocellus and usually reflexible on prosternum 3

3. Hind coxa normal, evidently extending laterally at least as far as outer edge of metasternum, femoral plates distinct. Pronotum narrowed in front, hind angles often more or less acute . . . . . DERMESTIDAE (p. 795)
–. Hind coxa more or less ovate, hind margin of metasternum emarginate to receive it, its outer end not appearing to extend to outer edge of metasternum, femoral plates obsolete. Front margin of pronotum as wide as hind margin (or nearly), hind angles obtuse . . . . . THORICTIDAE (p. 795)

FAM. NOSODENDRIDAE.—The 30 species of this family are widely distributed and all stages are found under bark, especially where sap is exuding. The larva has been figured by Ganglbauer.

FAM. DERMESTIDAE.—A family of small or moderate sized beetles usually invested with fine hair or with scales. They mostly inhabit furs, hides, wool and other integumentary substances as well as bacon, cheese, etc., and are exceedingly destructive as larvae. Some, from their habits, have become almost cosmopolitan and 16 species occur in Britain. Out in the field many act as scavengers in removing offensive animal matter. The adults of *Anthrenus* have been found in natural history specimens and also on flowers: its larvae are extremely destructive, and are the enemy of the collector. *Tiresias* occurs under loose bark among cobwebs, probably feeding upon the insect remains present. *Thaumaglossa* is predatory on the eggs of Mantids. The strange genus *Thylodrias*, with very aberrant adult structure and a larviform female, has a normal Dermestid-type larva which feeds principally on dead insects. *Dermestes* includes many species, some of which occur in dead animals and others are more frequently met with in dwellings, museums, etc., where they attack hides, furs, bacon, etc. The larvae of this family (Rees, 1943; Hinton, 1945) have their upper surface covered with a complex clothing of hairs of various lengths. The hairs are often aggregated into terminal or lateral tufts which, in some cases at least, can be raised at will or even rapidly vibrated: the function of this investment is perhaps protective. When a larva is about to pupate the integument splits down the back and remains as a pupal covering.

FAM. THORICTIDAE.—There are about 80 species in this family, many of which are myrmecophiles. They are commonest in the Mediterranean region but *Thorictodes* has been widely spread in stored foods.

Superfamily 13. **Bostrychoidea**

The families united to form this group contain species often associated with timber and often very destructive. The adult integument is rather hard and the pronotum largely developed and hood-like; there are six cryptonephric Malpighian tubules and, as in the preceding group, their ends are said to be attached at one side of the gut. The larva has a soft body without sclerotized dorsal plates and without setae and it maintains a C-like posture.

Table of families:

1. Trochanters distally truncate. Antennae usually 11-segmented, rarely with a compact club, their sockets closely approximated (or femoral plate of hind coxa distinct) 2

–. Trochanters distally obliquely joined to femora. Antennae usually with less than 11 segments and with a club, their sockets not approximated. Hind coxa with no femoral plate 3

2. Prosternal intercoxal process not received into the mesosternum. Antennal sockets more or less under sides of frons, separated by more than length of segment 1. Hind coxae contiguous . . . . . ANOBIIDAE (p. 796)

–. Prosternal intercoxal process received by the mesosternum. Antennal sockets on the frons, separated by less than length of segment 1. Hind coxae more or less separated . . . . . PTINIDAE (p. 796)

3. Fore coxae projecting, their cavities apparently open behind. Antennae with club of 3 segments. Pronotum hood-like. Hind coxae contiguous BOSTRYCHIDAE (p. 796)

–. Fore coxae rounded, their cavities evidently closed behind. Antennal club normally of 2 segments. Pronotum flattened. Hind coxae separated . LYCTIDAE (p. 797)

FAM. ANOBIIDAE.—The 1,100 species which make up this family are often very destructive to wood, less often to other kinds of stored products. Their larvae (Munro, 1915) resemble those of the Scarabaeids in their crescentic form; they are likewise fleshy and the terminal abdominal segments are generally larger than those preceding. The antennae are very short and there are no anal processes or cerci. *Anobium punctatum* (*striatum*) and *Xestobium rufovillosum* (*tessellatum*) are very destructive to furniture, rafters and flooring, their larvae boring into the solid wood (Fig. 591): the small round exit holes made by the adult beetles are very familiar objects. The name of 'death-watch' is often applied to both these species but belongs more properly to the latter insect. The tapping noise is a sexual call and is heard most often in April to May when pairing takes place. The beetle jerks its body forward several times in rapid succession, each time striking the lower part of the front of the head against the surface upon which it is standing (Gahan). *Lasioderma serricorne* and *Stegobium paniceum* are cosmopolitan: they injure a great variety of stored materials, etc. The former species attacks cigarettes, cigars, drugs, ginger, etc., and the latter is destructive to biscuits, flour, bread, many drugs including opium and aconite, together with a wide range of other substances.

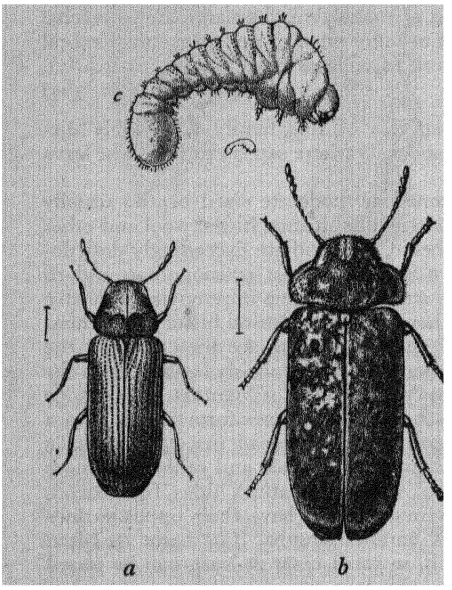


FIG. 591.—*a*, *Anobium punctatum*; *c*, its larva; *b*, *Xestobium rufovillosum*

After Gahan (reproduced by permission of the Trustees of the British Museum).

FAM. PTINIDAE.—No member of this family seems to be a wood-borer, but they are associated with stored foods, dead insects, excrement, or dry vegetable matter. The larvae (Manton, 1945) are superficially similar to those of Anobiids but the abdominal tergites lack rows of spinules and the anterior spiracle is in the prothorax and not intersegmental. There are about 500 species of which 20 have been recorded in Britain, some as introductions. The Australian Ectrephidae (5 spp.) and the Neotropical Gnostidae (2 spp.) are probably specialized, myrmecophilous Ptinids.

FAM. BOSTRYCHIDAE.—The members of this family make cylindrical burrows in felled timber or dried wood, and occasionally attack unhealthy standing trees. They exhibit a great variety of sculpture while the body is often truncated posteriorly and armed with small projections. Species of *Sinoxylon* and *Dinoderus* are very destructive to felled trees and bamboo in India. Their larvae resemble those of the Anobiidae and are similarly curved posteriorly, but the head is greatly reduced and the thorax more enlarged: the larva of *Bostrychus capucinus* is figured by Perris, and Anderson (1939) has tabulated those of many genera. The family is worldwide (550 spp.) but represented in Britain only by a few rare species.

FAM. LYCTIDAE (Powder Post Beetles).—This family is closely allied to the one preceding and is often merged as one of its groups. The larvae also are very similar and Lameere was of opinion that this similarity overweighed any adult differences. They are small elongate insects, found both in freshly cut and old timber, palings and furniture; only the wood of broad-leaved trees appears to be attacked. *Lyctus* larvae are often mistaken for those of the Anobiidae but may be easily distinguished by the more retracted head and large 8th abdominal spiracle. The Lyctidae have 90 species and several occur in the British Isles (Fig. 592).

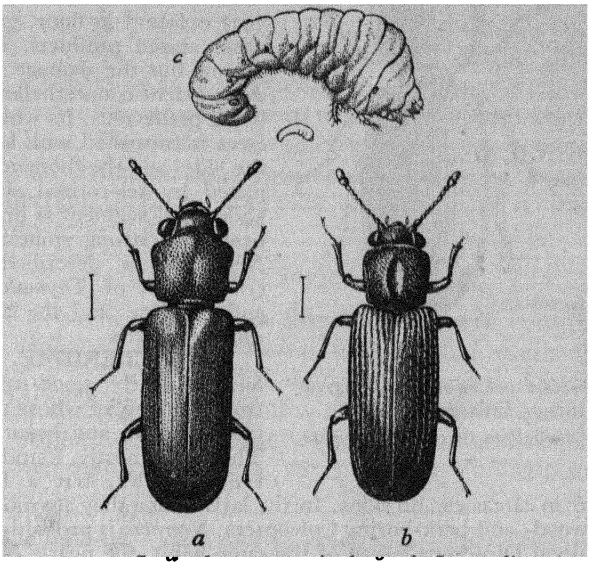


FIG. 592.—*a*, *Lyctus brunneus*; *c*, its larva; *b*, *Lyctus linearis*
After Gahan (reproduced by permission of the Trustees of the British Museum).

Superfamily 14. Cleroidea

The adults of this group have five tarsal segments, no femoral plate on the hind coxa, the prosternal intercoxal process is not received by the mesosternum, and there are six cryptonephric Malpighian tubules whose ends are attached regularly round the gut. The larval mouthparts are more or less protracted and there are two horny urogomphi. Their habits are nearly always predatory, at least in the larva.

Table of families:

1. Fore coxa strongly transverse. 1st tarsal segment much shorter than 2nd, no segment with lobes beneath; empodium conspicuous, bisetose. Gular sutures at least partly confluent 2
–. Fore coxa projecting. If tarsal segment 1 is shorter than 2 or 3, then these latter are lobed beneath or the empodium is indistinct. Gular sutures separate . . 3
2. Antennae clubbed. Abdomen normally with 5 visible sternites. Body not setose TROGOSITIDAE (p. 798)
–. Antennae filiform. Abdomen usually with 6 visible sternites. Body setose (3 N. Zealand genera) . . . . . CHAETOSOMATIDAE
3. Tarsi never 5-segmented and filiform. Antennae usually clubbed, rarely serrate or filiform. Gular sutures approximated. Labial palpi with last segments triangular . . . . . CLERIDAE (p. 798)
–. Tarsi 5-segmented, filiform. Gular sutures not approximated . . . 4
4. Antennae almost always filiform or serrate. Tarsal claws nearly always toothed or appendiculate, or with membranous appendages. Body nearly always setose MELYRIDAE (p. 798)
–. Antennae with last 3 segments forming a loose club. Tersal claws simple, with a bisetose empodium. Body not setose . . . PHLOIOPHILIDAE (p. 798)

FAM. TROGOSITIDAE.—Although there are over 500 species in this family, they are mostly tropical, only three genera and as many species being British. They vary greatly in form, some being elongate and cylindrical, others almost hemispherical. Several genera inhabit decaying trees, and prey upon the larvae of other lignicolous insects, while others occur in fungi. The cosmopolitan 'Cadelle' *Tenebroides mauritanicus* (Fig. 593) is found in flour, grain and many other stored products: it is often injurious but the damage it causes is to some extent counterbalanced by its also being predacious. Its whitish cylindrical larva is furnished with long setae along the sides and the thoracic terga are protected by sclerotized shields: the last abdominal segment is brown-black and bears two strong spines. The larva of *Nemosoma* is described by Erichson (1848): that of *Thymalus* by Chapuis and Candèze: and the larva of *Temnochila* by Perris.

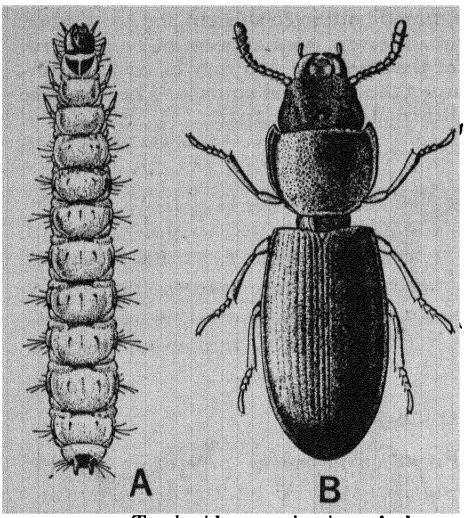


FIG. 593.—*Tenebroides mauritanicus*. A, larva; B, imago. Enlarged

After Fletcher & Ghosh, *Proc. 3rd ent. Meeting, Pusa*, 1919.

FAM. CLERIDAE.—An extensive family (nearly 3,000 species), mainly tropical, many of whose members are of graceful form and beautiful coloration. They are mostly found on plants or tree-trunks, but a few (*Necrobia*, *Corynetes*) occur in carcasses and skins. In the larval stage they are mostly predacious and feed upon wood- and bark-boring Coleoptera. *Necrobia* is probably saprophagous and also feeds upon Dipterous larvae of the same habit; the nearly cosmopolitan *N. rufipes* is destructive to stored hams. *Corynetes* sometimes preys upon *Anobium*, and *Trichodes* is known to infest the nests of *Apis*, *Chalicodoma* and other bees. The general appearance of Clerid larvae can be gathered from a valuable paper by Böving & Champlain (1920). They are frequently bright red, brown, pink or otherwise vividly coloured, and are more or less elongate and cylindrical, or slightly flattened. The pronotum is strongly sclerotized but the remaining segments are usually fleshy except the 9th, which carries a hard shield bearing two corneous processes, and the abdomen often has ambulatory swellings.

