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THE INVERTEBRATES:

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The acoelomate Bilateria

The acoelomate bilateria

VOLUME II

Volume II

BY

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THE INVERTEBRATES: PLATYHELMINTHES AND RHYNCHOCOELA

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PREFACE

Following the publication in 1940 of *The Invertebrates: Protozoa through Ctenophora,* the second volume of my invertebrate treatise, planned to include the acoelomate and pseudocoelomate Bilateria, was projected. It was interrupted by work on my volume on *Comparative Vertebrate Anatomy,* published in 1942. I then resumed work on the treatise; the task proved long and laborious, for in these groups are included all the parasitic worms on which there exists a vast literature that had to be read, digested, and organized into an adequate account. In addition, the preparation of the numerous figures required great expenditure of time. The task was finally completed by the end of 1949, but, upon examination of the material, the publishers ruled for its division into two volumes. Although I should much have preferred retention of the original plan of presenting the material in a single volume, practical considerations naturally took precedence, and therefore the present volume is limited to the acoelomate groups, to be followed shortly by the third volume dealing with the pseudocoelomate phyla.

Although the present volume contains a good deal of original material, like the preceding volume it is essentially a compilation from the literature. As such it should not be referred to, as some zoologists have done, as if it were a piece of original research for the statements in which I am personally responsible. In general, the contents of these volumes reflect a majority opinion or the opinion of outstanding specialists in a given group and are not to be ascribed to me as an individual. My own opinions are always accompanied by the phrase "in the author's opinion."

I have made all the illustrations of the present volume, except those that have been reproduced by photography. I realize that the quality of the figures is inferior to the work of a professional illustrator, but I think the figures adequately show the points intended. Probably the greatest difficulty in the way of writing zoological books resides in the matter of preparing the illustrations, and doing the latter myself has seemed the most practical method of disposing of this difficulty.

I wish to thank all those who took the time and trouble to write me encouraging letters with regard to the first volume. The letters and comments received by me and my publishers from zoologists the world over prove clearly enough the desperate need for a treatise of this kind in the English language. I trust these well-wishers will not be disappointed in the present volumes for which they have waited so long and so patiently.

LIBBIE HENRIETTA HYMAN

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CHAPTER IX

INTRODUCTION TO THE BILATERIA

I. THE BILATERAL PHYLA

The remaining phyla of the animal kingdom are characterized by bilateral symmetry which appears early in development or even in the uncleaved egg and persists throughout life, except in the phylum Echinodermata in which the bilateral larva undergoes a remarkable metamorphosis into a secondary radial condition. Less extensive modifications of bilateral symmetry are common, as the spiral twisting of many Mollusca. The general occurrence of bilateral symmetry, typical or modified, throughout these phyla justifies their designation as the Bilateria (or Bilateralia), in contrast to the Radiata. The essential feature of bilateral symmetry is that a section along one plane, and one plane only, the *median sagittal plane,* divides the body into right and left halves which are mirror images of each other. The body parts either lie in the median plane and are cut in half by it, in which case they are termed *unpaired* structures; or they lie on a transverse plane to either side of and equidistant from the median plane, being then termed *paired* structures. Bilateral animals also have differentiated dorsal and ventral surfaces and anterior and posterior ends. The median sagittal plane runs from the middle of the dorsal to the middle of the ventral surface. The main body axis runs in the median sagittal plane from anterior to posterior end and is termed the *anteroposterior axis.* (See further P–C, pages 19, 20.)[1]

The assumption of bilateral symmetry appears to have been an important forward step, since radial animals tend to lead a sessile or sedentary life, which is not conducive to evolutionary advance; or, if free-swimming, they do not direct any particular part of the body forward and hence fail to profit from the stimulating action of the environment. Concomitant with the appearance of bilateral symmetry, the anterior end comes to be consistently directed forward and differentiates into a head with concentrated nervous tissue and highly efficient sense organs. With the development of such a nervous center, body activities become more coordinated, response to external conditions is quicker and more precise, and all the systems differentiate rapidly to a more efficient morphological condition. It is to be noted that there is a tendency to bilateral symmetry among the higher Radiata (P–C, pages 372, 640).

[1] The first volume of this treatise, entitled *The Invertebrates: Protozoa through Ctenophora,* will be referred to as P–C.

With the differentiation of dorsal and ventral surfaces, the ventral surface becomes locomotory and is generally held against the substratum. At first cilia continue to serve as the locomotory mechanism, especially while the animal remains of small size; but with increasing size and complexity, movement becomes muscular and the muscular system differentiates correspondingly.

We have seen that the Porifera and the Radiata remain at the tissue grade of construction and have progressed very little in the direction of organ formation. The Bilateria, on the other hand, are anatomically of the *organ grade* of construction. Even the lowest Bilateria show a considerable development of organs, and the differentiation of organs and of organ-systems makes rapid strides as one proceeds toward the higher bilateral groups. The formation of organs is closely related to the presence of *mesoderm*, a characteristic feature of the Bilateria. While, as previously emphasized (P–C, pages 263–268), a form of mesoderm, the mesenchymal ectomesoderm, is present in sponges and most Radiata, the mesoderm there never reaches the extensive development which it attains in the bilateral phyla. The Bilateria are further characterized by the possession of "true" mesoderm, that is to say, *entomesoderm*, mesoderm of entodermal origin. Among a number of bilateral groups (the Protostomia, see below), there is also an early formation of ectomesoderm, also called the *larval mesoblast*, which contributes to larval structures and may persist in adult structures. This larval mesoblast is strictly comparable to and apparently reminiscent of the ectomesoderm of the radial phyla, and in some groups, as the rotifers, comprises the entire mesoderm. But in most Bilateria, after the ectomesoderm has been given off, there is a formation of mesoderm from the entoderm, and it is this mesoderm which is the chief source of the muscles, connective tissues, reproductive system, and other parts of the adult. Nevertheless, the distinction between ectomesoderm and entomesoderm, like most morphological distinctions, must not be taken too literally. The mesoderm provides material and space for the development of many organs and relieves the ectoderm and entoderm from the necessity of forming such parts as muscles and gonads, freeing them for further differentiation along their own special lines, protective-nervous, and digestive, respectively. The mesoderm also makes the body firmer and more solid and permits increase in size and complexity.