FAM. MELYRIDAE (including **Malachiidae, Dasytidae, Prionoceridae** and **Rhadalidae**).—This large family of nearly 4,000 species of which about 20 are British shows considerable diversity in structure and needs thorough revision. Many of them superficially resemble Cantharidae but this is probably due to convergence. Their habits generally resemble those of Clerids. *Malachius* frequents flowers and is characterized by the presence of lateral protrusible vesicles at the sides of the thorax and abdomen (cf. Schmidt, 1949).

FAM. PHLOIOPHILIDAE.—The British species *Phloiophilus edwardsii* is the only one certainly attributable to this family. It has been found very locally under bark but the larva, which might throw much light on its affinities, has not yet been described.

Superfamily 15. **Lymexyloidea**

This group is restricted by Crowson to the single family, the **Lymexylidae.**

They are elongate insects with soft integument. The maxillary palpi are flabellate in the male. The larva has an enlarged prothorax, well-developed legs and the 9th abdominal tergite though often greatly modified does not bear paired processes. There are said to be six cryptonephric Malpighian tubules. These are about 50 species of world-wide distribution. They are capable of boring into hard wood, doing at times considerable damage by drilling cylindrical holes and also through associated fungus infections. The curious larvae of the British *Lymexylon* and *Hylecoetus* are

figured by Westwood (1839) and that of *Melittomma* by Gahan (1908). *M. insulare* has done much damage to palm-trees in the Seychelles. *Atractocerus* has rudimentary elytra but ample wings, and its long flexible abdomen gives its species the appearance of Staphylinids. In tropical regions it is sometimes attracted to light.

Superfamily 16. **Cucujoidea**

Different authorities vary greatly in their treatment of the vast number of species assembled here. In the system proposed by Crowson the group is divided into two, not very clear-cut sections, corresponding roughly with the older groupings—Clavicornia and Heteromera. The further division of these into families is a matter of so much difficulty, subject to such differences of opinion, and so difficult to express in a concise and workable key that it has not been attempted here. The student is, therefore, advised to become thoroughly acquainted with the structure and appearance of the more easily recognizable families in the first instance, and gradually to identify the remainder with the aid of a reference collection.

Section **Clavicornia**

Tarsi never 5–5–4 in both sexes. Front coxae never projecting. If the trochanters are obliquely attached to less than the full width of the femur, then the tarsi are 5–5–5, 3–3–3 or apparently 3–3–3. Antennae usually clubbed. All visible abdominal sternites nearly always movably articulated to one another. Sometimes less than seven pairs of abdominal spiracles. Larva usually with a mandibular prostheca and rarely with a distinct median epicranial suture (cf. Verhoeff, 1923).

FAM. NITIDULIDAE.—*Tarsi* 5–5–5, *rarely* 4–4–4. *Fore and mid coxae very transverse, trochantins exposed. Abdomen usually with the last* 1 *or* 2 *tergites not covered by the elytra, with only* 6 (*rarely* 5) *pairs of functional spiracles.* A large family of about 2,200 species which are extremely variable in form, structure and habits (Fig. 594). A large number inhabit flowers and, in some cases, are restricted to particular species of the latter: others are found in fungi or in decaying animal matter. The larvae of various species have been studied by Perris. Those of certain species of *Meligethes* are sometimes injurious to cultivated Cruciferae while those of *Cybocephalus* attack scale-insects. The few tropical American species of *Smicrips* are very similar to the Nitidulidae though Crowson places them in a separate family.

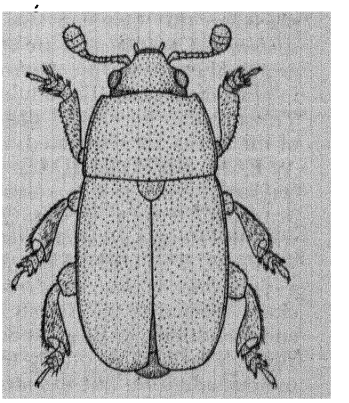


FIG. 594.—*Meligethes aeneus.* Europe. × 22

FAM. RHIZOPHAGIDAE.—*Antennal club of* 1 *or* 2 *segments* (10 *and* 11 *fused;* 9 *sometimes enlarged). Form usually parallel-sided, with elytra truncate and* 1 *abdominal tergite uncovered. Tarsi* 5–5–5, *or* 5–5–4 *in male, or* 4–4–4 *in both sexes. Fore coxal cavities closed behind.* A small family allied to and sometimes included in the preceding one. The adults and larvae are usually found under bark, often associating with Scolytinae on which they are predacious. *Monotoma* with nine British species is found in decaying vegetable matter and is sometimes placed in a separate family.

FAM. SPHINDIDAE.—*Tarsi* 5–5–5 *in* ♀, 5–5–4 *in* ♂, 1*st segment the smallest, empodium small. Fore coxae transverse, trochantins exposed, cavities closed behind.* About 30 small species (two British) which feed on Mycetozoa. Crowson (1952) has erected a new family the **Protocucujidae** with one Chilean and one Australian species which fall nearest to the Sphindidae but have the penultimate tarsal segment the smallest and a large bisetose empodium. The same author places the few and little-known species of *Hypocoprus* in a family with somewhat similar affinities.

FAM. PASSANDRIDAE.—*Gular sutures confluent. Tarsi* 5–5–5, *segment* 1 *usually small, no segment lobed beneath.* The members of this small family are very similar

to those of the next but the condition of the gular sutures is very unusual in this group. The species are mostly found in warmer climates and *Laemotmetus ferrugineus* is sometimes introduced into Britain with cargoes of grain, etc. The few larvae which are known are predatory on wood-boring beetles.

FAM. CUCUJIDAE.—*Aedegus inverted, with the parameres ventral. If mid coxal cavities are closed outwardly by the sterna, the 1st tarsal segment is much shorter than the 2nd. Antennae often filiform.* A family of moderate size with about 15 British species which are mostly found under bark or in borings of other beetles. Their habits seem most often to be predatory but in *Laemophloeus* both predacious and grain-eating species occur. The larva (vide Perris) has no epicranial suture, annular spiracles and a pair of urogomphi.

FAM. SILVANIDAE.—*Characters mainly as in preceding family but 3rd tarsal segment lobed beneath, 4th shorter than 1st. Tarsi 5–5–5 in both sexes. Antennae usually clubbed.* These beetles occur mostly on plants or amongst plant materials and several are found in warehouses. Some species of *Silvanus* are found under bark, often associating with some particular species of Scolytine or other beetle. Wheeler (1921) discovered in British Guiana two species (*Coccidotrophus socialis* and *Eunausibius wheeleri*) which live, along with their early stages, in the hollow leaf-petioles of *Tachigalia paniculata*. They are accompanied by a mealy bug (*Pseudococcus bromeliae*) whose honey-dew is solicited by the beetles and their larvae.

FAM. HELOTIDAE.—*Mid coxal cavities not outwardly closed by sterna, fore coxal cavities closed behind, trochantins hidden, all coxae rather widely separated. Elytra usually with metallic depressions, abdomen covered.* About 80 species are found in the warmer parts of Asia. The larva is undescribed but the species are said to be phytophagous. *Phycosecis* with a few Australasian species forms together with one Egyptian species of *Alfierella*, the family **Phycosecidae** of which the affinities are uncertain. The **Propalticidae** with about a dozen species, mostly in the warmer regions of the old world, is another small family of doubtful affinities. The beetles are said to occur under bark and to be capable of jumping.

FAM. CRYPTOPHAGIDAE.—*Mid coxal cavities closed outwardly by sterna. Elytral epipleura indistinct or developed only on anterior half. Tarsi usually 5–5–4 in the male. Elytra without scutellary striole, surface pubescent.* About 800 species are now placed in this family whose definition has gradually been refined. The numerous species of *Cryptophagus* are essentially fungus-feeders, but some of them are found in nests of bees or wasps. *Antherophagus* may be found on flowers but the larva is found in nests of *Bombus*. The adults occasionally cling to the legs of the bees when in flight. *Telmatophilus* lives in all stages on the heads of *Typha* and other water plants. Some of the larvae are illustrated by Hinton (1945).

FAM. BIPHYLLIDAE.—*Mid and hind trochanters of the heteromerous type* (*p.* 803). *Tarsi 5–5–5, claws simple. Fore trochantin hidden.* There are about 200 principally tropical species. Of the two found in Britain, *Biphyllus lunatus* is associated with the fungus *Daldinia concentrica* and *Diplocoelus fagi* is found under bark.

FAM. BYTURIDAE.—*Mid and hind trochanters of the heteromerous type. Tarsi 5–5–5, claws toothed. Fore trochantin exposed.* This family includes a few genera rather closely similar to the British *Byturus*. *B. tomentosus* infests raspberry and allied plants and the adults may do great damage to the blossoms and the larvae to the fruit (Massee, 1954). The larva according to Böving & Craighead shows, like the adult, some heteromerous affinities, but the tarsal formula, in particular, is in disagreement.

FAM. LANGURIIDAE.—*Fore coxal cavities open behind. Tarsi never 5–5–4, claws simple. Pronotum with more or less distinct posterior impressions. Form rather narrow and parallel-sided, elytral epipleura complete.* About 400 species, mostly found in Asia and in N. America (cf. Villiers, 1943), but one or two have been introduced into Europe in stored grain, etc. The adults can stridulate by rubbing the anterior margin of the pronotum against a file on the vertex. In some species, the female mandibles are strongly asymmetrical. The species seem to be phytophagous and the adults are found on leaves or flowers.

FAM. EROTYLIDAE.—*Fore coxal cavities closed behind. Tarsi with 5 segments, 4th small, claws simple. Pronotum without posterior impressions. Last segment of maxillary palpi broad. Form more or less broadly oval, elytral epipleura complete.* There are nearly 1,600 species (seven British) of this family of which about half are found in S. America. As far as is known, the early stages are always spent in the fruiting bodies of fungi.

FAM. PHALACRIDAE.—*Tarsal claws toothed or appendiculate. Fore coxal cavities open behind. Tarsi 5–5–5, 2nd and 3rd bilobed, 4th small. Small, convex, shining insects. Larvae with paired urogomphi.* The members of this family are easily recognized

when once known as they are all of very similar appearance. There are more than 500 species (17 British) widely distributed in all the main regions. The larvae of the genus *Phalacrus* develop on smuts on grasses, etc. (Friederichs, 1908). The species of *Olibrus* are found on flowers, especially those of Compositae. The larva develops in the flower and when full-grown bores down the stem to pupate in the ground. According to Heeger (1857) there may be six generations in the year.

FAM. CISIDAE.—*Head deflexed, more or less covered by the pronotum. Tarsi 4–4–4, 4th segment small. Fore coxae somewhat transverse, their cavities open behind and internally. Larvae with paired urogomphi.* The correct position of this family has been disputed; their superficial resemblance to the Bostrychidae is evident and the larvae show some resemblances to the Cleroidea. The reduced number of antennal segments in the adult (8–10) and the 3-segmented club suggest rather a position amongst the Clavicornia. The 360 species (26 British) are found in all the principal regions and they are all associated with woody fungi or with fungus-impregnated wood. Many of them seem to breed gregariously.

FAM. CERYLONIDAE.—*Tarsi 4–4–4, segments 2 and 3 similar and not lobed beneath. Mid coxal cavities broad, closed externally by sterna. Palpi with cylindrical segments.* This is a small group proposed by Crowson to contain species which have usually been placed in the Colydiidae. The species of *Cerylon* are usually found under bark and *Murmidius* is found in vegetable detritus, often in warehouses: its strange oval larva, fringed with spinulose setae, is figured by Böving & Craighead.

FAM. CORYLOPHIDAE.—*Very small beetles, head more or less concealed beneath pronotum. Tarsi 4–4–4, segment 3 much smaller than 2 which is more or less lobed beneath. Last segment of maxillary palpi not enlarged. Larval mandibles usually not falcate nor body setose.* These minute beetles are mostly found in rotting vegetation or decayed wood. *Sericoderus* has been reared on mould but some species associate with coccids. The pupa is obtect as in the next family. There are about 300 species of which 11 are British.

FAM. COCCINELLIDAE.—*Beetles of moderate size, convex, head partly concealed by pronotum. Tarsi 4–4–4, 3rd segment concealed in the deeply bilobed second. Last segment of maxillary palpi securiform. Larval mandibles normally falcate and body usually setose.* This very important family comprises nearly 5,000 species, for the most part brightly coloured and spotted. The greater number of the species are carnivorous and predacious, feeding during the larval and adult stages upon aphids, coccids and

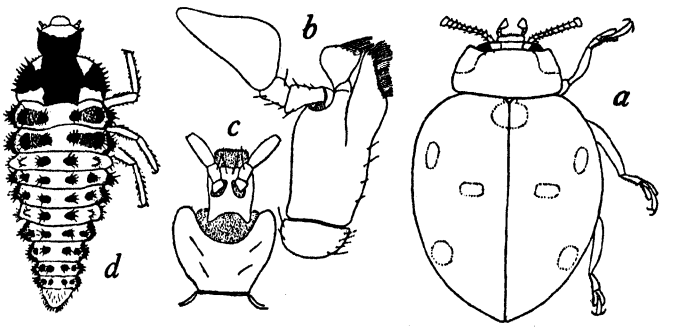


FIG. 595.—Coccinellidae

a, Coccinella septempunctata; b, maxilla; *c,* labium; *d,* a coccinellid larva. All magnified.

occasionally on other soft-bodied insects. They are, therefore, of very great importance in reducing the numbers of injurious species. A comparatively small group are phytophagous but they rarely cause serious damage. Structurally, the carnivorous forms (Fig. 595) (Coccinellinae) are characterized by the mandibles having simple or bifid apices and each jaw being armed with a basal tooth. Even in this group, however, *Psyllobora 22-punctata* feeds as a larva on mildews and others live in dung. The herbivorous species (Epilachninae) lack the basal tooth and the apex of the mandible is multidentate. The Tetrabrachinae form a third subfamily: very little is known about their habits but the mandibles are of the carnivorous type. They are distinguished by the tarsi being evidently 4-segmented.

When disturbed many members of the family discharge a bitter, amber-coloured

fluid. It is usually emitted through pores situated around the tibio-femoral articulations, but in *Epilachna* the pores have a much wider distribution. According to McIndoo (1916) the exuded liquid is a secretory product of hypodermal gland cells: other writers have regarded it as the blood of the insect. Porta (1903) found that the secretion had a poisonous effect upon vertebrates but had no influence upon insects. It is regarded as defensive in function, but it must be pointed out that Coccinellids are known to be eaten by several species of birds.

Several members of the family, notably the common species of *Adalia*, are remarkable for their wide range of colour variation. Another peculiarity is the markedly gregarious habits of certain species both during hibernation and when in the open: at times these insects have been found in 'masses' but the meaning of the phenomenon is obscure. One of the best known members of the family is *Rodolia cardinalis* which has been imported from Australia into California for purposes of controlling *Icerya purchasi*—a serious enemy of Citrus cultivation in the latter country. The beetle proved so effective a controlling agent that it has since been imported into all countries where the coccid has become injurious.

Coccinellid larvae (Böving, 1917) are soft-bodied and variously coloured: they are often of a leaden or other dark hue spotted with yellow or white. There are three ocelli on either side, the mandibles are sickle-shaped with molar bases (except in the Epilachninae) and the legs are long and slender. The terga are usually provided with segmental tubercles and spines and the abdomen tapers distally, but never bears the urogomphi so characteristic of other families. In some genera (*Hyperaspis*, *Scymnus* and *Platynaspis*) the spines are wanting and the whole body is covered with a white flocculent secretion. In *Chilocorus* (Fig. 596) the body is protected by long integumental processes.

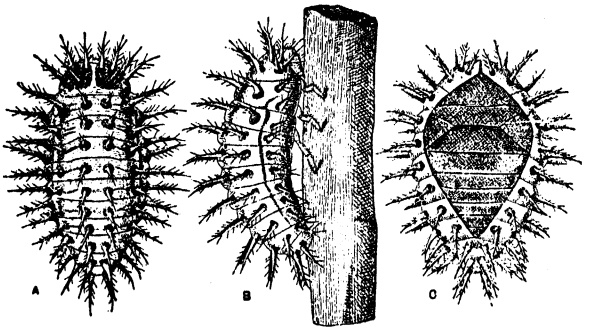


FIG. 596.—Larva of *Chilocorus*. A, dorsal; B, lateral; C, pupa *After* Silvestri.

The usual number of instars appears to be four, and the complete development of *Adalia bipunctata* in England was found to occupy about 34 days in captivity (Hawkes, 1920), an average of 20 days being spent as a larva. In California, Clausen (1915) found the average developmental period was 26 days. The eggs of Coccinellids are yellow, and disposed in batches, with their long axes perpendicular to the surface of the leaves upon which they are laid. Palmer found that the number laid by *Coccinella 9-notata* varied from 435 to 1,047: in *A. bipunctata* Hawkes states that the average number lies between 140 and 148 with 418 as the maximum. The number of aphids daily consumed by the larva of this species is stated by Clausen to be 14 while in *Coccinella californica* it is about 20. During the entire larval period he found that the number consumed varied between 216 and 475 for different species: the adults are usually even more voracious. *Hyperaspis binotata* is a coccid feeder and according to Simanton (1915) it will destroy 90 adults and 3,000 nymphs during its period of larval existence. When about to pupate, Coccinellid larvae usually suspend themselves by the caudal extremity which is attached by means of a secretion to plants, palings and other objects. The pupae are usually conspicuously coloured and are either surrounded by the larval exuviae, or the latter are pushed back to the anal extremity.

The larvae of the Epilachninae (Kapur, 1950) are invested with long branched processes of the body-wall. Members of this subfamily are often destructive to the foliage of potatoes, Cucurbitaceae, etc., especially in N. America. The only British member of the group is *Subcoccinella 24-punctata* whose larva gnaws the parenchyma of clover and other plants.

For further information on the biology of the family, vide Gage (1911; 1917; 1920), Palmer (1914) and papers by the latter writer on colour-inheritance in *Adalia*. Donisthorpe (1919; 1920) has followed the complete life-history of *Coccinella distincta*—a species found in association with ants.

FAM. ENDOMYCHIDAE.—*Species of moderate size, convex. Tarsi* 4-4-4, *3rd*

segment concealed in the deeply bilobed 2nd. Last segment of maxillary palpi not enlarged. Larva without branched setae on body, mandibles not falcate. A family of more than 600 species chiefly met with among fungi on timber in tropical forests. Many have brilliant colours and are variable in form and size. Among the few British species the black and red *Endomychus coccineus* and the small *Mycetaea hirta* are the best known. The latter occurs in dung, vegetable refuse and often in warehouses. The larvae may be ovate with the tergites expanded to conceal the pleura; the 9th segment occasionally bears urogomphi.

FAM. DISCOLOMIDAE.—*Tarsi* 3–3–3. *All coxae similar and strongly transverse, their lateral parts concealed by the sterna.* A small tropical family with about 30 species, many of them wingless, found on the bark of tree-trunks.

FAM. LATHRIDIIDAE.—*Tarsi* 3–3–3, *coxae not strongly transverse, with the outer part concealed by the sterna. Fore coxal cavities closed behind. Trochanters not elongate.* There are about 600 species in this widely spread family and apparently all of them feed in all stages on fungi, especially moulds, and on Mycetozoa. The numerous species found indoors, in cellars and warehouses, are probably attracted to fungal growth. Crowson (1952) proposes a family, the **Merophysiidae,** to include a few genera such as *Holoparamecus* and *Merophysia* which have usually been considered Lathridiids. In these adults, the fore coxal cavity is open behind and the trochanters are elongate. The larva of *Holoparamecus* has urogomphi which are not present in Lathridiids.

Section **Heteromera**

Tarsi 5–5–4 in both sexes, or 4–4–4 (very rarely 3–4–4 in males, or 3–3–3). Fore coxae usually projecting; if not, trochanters, obliquely attached to less than the full width of the femur (heteromerous type) and the first three visible abdominal sternites are fused. Abdomen with 7 pairs of spiracles. Larva rarely with a mandibular prostheca and often with a median epicranial suture.

FAM. COLYDIIDAE.—*Tarsi* 4–4–4 (*very rarely* 3–3–3). *Mesepimera not reaching middle coxal cavities. Fore coxae not at all protuberant. Antennal sockets usually beneath margins of front. Larval mandibles symmetrical.* A family of more than 1,400 species, found especially in the tropics, but well developed in New Zealand. There is great diversity of form and the definition of the family is still a matter of opinion. According to Crowson (1953), *Monoedus* (= *Adimerus*) clearly belongs here though some authors have placed it in a separate family. *Sarothias* (*Jacobsonianum*) has been reported on by the same author but its affinities are still dubious. For *Meryx*, with a few Australasian species, Crowson proposes a new family in which the mesepimera reach the mid coxal cavities and the antennae are 11-segmented with a weak 3-segmented club. Some Colydiids are found deep underground, associated with buried wood or roots. Others, e.g. *Bothrideres*, are parasitic in the larval stage on wood-boring beetles or bees. Probably most of the species are in some way predatory.

FAM. MYCETOPHAGIDAE.—*Tarsi* 4–4–4 in ♀, 3–4–4 in ♂. *Mesepimera reaching mid coxal cavities. Fore coxae somewhat projecting. Antennal sockets not beneath sides of front, antennal club usually with 4–5 segments. Larval mandibles asymmetrical.* A small family of about 200 species, mostly associating with fungi but *Berginus* develops on flowers. Some of the larvae are described by Hinton (1945): spine-like urogomphi may be present or absent.

FAM. PTEROGENIIDAE.—*Tarsi* 5–5–4, *no segment lobed. Fore coxae ovate, without concealed extensions, their cavities open behind. No antennal club.* Crowson (1953) proposes this family for two Indo-Malayan genera of very uncertain affinities.

FAM. NILIONIDAE.—*First* 3 *visible abdominal sternites connate. Trochanters not of the heteromerous type. Form broad and rounded, elytral epipleura very broad.* Insects somewhat resembling large Coccinellids in shape and associated with fungi on trees. There are about 40 species in tropical countries. *Nilio* is American but if the forms placed in the Leiochroini are also included, the family occurs also in the old world.

FAM. TENEBRIONIDAE.—*First* 3 *visible abdominal sternites connate—Trochanters of heteromerous type. Fore coxae not projecting. Claws simple.* One of the largest families of Coleoptera comprising more than 10,000 species which exhibit an extraordinarily wide range of superficial dissimilarity: the larvae on the other hand are strikingly uniform in character. Many are ground beetles, usually black in colour, and

often bear a superficial resemblance to the Carabidae. These forms are very often apterous, or have vestigial wings, and the elytra are frequently immovable. Many of the wood-feeding species have ample wings. The species of *Blaps* often occur in cellars and outbuildings. *Tenebrio molitor* and *T. obscurus* are nearly cosmopolitan: they are found in all stages in meal, flour and stored goods, their larvae being known as 'meal worms' (Fig. 597). *Tribolium* has very similar habits and *T. ferrugineum* and *T. confusum* are likewise widely spread, through commerce, in granaries and stores

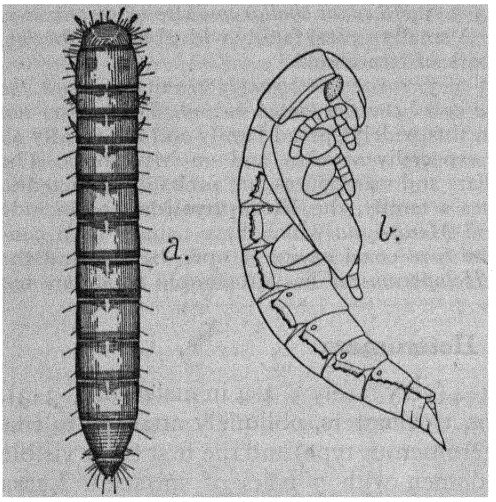


FIG. 597.—*Tenebrio obscurus*, larva and pupa: enlarged

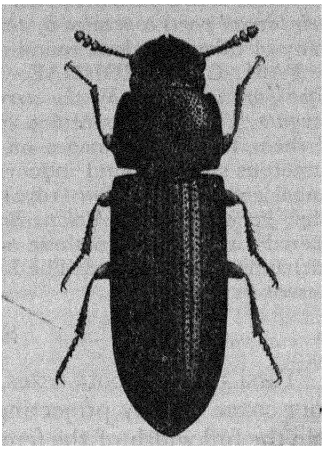


FIG. 598. — *Tribolium ferrugineum*, cosmopolitan. × 14

(Fig. 598). An account of the biology of *Tenebrio* is given by Cotton and St. George (1929). A very large number of species is found in desert habitats. Species of other genera live in dung, in dead animal matter, in fungi, under bark, etc. The larvae of this family bear a tolerably close resemblance to those of the Elateridae, but the labrum is plainly visible and the terminal segment of the abdomen rarely attains the complexity found in that family. For an account of Tenebrionid larvae see Korschefsky (1943).

The **Zopheridae,** a small and principally American group, were first separated from the Tenebrionidae by Böving & Craighead on the basis of larval structure, but the adult also differs in having movable abdominable sternites. The **Boridae** is another very small group usually placed in the Tenebrionidae but the fore coxal cavities are completely open. It has a wide distribution.

FAM. LAGRIIDAE.—*First 3 visible abdominal sternites connate. Trochanters of heteromerous type. Front coxae somewhat projecting, prosternal intercoxal process narrow.* There are nearly 600 species in this family which is widely distributed (except New Zealand). The only British representative is *Lagria hirta*: the larva of this species is somewhat broader and more active than those of the Tenebrionidae and the segments are furnished with lateral tufts of hairs (Schiödte). The head is very short and the last body-segment is bifid at the apex. The pupa is remarkable on account of the long broad clavate processes which project from most of the abdominal segments.

FAM. ALLECULIDAE (Cistelidae).—*Tarsal claws pectinate. Antennae filiform or pectinate. Fore coxae not projecting, prosternal intercoxal process broad.* The members of this family are easily recognized by the structure of their claws. There are about 1,100 species, found in all parts of the world, usually on flowers or leaves. The larvae are found in rotten wood or humus and that of *Gonodera* (*Cistela*) is figured by Westwood (1839). Binaghi (1949) describes the biology of *Omophlus lepturoides* which damages potatoes.

FAM. MONOMMIDAE.—*Fore coxae small, rounded, separated by a broad prosternal process, their cavities widely open behind. Propleuron grooved to receive antenna.* About 100 species found in most of the warmer parts of the world and breeding in rotten wood. *Monomma indicum* lives in decaying stems of the paw-paw.

FAM. ELACATIDAE.—*Fore coxae small, rounded to projecting, prosternal process between them usually broad, their cavities closed behind. Mesepisterna not nearly meeting in front of mesosternum.* Under this name Crowson unites several groups (*Othnius*, *Eurystethus* = *Aegialites*, and others) which have in the past been placed in separate families or scattered through other groups. *Othnius* is widespread in warm countries and lives in decaying vegetable matter. The species of *Eurystethus* are found on the coasts of western North America. Crowson has also erected a family **Inopeplidae** for *Inopeplus* which has usually been placed in the Cucujidae though it appears to be more allied to the Salpingidae.