Dependent on the presence of mesoderm is the occurrence of two other features limited to the Bilateria but by no means present in all bilateral groups, namely, the *coelom* and *segmentation*. The origin and nature of mesoderm, coelom, and segmentation are difficult questions considered further below.

Common to all the bilateral phyla except the Platyhelminthes is the

presence of a rear opening of the digestive tract, the *anus*. Connections of the digestive tract with the surface are not uncommon in the radiate phyla (medusae, P–C, pages 396, 421, 507; ctenophores, page 667); they also occur among several polyclad and trematode flatworms (pages 107, 228). Although there is no objection to considering such connections as anal openings, they are usually of haphazard occurrence, not terminal, and mostly two or more in number. The *definitive anus* is of general occurrence throughout whole phyla, is a single opening terminating the digestive tract, is situated in the median sagittal plane (at least in primitive members of a group), and is typically formed with the aid of an ectodermal invagination, the proctodaeum.[1] The advantages of an anus are obvious. In animals in which the digestive system opens only by the mouth, newly ingested food is continually mixed with partly digested or indigestible material, the entire gastrodermis must be capable both of digestion and absorption, and a high degree of efficiency is impossible. When an anus is present, the food is passed posteriorly, and different sections of the digestive tract can become specialized for various roles, such as mastication, digestion, and absorption.

With increase in size and complexity and the interpolation of many organs between epidermis and digestive tract, the primitive method of respiratory exchange, food distribution, and elimination of nitrogenous wastes by simple diffusion no longer suffices. Among the larger bilateral animals we see the gradual appearance of excretory, respiratory, and circulatory systems, all of which are completely absent in the Radiata. The reproduction system also differentiates, often achieving great complexity. Contrasting with the simple emission of sex cells through the mouth and external fertilization seen among the Radiata, the Bilateria usually have special ducts for conveying the sex cells to the exterior, glands or sacs for conserving and storing the sex cells, and some mechanism for introducing the sperm directly into the body of the partner.[2]

The number of bilateral groups is considerable, and attempts have naturally been made to unite them into larger assemblages. The scheme which seems likely to receive the most acceptance is that of Grobben (1908), who divides the Bilateria into the Protostomia and the Deuterostomia, a division previously suggested with other names by Goette (1902; see further P–C, pages 30–31). In the Protostomia, the blastopore becomes the mouth or the mouth forms about where the blastopore closed, there is a well-developed stomodaeum, embryonic development is of the determinate type with spiral cleavage and often a *trochophore* type of larva, the mesoderm originates by solid ingrowth of cells proliferated

[1] However, a proctodaeum seems to be sometimes absent in the lowest bilateral group to have a definite anus, namely, the nemertine worms.

[2] Recall, however, the beginning of sex ducts in ctenophores (P–C, pp. 684, 686).

from the entoderm, and the coelom, if present, is not an enterocoel. Among the Deuterostomia, the blastopore becomes the anus or the anus forms where the blastopore closed, the mouth is a new formation, cleavage is of the indeterminate type with a *dipleurula* larva, and the mesoderm and coelom originate by outfolding of the gut wall (*enterocoelous* method). The Deuterostomia include the phyla Chaetognatha, Echinodermata, Hemichordata, and Chordata. All the other bilateral groups belong to the Protostomia (although the Brachiopoda have an enterocoelous formation of the coelom). The protostomous phyla can be grouped further according to the type and mode of formation of the body cavity, presence or absence of segmentation, etc.

The foregoing scheme necessarily leads to the conception of a splitting of the bilateral phyla immediately after the origin of a bilateral ancestor from the Radiata into two main lines of ascent, one (Deuterostomia) leading to the vertebrates, and the other (Protostomia) leading to the arthropods and mollusks. This theory is termed the *diphyletic* theory of the relations of the Bilateria to each other and to the Radiata. The main alternative theories are the *polyphyletic* theory, which suggests that many of the invertebrate groups have evolved independently in a radiating manner from a remote bilateral ancestor; and the *annelid* theory, according to which annelids, arthropods, and chordates are closely related and lower bilateral groups may have arisen from annelids by degeneration. The diphyletic theory is at present widely accepted. It involves several important corollaries. It divorces the vertebrates from the annelids and arthropods to which they were for many years considered to be related, and it necessitates the assumption that mesodermic segmentation has arisen twice independently in the evolution of animals. A more important objection, which has not been met, is that *Amphioxus* has nephridia of a type found elsewhere only in some polychaete annelids. Serological tests performed by Wilhelmi (1942) indicated closer relationship between echinoderms, hemichordates, and tunicates than between these groups and annelids and arthropods, but the author has been informed by professional immunologists that the methods employed in such tests cannot be relied upon to yield convincing results.

A serological test is usually performed as follows. The animal to be tested is freed of foreign material and dried, and the dried material, either with or without removal of fats, is dissolved in an inert medium, usually saline. This solution, termed the *antigen*, is then injected into rabbits several times at short intervals; and then, after an appropriate lapse of time, blood is drawn from the injected rabbit, allowed to clot, and the serum removed. This serum contains substances called *antibodies* formed in the rabbit as a result of the injection of the antigen, and these will react with the antigen to produce a visible precipitate. This reaction is termed the *precipitin reaction* or *test*. It is very highly specific in that a precipitate appears even with very high dilutions of the antigen; a precipitate may also appear in less dilution

with substances related to the antigen but fails to appear with nonrelated substances. Hence the degree of dilution at which a precipitate appears has been commonly used as a measure of the degree of relatedness of the substances being tested. In carrying out the precipitin test, the undiluted rabbit serum carrying the antibodies is put into a test tube, and the solution to be tested diluted to varying amounts is carefully added so as to form a layer over the serum. At the boundary of the two fluids a ring or layer of white precipitate occurs if the test is positive. When the specific antigen used to obtain that particular serum (*homologous* test) is employed, a precipitate will usually be obtained in dilutions of a million or more. Related substances (*heterologous* test) give the reaction only in much stronger concentrations. In Wilhelmi's experiments, rabbit serum from sea-urchin antigen gave an homologous test with sea-urchin antigen at a dilution of 2,048,000; reacted with other echinoderm antigens at dilutions of 21,000 to 32,000; reacted with tunicate antigen at 4000 dilution, with hemichordate antigen at 2000 dilution, and with annelid and arthropod (*Limulus*) antigens at 100 to 200 dilution. Annelid and *Limulus* antigens gave homologous reactions at 250,000 to 2,000,000 dilution and heterologous tests with each other at 2000 to 4000 dilution.