FAM. SALPINGIDAE.—*Fore coxae rounded, separated by a broad prosternal process, cavities internally closed. Mid coxal cavities closed by sterna. Tarsal segments simple. Antennae clubbed.* A family of rather small size but of wide distribution. The British genera *Salpingus* and *Lissodema* superficially resemble Carabids, whereas *Rhinosimus* has a well-marked rostrum. The British species are found under bark but very little is known of their habits. The larval spiracles are biforous and there are complex urogomphi (vide Perris). Near the Salpingidae Crowson places the several genera forming his family **Cononotidae**: the adults have filiform antennae and the last segment of the maxillary palpi is securiform.

FAM. PYTHIDAE.—*Mid coxal cavities not closed externally by the sterna. Fore coxal cavities completely open both externally and internally. Antennae short or clubbed.* As now dismembered, this family is relatively small though widely distributed in Eurasia and America. One species of *Pytho* is British. The larva has cribriform spiracles and broad, almost lamelliform, urogomphi. The **Mycteridae** include a number of genera which have often been placed in the Pythidae though the mid coxal cavities are closed by the sterna. They are perhaps closer to the Salpingidae but the penultimate tarsal segment is lobed. *Mycterus* superficially resembles a weevil. It is found on flowers and is reputedly British.

FAM. HEMIPEPLIDAE.—*Tarsi with last 2 segments lobed beneath. Mid coxal cavities closed by sterna. Fore coxae oblique, not projecting.* This family which has been segregated from a position in the Cucujidae, has a small number of species in the warmer regions. The adults and larvae live together under the leaf-bases of palms.

FAM. TRICTENOTOMIDAE.—*Large, Prionid-like species. Mid coxal cavities closed by the sterna, fore coxae strongly transverse. Antennae long, last 3 segments differentiated.* About a dozen species are known from the forests of the Oriental region. The larva has been figured by Gahan (1908).

FAM. PYROCHROIDAE (Cardinal Beetles).—*Antennae long, filiform to pectinate. Tarsi with penultimate segment lobed beneath. Mid coxal cavities not closed outwardly by sterna, fore coxal cavities completely open both internally and externally.* A family of rather more than 100 species occurring principally in the north temperate region. They are of rather large size and often partly scarlet in colour. The adults are often found under bark where the larval life is spent but they also occur on leaves and flowers. The larva of *Pyrochroa* is figured by Schiödte (Fig. 599) and those of the three British species are distinguished by van Emden (1943).

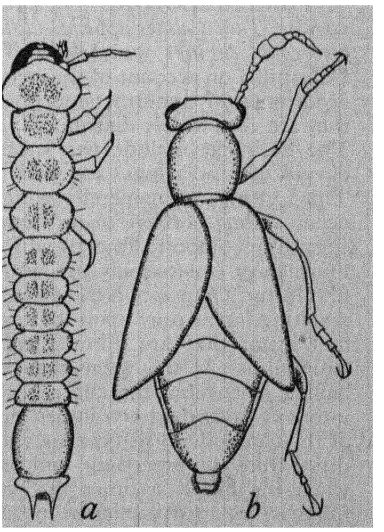


FIG. 599.—Heteromera

a, *Pyrochroa*, larva; *b*, *Meloë proscarabaeus*, Imago.

FAM. MELANDRYIDAE (Serropalpidae).—*Pronotum with well-marked side borders. Head not sharply constricted at neck. Tibial spurs simple or serrate, in former condition, antennae often with 4-segmented club.* About 450 species have been placed in this family which is principally found in woodland areas in temperate regions. The species are associated with decaying wood or with woody fungi; *Osphya*, however, is found in flowers. The species of *Orchesia* can jump actively with the aid of the tibial spurs. Some authorities recognize a family **Tetratomidae** for those genera in which these spurs are simple.

FAM. SCRAPTIIDAE.—*Pronotum with more or less distinct side borders, about as*

wide as elytra at shoulders. Tibial spurs pubescent. Tarsi with 3rd and 4th segments more or less lobed, claws simple. About 200 species of this family are distributed over most of the principal regions. The large genus *Anaspis* which has usually been referred to the next family is mainly Holarctic. The species of Scraptiidae are mostly associated with rotten wood or fungi, but the adults of *Anaspis* are abundant in flowers. The larva of *Scraptia* is principally characterized by the great length and spoon-shaped form of the last abdominal segment (Böving & Craighead).

FAM. MORDELLIDAE.—*Tibial spurs pubescent. Pronotum with more or less distinct side borders, about as wide as elytra at shoulders. Tarsi with penultimate segment not or slightly lobed, claws serrate and with bristle-like lobe beneath.* Most species of this family, of which there are about 650 species, can be recognized by having the 7th abdominal segment produced into a more or less long spine. The larva of *Tomoxia* (Schiödte) develops in decaying wood but that of *Mordellistena* is phytophagous and burrows in the stems of various plants. The adults of many species are found on Umbelliferae but they are rarely common in Britain. The genera of the family have been revised by Ermisch (1950).

FAM. RHIPIPHORIDAE.—*Antennae strongly flabellate, at least in ♂. Tarsal claws serrate but not appendiculate, penultimate tarsal segment simple. Pronotum posteriorly about as wide as elytra at shoulders.* This family with more than 400 species is noted for its specialized parasitic habits. The European *Pelecotoma*, whose larva is said to be predatory on those of other beetles in rotten wood, has probably the simplest type of life history. The Rhipiphorini are parasites of the larvae of aculeate Hymenoptera and exhibit hypermetamorphosis. *Metoecus paradoxus* is a parasite in nests of *Vespula*, particularly *V. vulgaris*. According to Chapman (1870; 1891) the newly hatched larva is black and campodeiform, resembling that of *Meloë*, but how it enters the nest of its host does not appear to have been ascertained, since the eggs are laid in old wood. Two hypotheses have been put forward—either the eggs are transferred along with wood fragments by the wasps to their nests, or the young larvae attach themselves to the wasps while the latter are gathering wood. Within the nest the larva becomes an endoparasite of that of *Vespula*: it subsequently becomes an ectoparasite, and gradually devours the whole of its host. Pupation takes place in the cell of the attacked individual, and the adult beetles are found up to the number of twenty or more in a single nest: more rarely they occur on flowers, etc., outside the nest. Among other genera *Macrosiagon* has a very similar life-history, but utilizes *Odynerus* as its host (Grandi, 1937). *Rhipidius* is an endoparasite of Blattids; the female is apterous and larviform and does not leave the body of its host (Stamm, 1936).

FAM. MELOIDAE (Oil Beetles, Blister Beetles).—*Head strongly deflexed, neck narrow. Tarsal claws appendiculate and usually serrate. Adult soft-bodied with long legs, fore coxal cavities open behind.* This is one of the most interesting of all groups of Coleoptera on account of the remarkable life-histories of its members and the general occurrence of hypermetamorphosis. About 2,000 species have been described and they are very widely distributed: *Meloë* (Fig. 599*b*), *Sitaris* and *Lytta* occur in Britain. The Meloidae include two subfamilies of which the Meloïnae are ground insects, devoid of hind wings, and with elytra frequently much shorter than the abdomen. The Lyttinae are generally winged and the elytra cover the abdomen; they mostly occur among herbage or on flowers. The female beetles lay a very large number of eggs (often 2,000 to 10,000) which is explicable on the grounds that the subsequent life-history is extremely precarious, and very large numbers of larvae perish in the first instar. Oviposition takes place in the soil or on the surface of the ground, and the resulting larvae prey upon the eggs of Orthoptera and aculeate Hymenoptera. In their first instar they are minute, active, hard-skinned, campodeiform larvae known as triungulins. At this stage they are principally engaged in seeking out their hosts: having discovered the latter, they subsequently undergo ecdysis and change either into soft-bodied, short-limbed eruciform larvae or, more rarely, into a modification of the campodeiform type known as the caraboid stage. The next succeeding instars differ from the preceding, and the second, or later larva, passes into a resting period when the insect assumes the pseudo-pupal or 'coarctate' condition. The latter is followed by a further larval instar which is succeeded by the pupa.

The biology of *Sitaris* has been investigated by Fabre (1857) and Mayet (1875). The eggs of *S. muralis* are deposited near the nests of *Anthophora* about August. The newly hatched triungulins remain lethargic and hibernate until spring when they become more active. A certain number succeed in attaching themselves to the hairy bodies of the male bees, which appear earlier than the females. When opportunity allows, they pass to the female bees and so get carried to the nests of the latter.

Anthophora constructs cells in the ground, in each of which there is a supply of honey and a single egg. When the bee deposits an egg on the honey, a triungulin slips off her body, alights on the egg, and becomes imprisoned in the sealed-up cell. It consumes the contents of the egg, and changes into a fleshy ovoid eruciform larva with vestigial legs. In this instar it feeds upon the honey stored by its host, and subsequently changes into the so-called pseudo-pupal condition within the larval skin. After about one month, a certain number of individuals pass through the subsequent instars and appear as beetles the same year. More usually, they winter in the pseudo-pupal condition and, in spring, assume a second eruciform stage, which differs comparatively little from the earlier one. No food is taken during this period, and the larvae soon change into ordinary coleopterous pupae from which emerge the adult beetles.

Riley (1878) has studied the biology of *Epicauta vittata* in N. America. This insect deposits its eggs in parts of the ground frequented by the locust *Melanoplus* (= *Caloptenus*). Triungulins emerge in due course, and explore the soil until they discover the egg-capsules of the Orthopteron. Having found the latter, a single triungulin eats its way in and commences to devour the contained eggs. After a few days ecdysis takes place, and the larva passes into the caraboid or second instar. After about a week, ecdysis again occurs, and the larva becomes curved in shape. From its general body-form this instar is known as the scarabaeoid stage. The succeeding instar is very similar and, when fully grown, the larva deserts the egg-capsule, and changes near by into the pseudo-pupal stage in which it hibernates. In spring it undergoes further changes, and in the sixth instar it is only slightly different from the scarabaeoid stages. From this condition it passes into the pupa and subsequently into the imago (vide Fig. 194).

The life-history of *Meloë* has been partially followed by Newport (1845–53) and is apparently very similar to that of *Sitaris*. Its triungulins do not appear to exercise much discrimination, and although their hosts are *Anthophora* and *Andrena*, they have often been found attached to other bees and also hairy Coleoptera and Diptera. Large numbers consequently perish through selecting the wrong host, while still greater numbers probably never discover a host at all. The second instar corresponds with Riley's caraboid stage, although it more closely resembles the scarabaeoid larvae in general form. In this condition it feeds upon the stored honey, and afterwards transforms into a legless pseudo-pupa. This form moults and the final larval instar is a thick-bodied apodous grub. Space excludes references to the biology of other members of the family, and the student should consult the work of Beauregard (1890) for further information, also numerous more recent papers by Cros.

The 'Spanish fly', *Lytta* (*Cantharis*) *vesicatoria*, of southern Europe is rarely found in England. It yields the pharmaceutical product cantharidin ($C_{10}H_{12}O_4$) which is prepared from the dried insects. The elytra are alone used in pharmacy and contain more of the active principle than the soft parts collectively. Species of *Mylabris* are known to yield a larger amount of cantharidin than *Lytta* and are also used commercially.

The family **Cephaloidae** with about 11 species in E. Asia and N. America is very like the Meloidae in the adult stage but the head is less deflexed and the neck broader; the larva is much more like a Mordellid and has no hypermetamorphosis.

FAM. OEDEMERIDAE.—*Claws simple or toothed, tarsi with 1 or 2 of the penultimate segments lobed. Head little deflexed, without a marked neck. Eyes emarginate.* The 600 species of this family are widely distributed but especially abundant in temperate regions. The larvae are soft-bodied and develop in timber. *Nacerdes* whose adult greatly resembles one of the Cantharidae breeds in water-logged timber, especially in maritime situations.

FAM. ANTHICIDAE.—*Head more or less strongly deflexed and usually constricted into a narrow neck. All visible abdominal sternites connate. Tarsi with penultimate segment lobed beneath, antepenultimate simple.* This large family has about 1,000 species, but some authorities place some of them in a separate family, the **Pedilidae.** The species are mostly found in vegetable refuse, often in damp situations. Some of them inhabit the burrows of *Bledius* (Staphylinidae) and a number are halophilous. The larvae are found with the adults but their food is not known. Several species of *Anthicus* and *Notoxus* are attracted to *Meloë* beetles and have been found hanging by their mandibles to the abdominal segments. Sometimes they have been attracted in large numbers to the dead bodies of *Meloë* put out to dry by coleopterists.

FAM. ADERIDAE (Xylophilidae).—*First 2 visible abdominal sternites connate. Tarsi with penultimate segment small, antepenultimate lobed beneath. Head deflexed and often constricted into a neck. Trochanters not of heteromerous type.* These small beetles

are widely distributed with about 350 species. Three of the large genus *Aderus* (*Xylophila*) are British. The beetles are usually found in dead wood or in vegetable refuse but very little is known of their habits (vide Baguena Corella, 1948).

The family **Petriidae** with a few species in C. Asia requires further elucidation. Several important structural details have not yet been recorded.

Superfamily 17. **Chrysomeloidea**

This vast assemblage of phytophagous or xylophagous insects is rather well defined. There is every gradation from the short squat Chrysomelid type to the elongate Cerambycids with long antennae. There are six cryptonephric Malpighian tubules. In the larva, the thoracic legs are more or less developed, the mandible lacks a mola, and the antennae have three segments.

Table of families:

1. Antennae usually at least two-thirds as long as whole body, capable of being flexed backwards and usually inserted on prominent tubercles. All tibiae with 2 spurs. Claws nearly always simple . . . . . CERAMBYCIDAE (p. 808)
–. Antennae usually shorter, not capable of being flexed backwards. If antennae are inserted on tubercles, there are usually fewer than 2 tibial spurs on one or more pairs of legs. Claws often split or appendiculate 2

2. Ligula not developed. Eyes deeply emanginate. Vertex not grooved. Pronotum with distinct side margins. Elytra with distinct striae but without a scutellary striole. Hind femora more or less thickened and toothed beneath. Spurs usually absent from fore and mid tibiae. Tarsal claws split or appendiculate. 1st visible abdominal sternite as long as the next 3 together . . BRUCHIDAE (p. 809)
. Several or all of these characters not developed. . CHRYSOMELIDAE (p. 810)

FAM. CERAMBYCIDAE (Longicornia).—The longicorn beetles number about 5,000 species mostly of elongate form and attractive coloration (Fig. 600). Some of ıe members, such as *Macrotoma heros* and *Titanus giganteus*, are among the largest f insects. The family exists throughout the world wherever there is woody vegetation, nd includes an almost infinite variety of shape and ornamentation among its species. lthough frequently dissociated into two or three divisions, each of separate family rank, it is scarcely necessary for general purposes to do otherwise than follow Sharp and regard these insects as forming a single family. The number of genera and species found in Europe is very small compared with those of the tropics. Only a few outlying representatives of this extensive group occur in Britain, and they comprise about 65 species, several being exceedingly rare or doubtfully indigenous. A number of forms are well known for their cryptic coloration, while others exhibit a close mimetic resemblance to insects of other families and also of other orders. One of the most striking cases of cryptic coloration is afforded by the African *Petrognatha gigas* whose whole upper surface resembles dead velvety moss and its irregular antennae are very like dried tendrils or twigs. The common British species *Clytus arietis* bears a close resemblance to a Vespid: it, furthermore, runs actively and exhibits antennal movements highly suggestive of those of a wasp. An interesting digression on these subjects will be found in the work of Fowler (1912) where a number of instances is enumerated. Many Cerambycidae possess the faculty of stridulating: in some cases the sound is caused by the hind margin of the prothorax working against a specialized striated area at the base of the scutellum: in others sound is produced by the friction of the hind femora against the edges of the elytra. In the Hawaiian *Plagithmysus* both types of organs are present in the same insect.

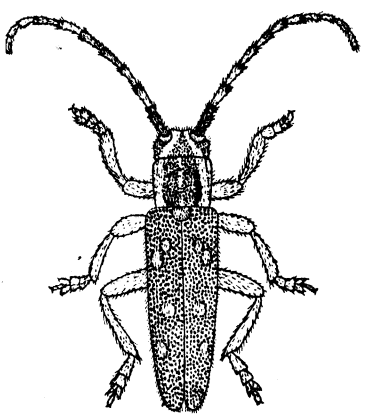


FIG. 600.—*Saperda populnea*, Europe and N. America. × 2

The larvae of the Cerambycidae bore for the most part into the wood of trees, but a few are confined to the roots or pith of herbaceous plants. Most species affect dead or decaying trees, some selecting moist and others dry wood. Certain species bore into the bark or into the sap or heart-wood of living trees and a few, such as *Saperda*, live in stems. The pupal habits are likewise varied, this instar occurring in the wood, between the latter and the bark, or in the bark. The pupa lies in the final larval burrow or in a special gallery leading therefrom and, in either case, a closed chamber is formed by the entrance being plugged with frass or fibrous chips. Many species adopt further measures for sealing up the pupal chamber (Beeson, 1919). In these cases a large amount of calcium carbonate is produced by the Malpighian tubes, this substance being mixed with gummy or silky matter and utilized for constructing an operculum which completely closes the pupal cell. In other cases the whole of the latter may be lined by an eggshell-like coating of the same substances. Cells which are closed or lined in this manner are protected from various enemies and are also probably enabled to maintain the requisite moisture-content. On account of their concealed mode of life, the larvae (Fig. 601) are soft and fleshy and of a whitish or yellowish colour: they are, furthermore, often finely pubescent. The form of the larvae is largely correlated with their habits, the bark-boring species being more or less flattened while those living in wood or stems tend to become cylindrical. The head is invaginated into the prothorax and is usually small and transverse, but in the Lamiinae it is longer than broad. The prothorax is large and is broader than the remaining trunk-segments. The 9th abdominal segment is often longer than those preceding and

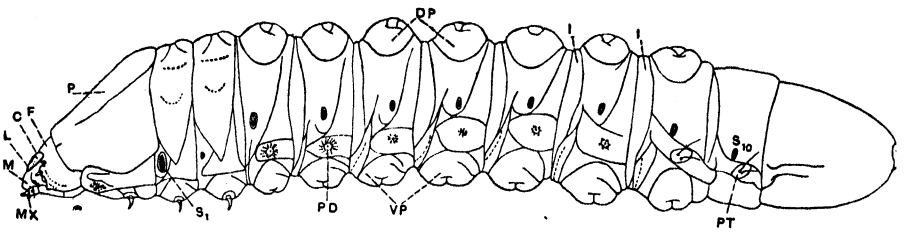


FIG. 601.—Cerambycidae: lateral view of a typical larva

C, clypeus; *DP*, dorsal pseudopods; *F*, frons; *I*, intersegmental region; *L*, labrum; *M*, mandible; *MX*, maxilla; *P*, pronotum; *PD*, pleural disc; *PT*, pleural tubercle; S_1, 1st thoracic spiracle; S_{10}, 8th abdominal spiracle; *VP*, ventral pseudopods. Adapted from Craighead, *U.S. Dept. Agric. Office of Sec. Report*, 107.

somewhat vesicular: in the Aseminae it bears a pair of spines. Thoracic legs are generally present, but are usually so much reduced as to be non-functional: in most of the Lamiinae they are wanting. Locomotion takes place by the aid of dorsal and ventral segmentally arranged abdominal swellings which, in some genera, bear cuticular asperities. In many larvae a variable number of the anterior abdominal segments bear small asteriform structures known as pleural discs which are the points of attachment of chorodotonal organs (vide p. 86).

The writings of Perris and Schiödte include descriptions of a number of larvae belonging to this family, while van Emden (1939) and Duffy (1953) have tabulated the British species and Craighead (1923) some of the Canadian ones. Among life-history studies those of Ritchie (1920) on *Saperda* and Crawshay (1907) on *Tetropium* may be mentioned. In *Saperda carcharias* the life cycle occupies about four years in Scotland, the first winter being passed in the egg stage. In *Tetropium gabrieli*, on the other hand, the life-history is of one year's duration and hibernation occurs in the larval stage. The shorter cycle is more usual, but the relative supply of moisture and the nutrient qualities of the food tend to increase or diminish the normal time by months or even years. Several instances are recorded in which wood, made into furniture many years, has been found to contain larvae which finally emerged as imagines (Craighead).

FAM. BRUCHIDAE (Lariidae).—The position of this family has often been discussed, many authors having regarded it as being closely related to the Anthribidae (p. 813) through the genus *Bruchela* (*Urodon*). On the other hand, the Bruchidae are also in many respects allied to the Sagrinae in the Chrysomelidae. Over 900 species are known and their larvae mostly live in seeds of Leguminosae, causing great injury to peas, beans, lentils, etc.: those of certain other species attack coconuts and palm-nuts. On account of this habit they are very often carried from one country to another

in cargoes of seeds. They are frequently, though erroneously, known as pea and bean 'weevils'. About a dozen species have been found in the British Isles, several being direct introductions from other lands (Herford, 1935).

The eggs of Bruchidae are usually laid on the young seed pods, as for example in *Bruchus pisorum*, and the larvae mine their way through until they reach the seed. In *Pachymerus chinensis* and *Acanthoscelides obtectus* the eggs are laid either upon the pods or the seeds, while *Bruchus pruinosus* lays them on the seed. In *B. pisorum* of the pea only a single larva enters a seed and dried peas are unattacked. *A. obtectus* readily attacks dried beans and in suitable climates six generations may occur in the year in the same batch of seed. The larvae in this family are eruciform and grub-like with thick bodies, becoming curved in the later development when they resemble those of the Curculionidae. The head is small and often narrower than the prothorax, with short stout mandibles. The first instar differs from those that follow in possessing legs and prominent spinous pronotal processes. In *B. pisorum* and *B. fabae* Riley states that the legs are slender and 3-segmented, but atrophy once the boring life within the seed is assumed. The retention of these appendages in certain species requires further investigation. Thus, in *A. obtectus* they are similarly present in the first instar, but most writers state that they subsequently atrophy. Razzauti, however, finds that they persist throughout life in the form of papilla-like vestiges. Owing probably to the nutritious nature of the endosperm upon which it feeds, a single larva usually devours only a small amount of nutriment, but where many occur in a single seed, as in *A. obtectus*, destruction is more complete. Pupation takes place as a rule within the seed.

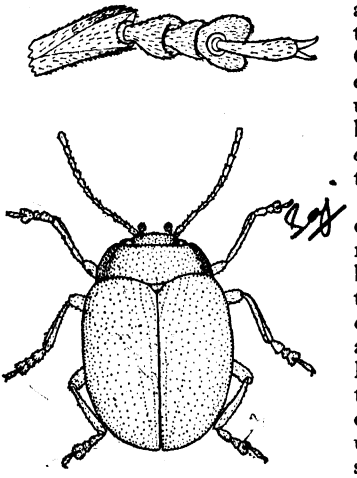


FIG. 602.—*Chrysolina staphylea*. Europe and N. America. × 4. Above — tarsus more highly magnified

FAM. CHRYSOMELIDAE. — This family competes very closely with the Curculionidae as regards number of species and over 26,000 have been described. They are extremely closely allied to the Cerambycidae, and there appear to be no definite and constant structural differences separating the two families. As a rule, the Chrysomelidae are very different in general appearance: their antennae are only of moderate length, and the eyes do not embrace their points of insertion: the upper surface of the body is generally bare and shining, frequently with metallic coloration.

Crowson recognizes eleven subfamilies, but many authors would separate the Halticinae from the Galerucinae and the Cassidinae from the Hispinae. The Sagrinae (Crowson, 1946) are large brilliantly coloured tropical insects with strongly thickened hind femora. According to Sharp the larva of *Sagra splendida* lives in swellings on the stems of *Dioscorea*. The Donaciinae are elongate and usually metallic insects common in temperate climates. They are aquatic in the pre-imaginal stages and in *Hæmonia* the adults also live beneath the water. The metamorphoses of *Donacia* have been investigated by MacGillivray (1903), Böving (1910a), and others. The larvae feed submerged at the roots or in the stems of water plants. They are elongate, subcylindrical whitish creatures with short, hooked thoracic legs. The abdomen is terminated by a pair of spinous processes, the structure and functions of which have been much discussed (Varley, 1939). They enable the insect to perforate the plant tissues and insert its caudal extremity into the air spaces for purposes of respiration. When feeding, they gnaw holes in the plants and, by means of their specially modified mouthparts, they extract the sap which is pumped into the digestive system by the aid of the pharynx. The pupae are enclosed in tough cocoons attached to the roots of the host plants. The Criocerinae are represented in Britain by a few species of *Lema*, *Lilioceris* and *Crioceris*. Their larvae are short, thick, fleshy grubs which feed externally on the leaves of plants. Some have the habit of concealing themselves with coverings of excrement while other, and often closely allied species, do not possess this trait. The asparagus beetle (*Crioceris asparagi*) is familiar to growers of that vegetable, and *Lema melanopa* is occasionally injurious to growing cereals.

The Chrysomelinae include the greater number of the species of the family and 40 are British (Fig. 602). Their larvae live exposed on plants and are short and convex,

frequently with leathery pigmented integument: those of *Orina* are well figured by Chapman (1903) and of *Leptinotarsa* by Tower (1906). The latter genus includes the well known Colorado potato beetle (*L. decemlineata*). The larvae and imagines of *Phaedon* are destructive to Cruciferae, particularly mustard, the former feeding in companies on the leaves. According to Champion & Chapman (1901) certain species of *Orina* are viviparous and this same method of reproduction is recorded by Williams (1914) in *Phytodecta viminalis*; see summary in Hagan (1951).

The Clytrinae are characterized by the peculiar structure of the abdomen which appears to be correlated with the formation of a case which envelops the egg. The larvae are also enclosed in cases which are composed, at least partially, of excrement. Owing to their concealed life they are usually devoid of pigment and resemble small Scarabaeid larvae in general form. The larval cases of *Cryptocephalus* and *Clytra* are described by Weise, Fabre and others: in the former genus they are carried almost erect and the larvae move with a jerky action. The life-history of *Clytra quadripunctata* has been studied by Donisthorpe (1902): its larvae live in nests of *Formica rufa* and their cases are composed of a mixture of earth and excrement.

The Galerucinae (Fig. 603) and Halticinae comprise a number of highly injurious species. Their larval habits are extremely varied: many feed openly on the parenchyma of leaves, others live in roots, and a considerable number are leaf-miners. The Turnip Flea Beetle, *Phyllotreta nemorum*, and other members of the genus, are exceedingly destructive to Cruciferae, especially to the turnip. This genus and other members of the Halticinae have greatly developed leaping powers which reside in the swollen hind femora.

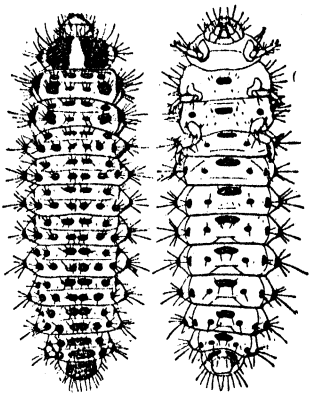


FIG. 603.—*Galerucella luteola*, larva, dorsal and ventral aspects. Enlarged
After Silvestri.