Serological tests offer a new and promising method of attack on problems of invertebrate relationships which are almost insoluble by morphological means, but great improvement in the technique of such tests is needed before dependable results can be obtained. According to information received by the author from immunologists, the dilution method is not a reliable index of relation of antigens, but rather the amounts of precipitate obtained at the dilution of antigen at which the homologous test yields the most precipitate must be compared. Further no decisive result can be expected when whole animals are employed in making the antigen. Instead related chemical substances must be isolated from the animals to be compared and these used as antigens. In any case, zoologists must persevere with embryological and morphological studies of invertebrates, as these will always be important for the evaluation of relationships.

Although the diphyletic theory is here adopted as a working hypothesis, the author is of the opinion that only the Protostomia constitute an assemblage of groups evidently related to each other. The Deuterostomia at present writing appear a heterogeneous assemblage of groups whose relationship to each other remains dubious. There seems to be very little concrete evidence for the widely assumed derivation of the chordates from the echinoderms.

As previously indicated (P–C, page 35), the Bilateria exist in three grades of structure: the acoelomate, the pseudocoelomate, and the eucoelomate. The present volume deals with the acoelomate phyla.

II. ORIGIN OF THE BILATERIA

Since the first Metazoa were almost certainly radial animals, the Bilateria must have sprung from a radial ancestor, and there must have been an alteration from radial to bilateral symmetry. This change constitutes a most difficult gap for phylogeneticists to bridge, and various highly speculative conjectures have been made. It is generally believed that bilateral symmetry originated in consequence of the assumption by

a radial ancestor of a creeping mode of life. We have already traced this ancestor to a planuloid form (P–C, pages 248–253; see further Hyman, 1942), resembling the planula larva of the Cnidaria (Fig. 2*A*). This planuloid ancestor was an elongated, radially symmetrical organism, without mouth or archenteron, and consisted of a ciliated or flagellated epidermis, probably composed of epitheliomuscular cells, and a solid interior mass of digestive cells. There was probably a nerve net under the epidermis with an accumulation of neurosensory cells at the anterior pole, and indifferent mesenchyme cells, capable of differentiating into sex cells and other types of cells, were scattered through the interior mass. Food catching and digestion remained wholly of the protozoan type so that the organism had no need of a mouth or archenteron. The creature was polarized with definite anterior or aboral and posterior or oral ends but lacked dorsoventral differentiation.

This planuloid organism may be supposed to have given rise to the coelenterate line by formation of a mouth at the site of the closed blastopore, hollowing out of the interior to form a primitive gut, and sprouting of tentacles, thus becoming a simple medusa similar to an actinula. It is here assumed also to have given rise to the Bilateria by adopting a creeping mode of life, then flattening out and developing bilateral symmetry and dorsoventral differentiation.

There are three chief theories of the steps from the radiate to the bilateral condition: the *ctenophore-polyclad*, the *ctenophore-trochophore*, and the *planuloid-acoeloid* theories. The ctenophore-polyclad theory was first suggested by Kowalevsky in 1880 as a result of his finding of the peculiar ctenophore *Coeloplana* (see P–C, page 685) but has been supported and elaborated chiefly by Arnold Lang, the eminent student of the polyclad flatworms, who based his conclusions on his studies of the anatomy and embryology of various turbellarians (1881–1884), and on the peculiar features of the aberrant ctenophores *Ctenoplana* and *Coeloplana*. These ctenophores resemble polyclads in their oval flattened shape with dorsoventral differentiation; in the presence of two dorsal tentacles; in creeping upon the entire ventral surface; in the centrally located ventral mouth and branched, blindly ending digestive canals; and in the radiating, anastomosing nervous system. There is a certain amount of resemblance in the embryology, as both ctenophores and polyclads have determinate cleavage with the formation of micromeres and macromeres, and in both there is a large stomodaeal invagination which in both contributes to the ventral surface. Many polyclads have a swimming larval stage with eight ciliated lobes which seem comparable to the eight comb rows of ctenophores. However, as Lang fully realized, *Coeloplana* and *Ctenoplana* have no trace of real bilateral symmetry, being in fact biradially symmetrical, and their nervous center is in the middle of the dorsal

surface, whereas it is characteristic of the Bilateria that the nervous center is anteriorly located. To bridge these differences, Lang postulated a series of stages (Fig. 1) from the platyctene ctenophores to the polyclads by a forward shift of the nerve center and tentacles and extensive branching of the digestive canals.

Lang's theory of the ctenophores as intermediate forms between the radiates and the polyclad flatworms had a wide and extended acceptance but is to be rejected on the following grounds. First, it is agreed by all students of ctenophores that the Platyctenea are simply highly aberrant ctenophores without phylogenetic significance. Second, the embryology of the two groups is in fact very different and the cleavage patterns follow