The Hispinae and Cassidinae are closely allied. The species of *Hispa* are usually covered with long stout upright spines: they are mainly tropical and their subfamily is unrepresented in the British fauna. Their larvae so far as known are leaf-miners. The Cassidinae include the 'tortoise' beetles, and have the lateral margins of the body greatly expanded which gives these insects a flattened shield-like appearance. Many are notable for their extremely brilliant coloration which fades very quickly after death. Their metamorphoses are of a remarkable character (Muir & Sharp, 1904): in certain species the eggs are enclosed in an ootheca often of complex structure, in others the ootheca is very small and imperfect and a layer of excrement is laid over it. The larvae are short and oval, somewhat flattened and spiny, often assuming bizarre forms: they usually cover their bodies with excrement which is supported and attached by a forked caudal process. The cast skins also form part of this adventitious covering, and the excrement may either form a solid pad, attached to the exuviae, or assume the condition of long filaments.

Superfamily 18. **Curculionoidea**

In number of species this is one of the largest of all the groups of the Coleoptera and can in many respects be regarded as the most highly evolved. They are allied to the Chrysomeloidea as shown by the resemblances between the Anthribidae and the Bruchidae. The antennae, however, are nearly always clubbed or the last segments are to some extent differentiated. The head is characteristically produced into a rostrum but this is hardly developed in such forms as the Scolytinae. The gular sutures are commonly confluent, but they are separate in the Belidae and obsolete in the Anthribidae. In the larva, the hypopharyngeal bracon, a transverse bar on the inner side of the labium, is a characteristic structure which is absent in the Chrysomeloidea. The thoracic legs are nearly always absent and when developed, as in the

Anthribidae, have no more than two segments. Only the head and occasionally the pronotum are at all well sclerotized, and urogomphi are absent. In nearly every species the larvae are phytophagous.

The number of families into which the group should be divided is a matter still not completely settled. In the tabulation below, which follows Crowson, certain families (e.g. Belidae, Apionidae) are recognized which most authors have treated as subdivisions of the Curculionidae, whereas the Scolytinae and Platypodinae are usually given family rank.

Table of families:

1. Maxillary palpi normal, flexible. Labrum distinct and separate 2
–. Maxillary palpi more or less rigid. Labrum never fully free. 3

2. Gular sutures more or less obsolete. Side borders of pronotum more or less distinct. Mid coxal cavities broadly closed outwardly by the sterna. First 4 visible abdominal sternites more or less connate . . . ANTHRIBIDAE (p. 813)
–. Gular sutures distinct and separate. Pronotum without side borders. Mid coxal cavities not or incompletely closed by the sterna. 5 free visible abdominal sternites . . . . . NEMONYCHIDAE (p. 813)

3. Gular sutures either more or less separate or obsolete, very rarely a single median suture. 5 free visible abdominal sternites. Antennae not geniculate and when clavate, the pronotum has side borders. Tarsal claws free, simple . . . 4
–. Gular suture single and median, or else the antennae are geniculate. First 2 or 4 of the visible abdominal sternites connate. Antennae usually with a club of 3 segments 6

4. Elytra with a flange on their inner surface arising from the epipleura near the shoulders. Gular sutures short but separate. Antennae more or less filiform. Tarsi apparently 4-segmented, all coxae more or less contiguous. Pronotum without side borders . . . . . BELIDAE (p. 813)
–. Elytra without a flange on their inner surface. Gular sutures rarely distinct and separate: if so, pronotum with side borders. Antennae clavate or tarsi apparently 3-segmented 5

5. Tarsi apparently 4-segmented, the 2nd broadly lobed like the 3rd. Antennal club of 2 or 3 segments, antennal sockets facing ventrally and placed at base of the long rostrum. Pronotum with side borders. Elytra with epipleura OXYCORYNIDAE (p. 813)
–. Tarsi apparently 3-segmented, only the 2nd broadly lobed. Antennae usually filiform, not inserted at base of the short rostrum. Elytra without epipleura AGLYCYDERIDAE (p. 813)

6. Maxillary palpi 4-segmented (excluding palpiger). Labial palpi inserted on the mentum ventrally, not in deep pits. Antennae not geniculate, club 3-segmented. Mandibles more or less dentate on outer edge or first 4 visible abdominal sternites connate. Species usually shining and glabrous, without scales ATTELABIDAE (p. 813)
–. Maxillary palpi 2–3 segmented (excluding palpiger). Labial palpi inserted on the mentum apically or dorsally, or sunk in deep pits. Antennae often geniculate, club usually compact. Mandibles not toothed on outer edge. First 2 visible abdominal sternites connate. Species often dull, with scale-like vestiture . 7

7. Antennae not geniculate and not or scarcely clavate. Labial palpi minute, lying in deep pits. Trochanters normal. Species usually elongate and glabrous, rostrum often strongly sexually dimorphic. Prosternum elongate in front of fore coxae BRENTHIDAE (p. 813)
–. Antennae clavate. Prosternum less elongate in front of fore coxae . . 8

8. Antennae not geniculate or else the trochanters are elongate. Ventral surface of mentum usually with a distinct projecting seta or tuft of bristles on each side APIONIDAE (p. 813)
–. Antennae nearly always geniculate, trochanters very rarely long. Ventral surface of mentum without projecting setae . . . . CURCULIONIDAE (p. 814)

FAM. NEMONYCHIDAE (Rhinomaceridae).—This small group has usually been included in the Curculionidae or the Attelabidae though the larva shows marked affinities to the Anthribidae: in both groups the larval mandible has a molar area which is otherwise lacking in the superfamily. The single British species of *Cimberis* (*Rhinomacer*) lays its eggs on the male blossoms of the pine.

FAM. ANTHRIBIDAE.—This large family with nearly 2,400 species is mainly tropical and is particularly numerous in the Indo-Malayan region. Its species are chiefly met with in old wood, dead branches and in fungi, but *Brachytarsus* is predacious on scale-insects. The anomalous genus *Bruchela* (*Urodon*) has been placed in the Bruchidae but it seems to have the essential characters of the present superfamily. The larva develops in the seed-capsules of *Reseda*. A few Anthribids such as *Xenocerus* have very elongate antennae and closely resemble Cerambycidae. The Anthribid larvae have been tabulated by Anderson (1947).

FAM. BELIDAE.—This small group has not generally been given family status though the adult characters seem to be distinctive. The species are found in Australia, New Zealand and S. America and are attached to a considerable variety of plants. The **Oxycorynidae** recognized as a family by Kolbe and more recently by Crowson contains the genera *Oxycorynus* of S. America developing in the flowers of *Prosopanche* (Hydnoraceae), *Metrioxena* (E. Indies) living in palm fruits and *Allocorynus* of tropical America which breeds in the male cones of the Cycad, *Zamia*.

FAM. AGLYCYDERIDAE (Proterhinidae).—The members of this family, which has about 120 species, are known from their allies by having apparently 3-segmented tarsi, otherwise only known in some Apionidae. The species of *Proterhinus* are mostly found in the Pacific region, especially in Hawaii, but *Aglycyderes* which is sometimes placed in a separate family has a single species in the Canary Is. The larvae of *Proterhinus* (Anderson, 1941) may live in dead branches, under bark, in stems, or as leaf-miners.

FAM. ATTELABIDAE.—The weevils placed in this family are responsible for some of the familiar 'leaf-rolls' on various species of trees. These are constructed by the female after making certain cuts in the leaf-blade and an egg is laid in the centre of the roll. This is seen in *Attelabus*, *Apoderus* and *Rhynchites* and Buck (1952) has given an account of the behaviour of *Deporaus betulae*. In species of *Caenorhinus*, such as *C. germanicus* which attacks strawberry and raspberry, a leaf or shoot is girdled so that withered material is provided for the development of the larva. In that stage, the vertex is overlapped by the prothorax, the frontal sutures reach the articulations of the mandible and the abdominal segments each have two dorsal folds. The group is of moderate size but there are 20 British species.

FAM. BRENTHIDAE.—A group of elongate narrow insects numbering about 1,700 species which are almost confined to wooded tropical countries, with one species in the Mediterranean region. The size of the individuals of a species is often subject to a great range of variation and the males are usually much larger than the females. In many species the two sexes are structurally very different (Fig. 604). In such instances the rostrum of the male is broad and rudimentary and the mandibles are large and are said to be used in seizing and carrying about the female before pairing. The females have minute jaws, but the rostrum is very slender, often equalling or exceeding the body in length. The early stages, so far as is known, are passed in wood, and the rostrum of the female is used for boring holes in which the eggs are laid. The larvae have the frontal sutures reaching the articulation of the mandibles, the abdominal segments each have 3–4 dorsal folds, and thoracic legs (otherwise only found in the Nemonychidae and most Anthribidae) are usually present.

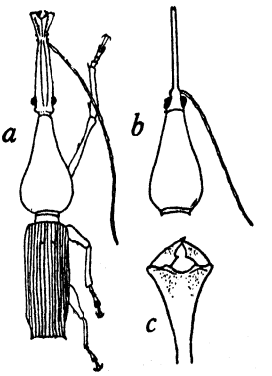


FIG. 604.—*a*, *Ectocemus cinnamonii*, male, Borneo; *b*, head and thorax of female; *c*, *Euctrachelus*, Sumatra, extremity of head of male

FAM. APIONIDAE.—The familiar genus *Apion* is easily recognized by its non-geniculate antennae, but *Nanophyes* which has usually been located elsewhere in the Curculionidae has antennae of the common weevil type though it resembles *Apion* in its long trochanters. Another subfamily, the Eurhynchinae, includes the well-known Sweet Potato Weevil, *Cylas formicarius*: the antennal club is considerably less compact than in *Apion* and the trochanters are short. Most of these weevils do not

have the strongly sclerotized proventriculus which is characteristic of most Curculionidae. In the larva, the abdominal segments have only two dorsal folds and the frontal sutures extend to the mandibular articulations. The genus *Apion*, of which there are 79 British species, develops in seeds, stems or roots of plants: several species are injurious to leguminous crops.

FAM. CURCULIONIDAE (Weevils) (including the bark beetles, **Scolytinae** and **Platypodinae**).—Even after removing the several groups which have here been treated as families, the weevils are still an immense group with more than 35,000 species. Their arrangement in a logical system of subfamilies and tribes is a matter of great difficulty. In one section which comes nearest to the Apionidae the larva has only two dorsal tergal abdominal folds and the adult is without a differentiated proventriculus: this group includes such British genera as *Rhynchaenus*, *Stenopelmus* and *Mecinus*. The other larger section includes species in which there are three or four larval tergal folds and the adult has a sclerotized proventriculus with eight valves. Two large subdivisions can be recognized (van Emden, 1938; 1952) in this section: the Adelognatha (Otiorrhynchinae, Brachyderinae, etc.) in which there are provisional mandibles (p. 753), the rostrum is short, the mentum is expanded so as largely to conceal the maxillae, the larval antennae do not project and the larva lives in the soil, feeding on the roots of plants. In the Phanerognatha, there are no provisional mandibles, the maxillae are not hidden by the mentum, the larva has conically projecting antennae, and very rarely lives in soil, feeding upon roots.

The vast majority of weevils can be recognized by the pronounced rostrum, the geniculate clubbed antennae, and the reduced rigid palpi. The function of the rostrum in the female is often that of a boring instrument, a hole being drilled by it for placing the eggs: in some species the eggs are inserted far into holes previously made by the ovipositor, but whether the rostrum plays any part in this act or not is uncertain: in a number of species it is not used for either of these purposes and its function, like that of the male rostrum, is not known. In many instances this organ exhibits sexual differences, being better developed in the female than in the male. This dimorphism is well exhibited among British weevils in *Balaninus* and in the S. African *Antliarrhinus* which oviposits in cones of cycads the rostrum in the female is about three times the whole length of the body and six times the length of the corresponding organ in the male. Unlike other Coleoptera, an exceptionally large proportion of the species are clothed with scales, but very little attention has been devoted to their form and structure. As a rule weevils have a sombre coloration, but most of the common British species of *Phyllobius* and *Polydrosus* have bright green scales and the Papuan *Eupholus* is sky-blue and the brilliancy of this colour rivals even that of the Lycaenidae. The diamond beetles (*Cyphus* and *Entimus*) of Brazil are probably the most resplendent of all Coleoptera. In some weevils the colour is produced by a fine powdery exudation which is readily abraded and, in a few cases at least, it is stated to be renewed during the life of the insect.

The larvae of Curculionidae are apodous and exhibit great similarity of form. The vast majority are internal or subterranean feeders; *Phytonomus*, however, has larvae which feed externally on leaves. No part of plants, from the roots to the seed, is entirely free from the attacks of one or more species of weevil. A few genera are aquatic, their larvae inhabiting the submerged parts of water plants. The imagines of such genera as *Bagous*, *Eubrychius* and *Litodactylus* are likewise aquatic and the two first mentioned swim by means of the hind legs. In some of the genera whose larvae feed openly, the larvae maintain their position by means of a viscous secretion, as in *Phytonomus* and *Cionus*. The larvae of *Hylobius* and of some species of *Pissodes* burrow in the wood of the Coniferae, either in the larger roots or in the trunk. Many *Otiorrhynchus*, *Sitona*, etc., affect roots. *Calandra* is entirely a seed feeder, and species of *Gymnetron*, *Ceuthorrhynchus*, etc., form either stem or root galls. *Rhynchaenus* mines leaves. When about to pupate, certain species construct cocoons from a product of the Malpighian tubules which is worked up by means of the larval mouthparts (Knab, 1915). It exudes from the anus and forms the reticulate cocoons of *Phytonomus*, the parchment-like capsules of *Cionus*, the chalky nodular cocoons of certain species of *Larinus*, and the felted cocoons of *Rhynchaenus*. In the two first mentioned genera the material is the same as that which enveloped the larvae (see above). Labial spinnerets occur in some weevil larvae, and it is likely that the latter may spin cocoons in the strict sense of that operation or contribute material from stomodeal glands to the cocoon-forming substance. The bulk of Curculionid larvae pupate in the soil or in the substance of the food-plant.

In a family of the size of the Curculionidae it is scarcely remarkable that a number

of the species are highly injurious, either as larvae or as imagines also. The Granary Weevil (*Calandra granaria*) deposits its eggs in the grains of maize, wheat or barley and has become widely distributed through commerce. The cosmopolitan Rice Weevil (*C. oryzae*) affects a great variety of food substances including rice and other cereals, dried peas and beans, flour, meal, etc. *Anthonomus grandis* is the Mexican Cotton Boll Weevil—the most serious enemy of the cotton crop in America, where it is estimated to destroy an equivalent of 400,000 bales annually. It is a comparatively recent introduction, having entered Texas about 1892 from tropical America. The eggs are laid in cavities made in the flower buds which usually fail to develop. Under suitable conditions the whole life-history only occupies two to three weeks. *Anthonomus pomorum* is the Apple-blossom Weevil, locally destructive in many parts of England. It is univoltine and the eggs are laid in the unopened blossom buds. The larvae feed upon the inner parts of the flower and on the receptacle: growth of the flower ceases, the petals dying and forming a kind of brown cap, hence the name of 'capped blossom' for this affection of the tree. *Rhynchophorus ferrugineus* is the Palm Weevil, which infests the toddy and coconut palms. The eggs are laid in the soft tissue at the bases of the leaf-sheaths, in wounds, or in cuts made by the toddy drawer. The larvae tunnel the stems in all directions and pupate in fibrous cocoons.

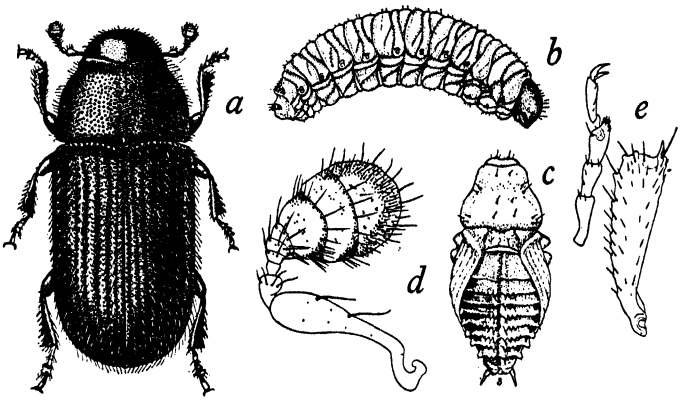


FIG. 605.—Scolytinae

a, *Dendroctonus*; *b*, larva; *c*, pupa; *d*, *Gnathotrichus*, antenna; *e*, hind tibia and tarsus. (*a*, *b*, *c after* Hopkins: *d*, *e* after Schedl.)

Hylobius abietis is extremely injurious to young conifers: the weevils gnaw the bark and cambial layer, thus reducing or stopping the flow of sap. The larvae, on the other hand, are not injurious and mostly live below ground in the roots of trees that have been felled. Certain species of *Sitona* are pests of leguminous crops, and the larvae of *Ceuthorrhynchus pleurostigma* form conspicuous galls on the roots of cabbages and swedes.

The subfamilies Scolytinae and Platypodinae have usually been given family rank; the cylindrical shape (Fig. 605) of their more typical members is characteristic of wood-borers and recurs in the Anobiidae and Bostrychidae. The majority of species bore into the bark and between the latter and the wood: others may attack the roots, solid wood, or twigs, while still other species attack shrubs and a small number select herbaceous plants. A few species bore into the fruit or seed of palms, etc., young fir cones, or the wood of casks and barrels. The larvae and adults feed upon the starches, sugars, etc., found in the host plants, or upon fungi which grow in the brood galleries. Owing to such habits these insects are among the most serious enemies the forester has to contend with. The method of attack is first to construct an entrance tunnel through the bark which, in the wood-boring forms, is carried deeply into the tree: in the bark-feeding species it does not reach further than the surface of the wood. From the inner end of the entrance tunnel two or more egg-tunnels are cut vertically, transversely, or radially between the bark and wood (Fig. 606). With many species a nuptial chamber is excavated at the end of the entrance tunnel and, in such cases, the egg-tunnels originate from it. In most species this chamber is probably constructed by the male. The eggs are laid in niches along the walls of the egg-tunnels

and the larvae excavate slender mines or larval burrows usually at right angles to them. The larval burrows are generally filled with excrement and their calibre increases as the larvae grow. The form and arrangement of the egg-galleries and larval burrows exhibit various features characteristic of each species or group of species and consequently these excavations are of particular taxonomic value. The extremities of the larval burrows are widened to form the pupal cells, and the adult beetles finally construct exit burrows leading from the pupal cells to the exterior. 'Ventilating burrows' are also often constructed: they are located in the roof of an egg gallery and extend to or near the exterior of the tree. Although perhaps serving for ventilation in some cases, they appear to serve more usually for the storage of boring dust, or as an opening through which this material may be ejected.

The social habits and relations of the sexes in this family are of a remarkable nature. As Hopkins remarks, there is a wide range of variation from simple or unorganized and intensive polygamy to specialized or organized polygamy, and a gradual reduction in the number of females associated with a single male from one male and sixty or more females (*Xyleborus*), to one male and two females (*Ips*) and finally to specialized monogamy (*Scolytus*). With many species copulation takes place on the bark of old trees or after alighting on the new host tree. Monogamous species often pair in the entrance tunnel and polygamous species in or near the nuptial chamber.

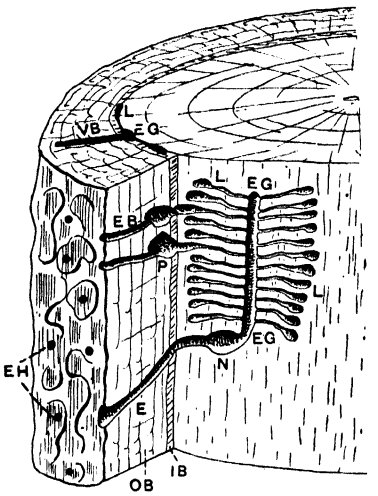


FIG. 606.—Schematic figure illustrating the tunnellings of a bark beetle in a branch of a conifer

E, entrance burrow; *EB*, exit burrow; *EG*, egg-gallery; *EH*, exit holes; *IB*, inner bark; *L*, larval galleries; *N*, nuptial chamber; *OB*, outer bark; *P*, pupal cell; *VB*, ventilating burrow.

The ambrosia beetles penetrate the wood and their larvae are nourished by certain fungi which develop upon the walls of the burrows. A carefully prepared bed or layer of chips and excreta is provided by the female beetle, upon which the fungus develops—ambrosia being the name applied to this fungus-food. The mycelium spreads to the various galleries staining them dark brown or black owing to the action of the fungus upon the wood. Certain species of fungi appear to be associated with individual species of beetles. Unless eaten off regularly, the fungus develops and spreads rapidly and during wet weather it may block up the galleries and kill the occupants. The transportation of the reproductive bodies of the fungus from one tree to another has received diverse explanations and takes place, either fortuitously or intentionally, through the agency of the beetles themselves. In the case of *Xyleborus* it has been stated that the conidia are either voided in the excreta or carried in the crops of the female beetles, and regurgitated when a fungus-bed is being prepared. In other cases it has been found that the brushes on the front of the head in the female of certain species retain the conidia among their hairs, and facilitate transportation. In *Diapus furtivus* Beeson (1917) has observed the same method of conveyance. He also states that groups of large prothoracic pores are found in many Platypodinae and are each filled with a globule of fatty secretion to which the spores readily adhere. He has observed the latter germinating *in situ* but they speedily become separated from the insect once the latter is established in its tunnel. Among the best known genera of ambrosia beetles are *Xyleborus*, *Trypodendron*, *Crossotarsus*, *Diapus* and *Platypus*.

Scolytine larvae are apodous and usually closely resemble those of other Curculionidae. The literature on the family is very extensive; among the more important contributions are those of Hopkins (1909; 1915), which are accompanied by a full bibliography, and the writings of Hagedorn, Swaine, Nüsslin, Fuchs, etc.: works on forest entomology should also be consulted. Kleine (1939) has collected the literature up to 1938: see also Chamberlain (1939) and Balachowsky (1949).

For the Curculionidae as a whole, the classification has been discussed by Marshall (1916) and the French species have been treated by Portevin (1935). From the morphological standpoint, Hopkins' study of the larval and imaginal structure of *Pis-*

sodes (1911) is valuable. Important life-history studies are those by Trägårdh (1910) on *Rhynchaenus* (*Orchestes*), Jackson (1920–22) on *Sitona*, and Günthart (1949) on *Ceuthorrhynchus*.

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Order 29. **STREPSIPTERA** (Stylopids)

Small, endoparasitic insects: males free-living, mouthparts of a degenerate biting type, antennae conspicuous and flabellate, fore wings reduced to small club-like structures, metathorax greatly developed, hind wings large and fan-shaped trochanters absent. Female normally remaining in host, enclosed in a puparium, sexual openings segmental, 3 to 5 in number: a few females leave the hosts and have a larviform structure with terminal gonopore; larval development hypermetamorphic.

The order Strepsiptera comprises a small number of very anomalous insects whose larvae are endoparasitic. The majority of females remain all their lives in a puparium which protrudes slightly from the body of the host. In common parlance the adults are termed 'stylops' and an insect harbouring these parasites is said to be 'stylopized'. Their hosts consist principally of members of the Homoptera Auchenorrhyncha and superfamilies Vespoidea, Sphecoidea and Apoidea among the Hymenoptera. Among the most extensively parasitized hosts are species of some of the common genera of the Homopterous Delphacidae and the genera *Polistes*, *Halictus* and *Andrena* among Hymenoptera. The last-mentioned genus is more often attacked than any other and it includes a very long list of parasitized species. The majority of writers have included the Strepsiptera among the Coleoptera, placing them near the heteromerous families Meloidae and Rhipiphoridae, mainly on account of similarities in the larvae and metamorphosis. The resemblances to these families with specialized life-histories may well be due to convergent evolution and probably do not indicate close relationship. The characters of the Strepsiptera are so peculiar that it seems best to treat them as a separate order. They may perhaps have been derived from the same general stock as the Coleoptera but such a view is largely speculative (Pierce, 1909; 1936; Bohart, 1941; Jeannel, 1945; Crowson, 1955).

About 300 species are known, the majority from the Holarctic region, though the order is also represented in the remaining zoogeographical regions: a synopsis of British species of *Stylops* and *Halictoxenos* is given by Perkins (1918). The classification at the generic and specific level has been much confused by the too easy assumption that each parasite is confined to a single host species, which is certainly untrue (cf. Hassan, 1939). All members of the order are very small or minute, the males commonly measuring about 1·5–4·0 mm. in length. In colour they are either black, or some shade of brown, and the protruding female puparium is usually yellowish-brown.

External Anatomy (Fig. 607).—In the males the integument is very thin and in many parts transparent. The head is transverse, the compound eyes (Strohm, 1910) are very protuberant, and there are no ocelli. The antennae are 4- to 7-segmented, but are variable in form and of peculiar structure: the 3rd segment is flabellate, giving the antennae a bifurcate appearance, and the

succeeding segments may also be similarly produced, the antennae then appearing as if branched. The surface of the segments is studded with complex sensory organs. The mouthparts exhibit modification and great reduction

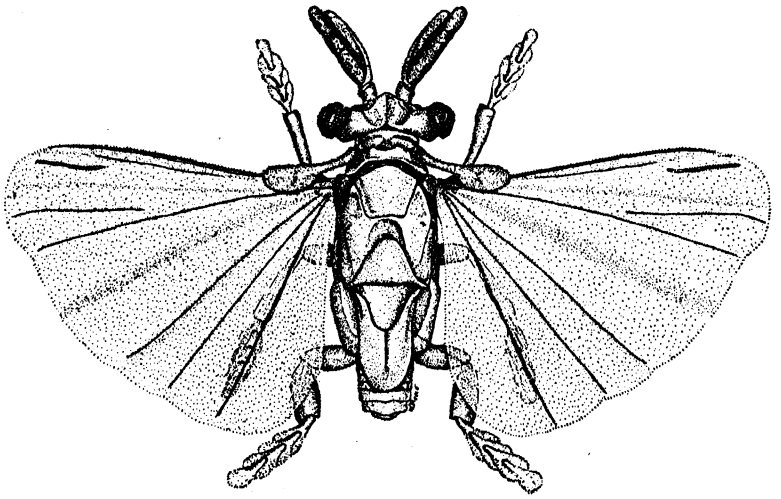


FIG. 607.—*Stylops shannoni*, N. America: male, enlarged
After Pierce, *Proc. U.S. Nat. Mus.*, 54.

from the normal biting type. Only vestiges of parts corresponding with the labrum and labium are recognizable; the mandibles are usually narrow and sickle-like or, more rarely, they are almost bristle-like, while a pair of 2-segmented palpi alone represent the maxillae. In the thorax the first two segments are greatly reduced, but the metathorax is very large, occupying at least half the length of the body. The legs are chiefly used for clinging to the female during copulation: the tarsi are ordinarily 2- to 4-segmented, without claws (except Mengeidae), and usually each segment is provided with a ventral adhesive pad. The anterior wings are represented by small club-like processes which function like the halteres of Diptera (Ulrich, 1930), but the hind wings are relatively large and fan-shaped, with radiating veins. The venation is degenerate; in the most generalized forms eight simple longitudinal veins are recognizable but their homologies in relation to the pupal wing-tracheation have not been determined, and there are no cross-veins. The abdomen is 10-segmented: an aedeagus is located on the 9th sternum: cerci are absent.