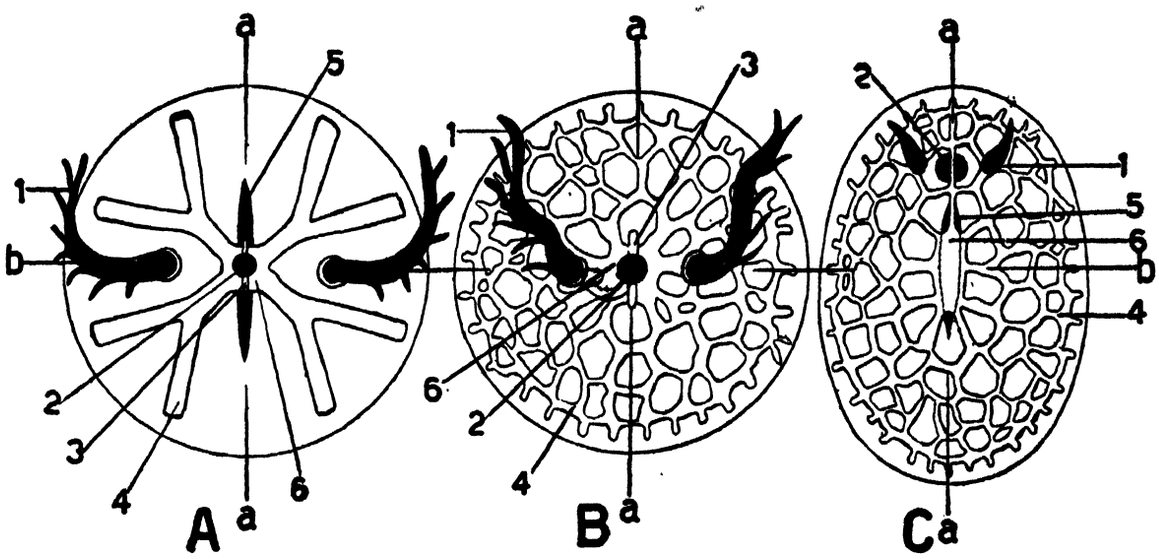

FIG. 1.—Diagram to show change from a ctenophore to a polyclad (*after Lang*, 1884). *A*. Ctenophore. *B*. Hypothetical intermediate stage. *C*. Polyclad. 1, tentacle; 2, nervous center; 3, polar field; 4, gastrovascular branches; 5, pharynx; 6, main canal of gastrovascular system. *aa*, sagittal axis; *bb*, transverse axis.

very diverse plans, that of the ctenophores being biradial, and that of the polyclads spiral. Third, in the theory of Lang, the polyclads are necessarily regarded as the most primitive existing Bilateria; this is a mistaken idea, since it is now clear that the order Acoela occupies that position and the polyclads stem from acoel ancestors.

The ctenophore-trochophore theory is a variant of the trochophore theory, discussed below, and is based on alleged resemblances between ctenophores and the trochophore larva. These resemblances are best stated after the anatomy of the trochophore larva has been described. Here it may be pointed out that this theory proceeds from the ctenophores to the annelids and other higher Bilateria and fails to account for the origin of the lower Bilateria. Supporters of the theory have realized this difficulty and take one or the other of the two possible explanations. Some regard the larvae of the acoelomate Bilateria (i.e., the flatworms and the nemertines) as earlier stages of the trochophore larva. But then, such stages would necessarily fall between the ctenophore and the trochophore and should more nearly resemble the ctenophore than does the

trochophore larva. This, however, is not the case for in fact the ctenophore similarities are manifested only in the fully developed typical trochophore larva. The second explanation is to the effect that the acoelomate Bilateria are degenerated from the higher Bilateria. This cannot possibly be admitted. It may be regarded as firmly established that the free-living flatworms, especially the order Acoela, are of exceedingly primitive structure, positively not degenerated from or modified from a higher anatomical type. The ctenophore-trochophore theory therefore appears to the author unacceptable, although it has been widely supported.

The planuloid-acoeloid theory is based upon the remarkable features of the flatworm order Acoela, whose primitive structure was first recognized in 1882 by Ludwig von Graff, the distinguished pioneer in the study of the free-living flatworms. The Acoela were nevertheless long regarded as degenerate forms and hence of no phylogenetic importance until recent years when their primitive nature has again been recognized by all students of the Turbellaria. The Acoela are a group of very small flatworms with the following primitive characteristics. The ciliated epidermis is often syncytial, as in many coelenterates, and in several members has basal muscle fibers, as also in coelenterates. There is no distinct basement membrane beneath the epidermis. The interior is a solid mass of cells as in the planula larva without a digestive cavity, and comparison of the embryonic development with that of other flatworms indicates that this interior mass represents entoderm and ecto- and entomesoderm. There is a mouth in the center of the ventral surface, and this leads into the interior mass either directly or by way of a simple tubular pharynx. These worms feed by ingesting small animals through the mouth into the interior mass where intracellular digestion occurs; thus it is directly proved that an archenteron is not a necessity for the early bilateral holozoic animal, as supposed by the Haeckelian gastrula theory. The nervous system is of primitive construction, consisting of a plexus beneath the epidermis with several more or less distinct longitudinal strands radiating from an anterior brain mass; but in some acoels (see page 83) the nerve plexus is situated in the basal part of the epidermis and the brain is a mere thickening also epidermally located. Most of the Acoela have a statocyst near or embedded in the brain; this structurally is more like the statocyst of a medusa than of a ctenophore. There are no distinct gonads, but the sex cells differentiate out of the cells of the interior mass. Female ducts are wanting, and the eggs discharge either through the mouth or by rupture of the body surface. There are usually indistinct male ducts which lead to a copulatory organ. Although the animals are hermaphroditic, cross-fertilization is the rule and is internal. The Acoela lack an excretory system.

It is evident that there is no difficulty in passing from a planuloid type of ancestor to an acoeloid form (Fig. 2). Epidermis, muscular system, interior mass, nervous system, and sex cells are, even in present Acoela, distinctly at a coelenterate stage or but slightly advanced from this stage. Consequently we accept the theory of the origin of the Bilateria from a planuloid ancestor by way of an acoeloid form. The main changes necessary are the alteration from radial to bilateral symmetry and the forward shifting of the nervous center. As no intermediate forms are

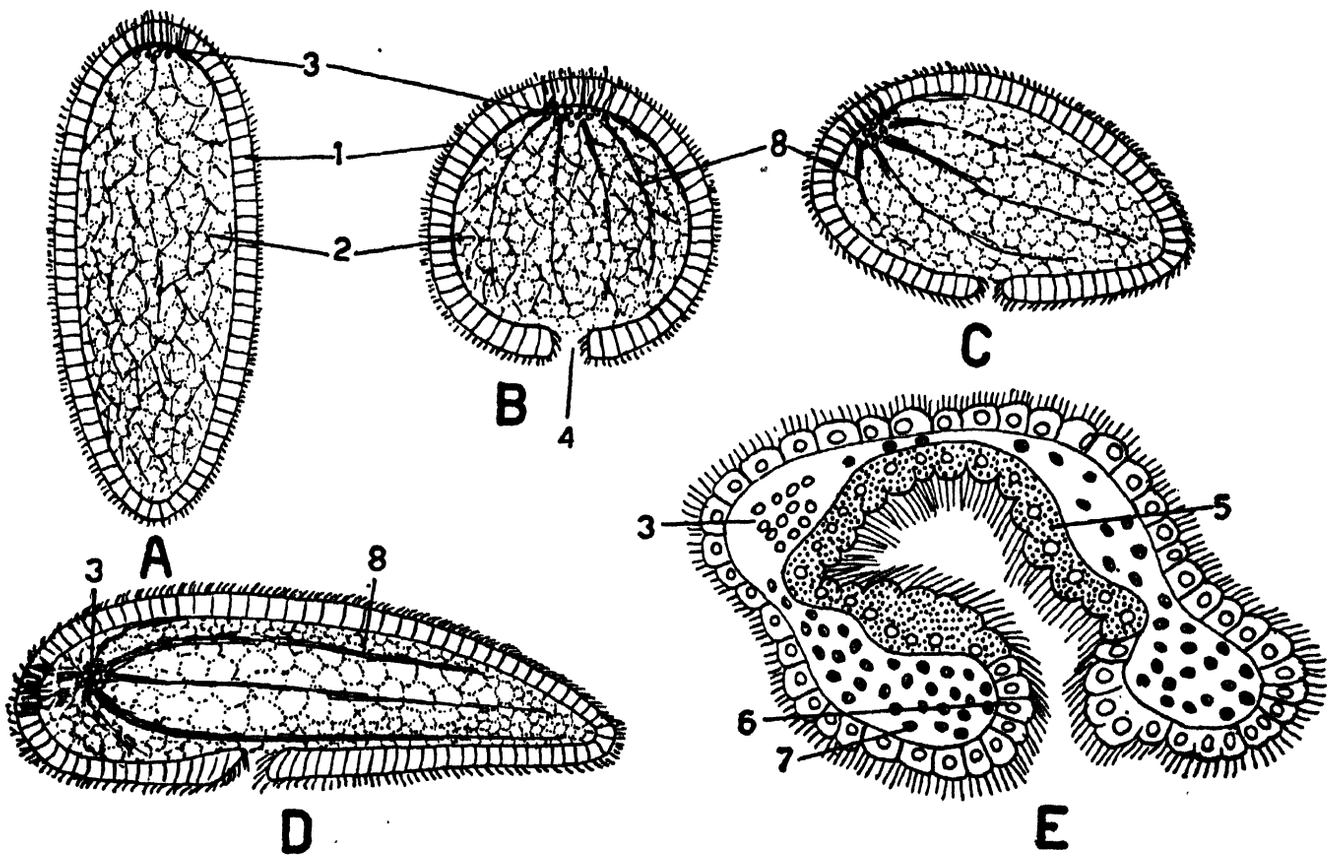

FIG. 2.—Diagrams illustrating the planuloid-acoeloid theory of the origin of the Bilateria. *A*. Planula larva, mouthless with apical nerve center. *B*. Mouth formed, oral-aboral axis shortening. *C*. Body elongating in a sagittal (originally transverse) plane, nervous center shifting forward. *D*. Acoeloid stage, a bilateral creeping worm with anterior nerve center. *E*. Later stage, archenteron formed; actual embryonic stage of a polyclad (*after Surface*, 1907). 1, ectoderm; 2, entodermal mass; 3, nervous center; 4, mouth; 5, archenteron; 6, stomodaeum; 7, mesoderm; 8, nerve cords.

known, the steps by which these changes occurred may be inferred from the embryology of the lower Turbellaria. As the mouth of the Acoela occupies the site of the blastopore, it may be taken as a fixed point. It is then evident that, as postulated by Lang, the planuloid form must have flattened down in the oral-aboral axis and at the same time there must have occurred a forward migration of the sensory center, as actually happens in the development of polyclads, through processes of differential growth (Fig. 2). The result is a simple flatworm with bilateral symmetry, ventral mouth, and anteriorly located brain and sense organs. A later stage, represented by the higher Turbellaria, is attained by the hollowing out of the central part of the interior mass to form an archenteron (Fig. 2*E*) and the greater differentiation of the anterior region as a head.

It is thus seen that the oral surface of the Radiata becomes the ventral surface of the Bilateria while their sagittal plane is retained as the sagittal plane of the latter. But the dorsoventral flattening is not a mere shortening of the oral-aboral axis, for this axis has been curved forward by the anterior shifting of the nervous center. Thus, whereas in the Radiata the oral-aboral axis of the larva is retained as the oral-aboral axis of the adult, in the Bilateria the gastrular axis has no direct relation to any of the adult axes.

III. SPIRAL CLEAVAGE AND DETERMINATE DEVELOPMENT

Determinate or *mosaic* development, characteristic of most of the Protostomia, is usually associated with the spiral type of cleavage, found in polyclad flatworms, nemertines, annelids, and mollusks. Among these groups the cleavage pattern and the fate of the various blastomeres are so nearly identical that a common descent is scarcely to be doubted. In spiral cleavage, the spindle axes are oriented obliquely with respect to the polar axis of the egg. As a result successive tiers of blastomeres alternate, the cells of one tier resting in the angles between the cells below them (P–C, page 257, Fig. 73*F*, *G*). This displacement may be either clockwise (dextrotropic) or counterclockwise (levotropic). Spiral cleavage is commonly holoblastic but unequal, and this inequality is often evidenced even at the first cleavage. In spiral cleavage, the fate of each blastomere can be determined, a type of study known as *cell lineage* and pursued with brilliant results by American embryologists. For clarity in describing the course of events, each blastomere is named. The four blastomeres formed by the first two meridional cleavages are labeled *A*, *B*, *C*, *D*. The third division is transverse and latitudinal and results in eight cells, four small animal ones called the *first quartet of micromeres* and four large cells below, called *macromeres* (Fig. 3*A*). The micromeres are named 1*a*, 1*b*, 1*c*, 1*d*, and the macromeres 1*A*, 1*B*, 1*C*, 1*D*. At the next cleavage, the macromeres give off above a *second quartet* of micromeres, called 2*a*, 2*b*, 2*c*, 2*d*, and are themselves then designated as 2*A*, 2*B*, 2*C*, 2*D* (Fig. 3*B*); and at the next cleavage the latter again divide, giving off a *third quartet*, 3*a*, etc., themselves becoming 3*A*, etc. (Fig. 3*C*). Meantime the first and second quartets have cleaved, and their offspring are also numbered by a definite system. Thus the two daughter cells of 1*a* become $1a^1$ and $1a^2$; the exponent 1 is applied to the cell nearer the animal pole. When these divide again, exponents are added; thus the daughter cells of $1a^1$ are numbered $1a^{11}$ and $1a^{12}$, and of $1a^2$, $1a^{21}$ and $1a^{22}$, respectively. This system obviously is capable of indefinite expansion and serves to designate exactly the origin of any particular cell. All the cleavages are oblique and are alternately dextrotropic and levotropic. All the blastomeres bearing one letter, as *a*, are offspring of one of the