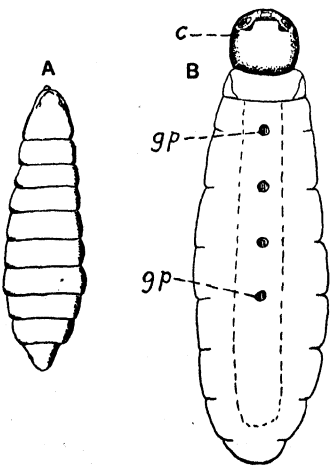


FIG. 608.—*Xenos vesparum*. A, fully-grown male larva. B, adult female

c, cephalothorax; *gp*, genital pores. Adapted from von Siebold.

The female (Fig. 608) is highly modified through degeneration in accordance with a permanently endoparasitic life. She is larviform, apodous, and enclosed in the persistent larval cuticle. The head and thorax are adnate, forming a cephalothorax which is separated by a

constriction from the long sac-like abdomen. Antennae and eyes are wanting and the mouthparts are vestigial: mandibles are always present. The thorax is separated ventrally from the head by the aperture of the brood canal, which is a passage between the body of the female and the last larval cuticle, leading from the genital apertures to the exterior. In the Mengeidae, however, the female is free-living and the head and thorax are distinct. The eyes, antennae and legs are functional and copulation and emergence of the first-stage larvae take place through a single posterior orifice.

Internal Anatomy.—Our knowledge of the internal anatomy of Strepsiptera is mainly due to Nassonow whose work forms the basis of the account given by Pierce (1909). The alimentary canal is an unconvoluted tube of simple structure. In the male it exhibits three well-marked regions—the fore, middle and hind intestine—but there is no communication between the two latter parts of the gut: in the adult female the hind intestine has atrophied, the posterior end of the stomach being in contact with the integument of the last abdominal segment, there being no anal opening. The Malpighian tubes are absent. The nervous system is highly concentrated in both sexes: in the male the brain assumes much larger proportions than in the female, owing to the presence of the antennary and visual centres. The para-oesophageal connectives pass to a common ganglionic mass formed by the union of all the ventral ganglia up to, and including, the ganglia of the 2nd or 3rd abdominal segment: a median abdominal nerve-cord terminates in a nervous centre formed by the coalescence of the posterior ganglia. The tracheal system opens to the exterior by one or two pairs of thoracic spiracles and, in the male and in female Mengeids, up to eight pairs of abdominal spiracles. The reproductive system is very similar in the larvae of both sexes and consists of a pair of tubes lying one on either side of the gut. In the adult male, these organs maintain their paired structure, and communicate with the exterior by means of a common duct. In the female, the reproductive organs are stated to disintegrate, and the egg-masses are scattered through the body space. Cuticular invaginations, which develop into funnel-like tubes, function as genital ducts. The number of these apertures appears to vary from two to five: they are segmentally disposed on the median ventral region of the 2nd and following abdominal segments. According to Noskiewicz and Poluszyński (1935) polyembyrony occurs in *Halictoxenos*.

Biology and Host Relations.—The biology of these insects has been mainly studied with reference to species parasitizing Hymenoptera. The only tolerably complete study of the life-history of any species is the account given by Nassonow (1892) (in Russian) of *Xenos vesparum*. Male Strepsiptera are free-living, and usually only survive a few hours after emerging from their hosts. The females, on the other hand, remain permanently endoparasitic, and only the cephalothorax is visible externally, where it protrudes through the body-wall of the wasp or bee. The males are by no means rare insects, but their small size and brief life cause them to elude the observation of most entomologists. They emerge from their hosts early in the morning, very soon after the latter have taken to the wing. Pairing takes place by the male alighting on the host, and inserting the aedeagus into the aperture of the brood canal of the female (Perkins); in some cases it appears probable that the eggs are able to develop parthenogenetically. The larvae hatch within the body of the female and issue in large numbers (sometimes several thousand) through the genital canals previously alluded to. They pass into the space (or brood pouch) between the ventral surface of the parent and

the persistent larval cuticle, ultimately emerging through the aperture of the brood canal. They then remain upon the body of the host until opportunity is afforded for escape. At this stage the young larvae bear a resemblance to the triungulins of *Melöe*: they are very minute, active creatures with a group of ocelli and well-formed legs (though without trochanters), and pairs of long caudal setae (Fig. 609). Their method of securing a new host has rarely been directly observed but, presumably, they leave the 'maternal' hosts when the latter are on flowers, in the nest, or in other situations. If liberated on to flowers, they probably attach themselves to other host individuals that come along, and become transported thereby to the nests. Within the latter, they seek out the larvae, and speedily burrow through the body-wall and become endoparasitic. In *Corioxenos*, however, the triungulins jump by means of their caudal bristles on to *Antestia* (Pentatomidae) to which they are apparently attracted by colour (Kirkpatrick, 1937). Having entered the host, the stylopid larvae undergo ecdysis, assuming an apodous maggot-like form in the second instar (Fig. 608). Their subsequent history has been followed by Nassonow in the case of *Xenos*. Nutrition appears to take place by the filtration of the host's blood through the delicate cuticle of the parasite. The parasite does not penetrate the organs of the host, but occupies the body space between them, pushing them out of position. At the 7th instar the parasitic larva works its way outwards, so as to protrude from the abdomen of the host and, at this stage, the wasp or bee has assumed the pupal condition. In the case of *Stylops* protrusion usually takes place through the intersegmental membrane between the 4th and 5th abdominal segments. The male parasite now undergoes pupation and the pupa is enclosed in the exuviae of the two preceding instars. The rounded tuberculated apex of the puparium, thus formed, is the only region visible externally and the winged insect emerges by pushing open an operculum. The female parasite is recognizable by the flattened disc-like cephalothorax, the large white grub-like after-body remaining within the abdomen of the host.

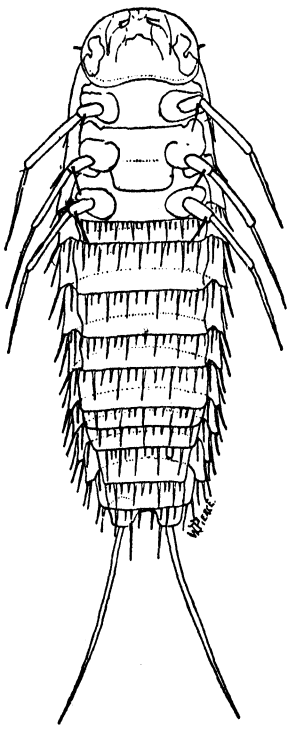


FIG. 609.—*Stylops californica*, triungulin, ventral view, enlarged

After Pierce, *loc. cit.*

Both sexes of the host are liable to parasitization but, in most cases, the largest number of attacked examples are females. As a rule, male parasites are the commoner, but both sexes may occur in the same individual host. The latter often nourishes several parasites: Pierce (1909) mentions the exceptional number of 31 larvae in a single host and states that the largest number of male puparia found exserted from the body of a host is 15. The effects of stylopization on the hosts have been studied by Pérez (1886), Smith & Hamm (1914), Perkins (1918) and others with reference to *Andrena* and by Salt (1931) in Vespids; the whole subject is also discussed by Pierce and by Wheeler. In the first-mentioned genus, stylopized examples often exhibit a shorter and more globular abdomen with increased pilosity, the

head is usually smaller than in normal specimens, while the punctation of the body becomes finer, but different individuals do not necessarily react similarly to the presence of the parasite. These changes are common to both sexes and affect the specific characters. Much confusion has consequently arisen through the founding of new species on stylopized individuals. The following changes affect the secondary sexual characters. (1) Parasitized females have the pollen-collecting apparatus so diminished that the hind legs resemble those of the males. (2) When the clypeus or frons in the males is normally marked with a greater amount of yellow than in the females, stylopization may result in the females acquiring the yellow coloration of the males, and individuals of the latter sex having the light colour very markedly diminished. (3) The sting is curtailed in size and the copulatory apparatus of the male suffers reduction. Certain minor changes may also occur and Pérez concludes that, in the case of *Andrena*, secondary sexual modifications induced by stylopization are inversions of development, and that parasitized examples are not merely diminished individuals, but that the female acquires certain characters belonging to the male and the male develops certain of those which pertain to the female.

Before maturity the parasites live on the fat-body and blood-tissues of the hosts. As already mentioned, they do not directly attack the other organs but the latter undergo partial atrophy through inadequate nutrition. The gonads become more or less reduced in size, and the oocytes degenerate in their follicles. There is no evidence that the females are ever fertile, but the males are known to be capable of producing spermatozoa, and parasitized examples of both sexes of *Andrena* have been taken *in copula*.

The effects of parasitism by *Elenchus* on Delphacidae are discussed by Hassan (1939) who shows that they are approximately proportional to the time which the parasite spends within the host. This varies with the season and is greatest in those hosts in which *Elenchus* overwinters. Here, as in other Strepsiptera, the effect of a male parasite is greater than that of a female.

If the observations of Ogloblin (1939) are correct, the family Myrmecolacidae has an extraordinary life-history. The genus *Myrmecolax* was long known from a single male bred from an ant in Ceylon about 100 years ago. Pierce (1909) described one more Mexican species from four males. Ogloblin pointed out that the family Stichotrematidae was known only from females; one species was a parasite of a Tettigoniid in New Guinea and he himself found several more as parasites of Gryllids and Mantids in Brazil. In the same region he found several Myrmecolacids, all males, attacking different genera of ants. The exuviae of first-stage larvae in the ants are of the same type as that stage in *Stichotrema*, and Ogloblin suggests that in the Myrmecolacids the males develop in ants, the females in orthopteroids. Quite recently Bohart (1951) described ten species of males from a collection of about 300 caught at light in the Philippine Islands. The Mengeidae are the only Strepsiptera in which the adult female is free living. The early stages are now known to develop in Lepismatids (Carpentier, 1939; Silvestri, 1942). The female puparium is found under stones and both sexes exhibit many generalized features. *Mengea* itself was originally described from a male in the Baltic Amber.

Classification.—The Strepsiptera may be divided into six families, following with slight emendations the classification of Bohart (1941). Seventeen species are known from Britain. Philip (1950) has recently revealed in America stylopized *Chrysops* (Tabanidae) which extends the host-list to a new order.

Table of males, females and first-stage larvae:

1. ♂ tarsi 5-segmented and clawed. Adult ♀ free living, with legs, antennae and eyes. First-stage larva with fore and mid tarsi pulvilliform, head with long backwardly projecting spines at its hind angles, and abdominal sternites posteriorly margined with bristles. (Parasites of Lepismatidae) . . . . . MENGEIDAE

–. ♂ tarsi with less than 5 segments, clawless. Adult ♀ enclosed in a puparium, most of body inside the host. First-stage larva without above characters in combination 2

2. ♂ tarsi 4-segmented. ♀ not parasites of Homoptera; if parasites of Grylloids, then the cephalothorax with hood-like projections behind the spiracles. First-stage larva with at least the first pair of tarsi pulvilliform 3

–. ♂ tarsi 2–3-segmented. ♀ parasites of Homoptera or of Tridactylidae. First-stage larva with all tarsi setiform 5

3. ♂ antennae 7-segmented, 4 very short, 5–7 very long. ♀ cephalothorax with hood-like projections behind the spiracles. First-stage larvae with mid and hind tarsi setiform. (Parasites of Formicidae (♂) or of Orthopteroids (♀)) MYRMECOLACIDAE

–. ♂ antennae with less than 7 segments. ♀ cephalothorax without hood-like projections behind the spiracles. First-stage larva with mid tarsi pulvilliform . 4

4. ♂ antennae 5-segmented, 3 and 4 laterally flabellate. First tarsal segment about as long as three following segments together. ♀ cephalothorax greatly elongate with 2 pairs of spiracles or with the head and thorax distinct; 4–5 genital tubes. First-stage larva with long spines projecting from posteroventral corners of head; abdominal sternites posteriorly dentate. (Parasites of Heteroptera) CALLIPHARIXENIDAE

–. ♂ antennae 4–6-segmented, only 3 laterally flabellate. First tarsal segment much shorter than the 3 following segments together. ♀ cephalothorax with 1 pair of spiracles, thorax not distinctly separate; 2–5 genital tubes. First-stage larva without long spines projecting back from posteroventral corners of head. (Parasites of Aculeate Hymenoptera) . . . . . STYLOPIDAE

5. ♂ tarsi 2-segmented. Antennae 4-segmented. ♀ brood-passage opening broad and semicircular, the thorax behind it forming only a narrow ring. (Parasites of Delphacidae) . . . . . ELENCHIDAE

–. ♂ tarsi 3-segmented. Antennae 7-segmented. ♀ brood-passage opening a narrow, linear or oblong slit, thorax behind it broader. (Parasites of Homoptera Auchenorrhyncha and of Tridactylidae) . . . HALICTOPHAGIDAE

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