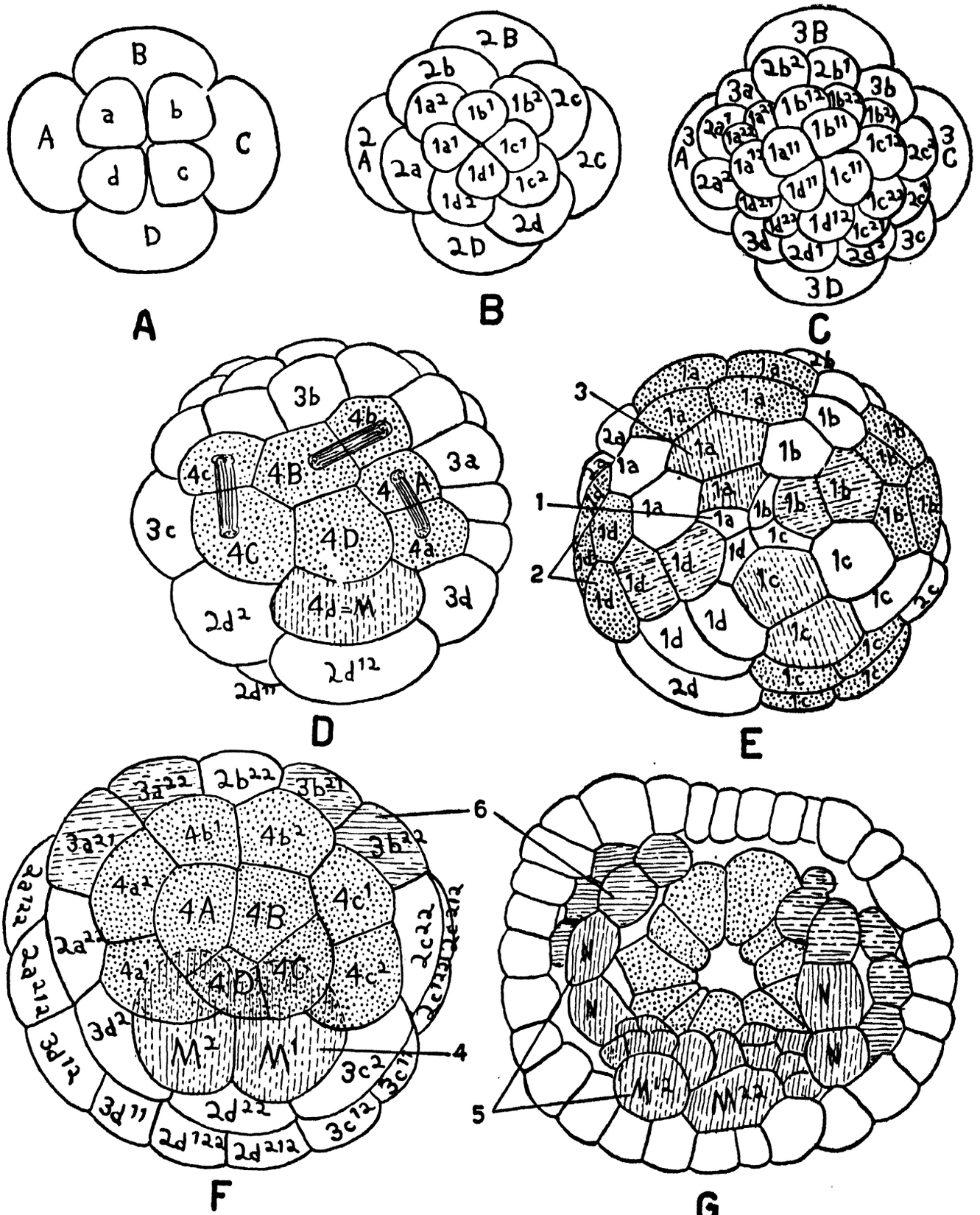

FIG. 3.—Spiral cleavage. *A*. Third cleavage, division into micromeres and macromeres. *B*. Formation of the second quartet of micromeres; first quartet has divided. *C*. Formation of the third quartet of micromeres; second quartet has divided again. (*A*, *B*, *C*, based on development of polyclads.) *D*. View from vegetative pole, showing the macromeres giving off the fourth quartet of micromeres; entoderm cells stippled, entomesodermal cell, $4d = M$, vertically hatched. *E*. View from the animal pole, showing the rosette and the annelid cross (cells of cross hatched); primary trochoblasts stippled; only the series to which each cell belongs is indicated. (*D*, *E*, polychaete *Arenicola*, *after Child*, 1900.) *F*. View from vegetal pole of embryo of the snail *Physa*, showing entoderm (stippled), the two teloblasts (vertically hatched), and the cells that give rise to the ectomesoderm (crosshatched). *G*. Later stage of *Physa*, looking into interior from animal pole, showing the teloblasts giving off the mesoderm bands (vertically hatched), of which the cells marked *N* become the metanephridia; entoderm stippled, ectomesoderm crosshatched. (*F*, *G*, *after Wierzejski*, 1905; the cleavage of *Physa* spirals in the reverse direction from that of the other forms figured.) 1, rosette; 2, primary trochoblasts; 3, cross; 4, teloblasts; 5, mesoderm bands; 6, ectomesoderm.

original four blastomeres, in this case *A*, and hence more or less occupy one quadrant of the embryo.

When the third quartet of micromeres has been given off, the germ layers are already fixed (usually 32-cell stage, as the first and second quartets have cleaved). The three quartets and their offspring form the whole of the ectoderm (and also the larval mesoderm, i.e., the ectomesoderm) and hence are often called *ectomeres*. The four macromeres, 3*A*, 3*B*, 3*C*, 3*D*, form the whole of the entoderm and the true or entomesoderm. At their next division, they give off at the vegetal pole a fourth quartet of micromeres, 4*a*–4*d*, three of which are also purely entodermal (Fig. 3*D*). The fourth cell, 4*d*, is larger than the corresponding macromere, 4*D*, is called the *mesentoblast* cell, or *M*, and is the entire source of the entomesoderm. It was originally supposed that all its offspring are mesodermal, but later researches have shown that a few of these remain entodermal and contribute to the gut wall. The main offspring of 4*d*, however, in annelids and mollusks, are two cells known as the *teloblasts*, *pole cells*, or *primordial mesoderm cells*. These take up a bilateral position just in front of the future anus and each proliferates a band of cells, the *mesoderm band*, the sole source of the entomesoderm (Fig. 3*F*, *G*).

The embryo becomes an inequal coeloblastula or, in the case of very yolky eggs, a stereoblastula. The ectomeres spread and grow down over the macromeres, which also invaginate. A typical invaginate gastrula thus arises partly by epiboly and partly by emboly. The mouth forms at the site of the blastopore by way of a stomodaeal invagination. In forms with an anus, the blastopore elongates and closes together medially so as to leave its anterior end as mouth and its posterior end as anus. The anal end usually closes temporarily but later reopens as the permanent anus. A stomodaeum is universal throughout the Protostomia. The mouth is usually shifted forward by growth processes elsewhere in the embryo. The embryo develops an apical tuft of cilia and an equatorial girdle of cilia and swims about as a free-living larva.

The fate of the various cells of the cleavage pattern may be stated briefly. The micromeres of the first quartet form the ectoderm of the aboral part of the larva. The $1a^{111}$–$1d^{111}$ series occupy the animal pole where they make a four-rayed pattern termed the rosette which becomes the aboral sensory plate with its tuft of cilia (Fig. 3*E*). Their sister cells, the $1a^{112}$–$1d^{112}$ series, in annelids alternate with them as a cross-shaped figure called the *annelid cross* (Fig. 3*E*). A similar *molluscan cross* occurs in molluscan development but there is formed of the cells which lie between the arms of the annelid cross, namely, the $1a^{12}$–$1d^{12}$ cells, with some assistance from second quartet cells. Thus the arms of the cross are interradial in annelids, radial in mollusks. The cross, very evident in early stages, eventually becomes obliterated and plays no special role in

development as such. It is often regarded as a ctenophore reminiscence, and the ctenophore resemblance is enhanced in some cases by the bifurcation of the tips of the arms to form an eight-rayed figure. The $1a^2$–$1d^2$ descendants of the first quartet are termed the *primary trochoblasts;* they form four groups of four cells each, one group in each quadrant of the embryo near the equator (Fig. 3*E*). Each cell develops a transverse tuft of cilia reminiscent of a ctenophore comb. These four groups of ciliary tufts constitute the primitive ciliated girdle, or *prototroch,* of the larva. Later the prototroch is completed by the formation of cilia on the cells between the primary trochoblasts, termed *secondary trochoblasts,* which come from the first or second quartet or both.

The cells of the second and third quartets contribute to the surface ectoderm, and certain ones, termed *stomatoblasts,* invaginate as the stomodaeum. In annelids, the cell 2*d,* known as the first *somatoblast,* gives rise to practically the entire ectoderm of the adult trunk. Cells are also given off from the second and third quartets into the blastocoel as mesenchyme which differentiates into larval muscles (Fig. 3*F, G*). This mesenchyme constitutes the larval mesoderm or ectomesoderm and is undoubtedly a reminiscence of the original ectomesoderm of the ancestral stem form of the Bilateria. Descendants of $3c^2$ and $3d^2$ give rise in annelids to the larval excretory organs, the *archinephridia.* In the most primitive case, that of the annelid *Polygordius,* the archinephridium comes from two cells, one forming the tubule, and the other the solenocyte.

The entoderm originates almost wholly from seven cells, namely, 4*a,* 4*b,* 4*c,* 4*A,* 4*B,* 4*C,* and 4*D* (Fig. 3*D*), which invaginate and produce the entodermal wall of the stomach and intestine of the larva. As already noted, a few cells descended from 4*d* become incorporated into the intestinal wall. The intestine (in the higher Protostomia) connects to the exterior by an anus formed at the site of the rear end of the blastopore. In producing the anus, the ectoderm invaginates slightly, and this ectodermal termination of the gut is called the *proctodaeum.*

The two teloblasts, offspring of 4*d,* lie in the blastocoel just in front of the anus (Fig. 3*F*). By repeated divisions each gives rise to a band of cells which extends forward into the blastocoel. These bilateral *mesoderm bands* (Fig. 3*G*) are the whole of the entomesoderm and give rise to muscle, connective tissues, gonads, excretory system at least in part, blood vessels, etc. The formation of typical mesoderm bands from teloblasts is confined to the phyla Annelida and Mollusca, but the bands are well evidenced in the Arthropoda.

In the annelids and mollusks, spiral cleavage often results in a characteristic larva, known as the *trochophore,*[1] and somewhat similar larvae

[1] Discovered in 1840 by the Swedish naturalist Loven and known for many years as Loven's larva. It was then called *trochosphaera* or *trochosphaere* by Ray-Lankester

occur in other protostomous phyla. As great phylogenetic significance has been attributed to the trochophore larva, it becomes necessary to describe its characters before proceeding further.

IV. THE TROCHOPHORE LARVA, THE TROCHOPHORE THEORY, AND THE GENERAL PHYLOGENETIC SIGNIFICANCE OF LARVAL TYPES

The trochophore larva (Fig. 4) is a somewhat biconical creature with a protruding equator. Its external surface consists of a one-layered epithelium (ectoderm) thickened at the apical pole into a sensory plate which bears a tuft of cilia. Around the equator there is a girdle of cilia termed the *prototroch* which passes above the mouth; and there may be present a second equatorial girdle, the *metatroch*, passing below the mouth, and sometimes also a ciliated circlet around the anus, the *paratroch*. A complete digestive tube is present extending in an L-shape from the mouth at the equator to the anus at the lower pole; it consists of a ciliated stomodaeum leading into an expanded rounded stomach from which the short narrowed intestine proceeds to the anus. Between the digestive tube and the ectoderm there is a spacious cavity which is the blastular cavity or blastocoel. This is more or less occupied by mesenchyme cells and well-developed muscle cells, all derived from the ectomesoderm. The muscular system is often quite complicated consisting not only of bands acting on the digestive tube and ciliary girdles but also of bands under the ectoderm accompanying the nerves (Fig. 5). The nervous system according to the best description (E. Meyer, 1901) may attain an astonishing degree of complexity (Fig. 5), consisting of a ganglionic mass under the apical plate, a variable number of longitudinal nerves radiating from this mass, and one to several nerve rings connecting the radial nerves. The main nerve ring underlies the prototroch. Various sense organs, including eyes and statocysts, may be present. To either side of the intestine lies a mesoderm band derived from a teloblast, and near this there is on each side a nephridium consisting of a tubule whose inner end is closed by one or more solenocytes. A solenocyte (Fig. 12*D*) is a long tubular cell having a flagellum playing in the tube. Solenocytes occur in several invertebrate groups and also in *Amphioxus*, and nephridia with solenocytes are undoubtedly only a variant of nephridia with flame bulbs (see below); the latter are general throughout the acoelomate and pseudocoelomate Bilateria.

The *trochophore theory*, elaborately developed by Hatschek (1878), is to the effect that the trochophore is the larva of an ancestral form, the *trochozoon*, which was the common ancestor of most, if not all, the bilateral phyla, and which, of living forms, most nearly resembled a rotifer. It

(1877), but this name was abandoned because it had earlier been used for a genus of rotifers. The name trochophore originated with Hatschek (1878).

is to be noted that the trochophore is regarded as recapitulating the *larva* of the ancestor, not as being itself a replica of the ancestor. The rotifer resemblances usually cited are the general pseudocoelomate grade of structure, the ciliary girdles, the structure and location of the brain and the nature of its attached sense organs, the muscle bands, the nephridia, the form of the digestive tract, and the presence of an anus. The rotifer-like nature of the hypothetical trochozoon was considered

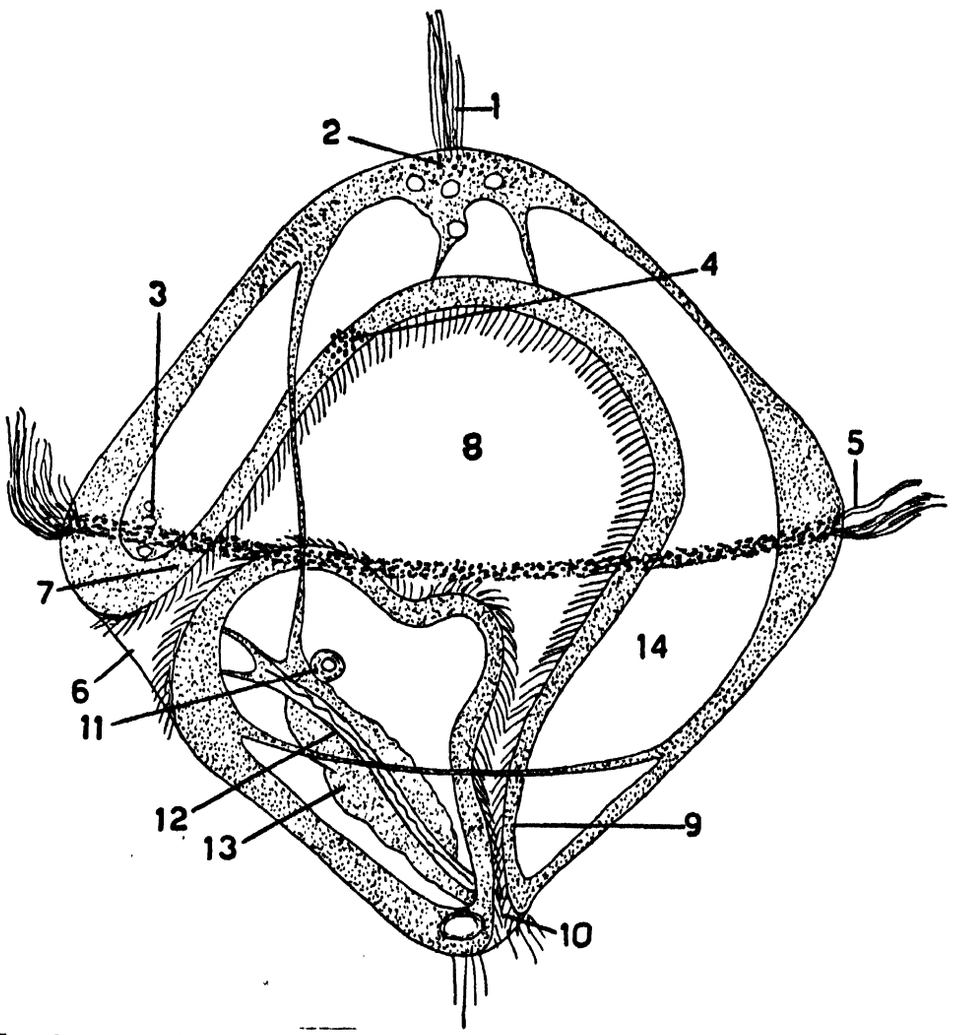

FIG. 4.—Trochophore larva of an annelid (*after Shearer*, 1911). 1, apical tuft of cilia; 2, apical sensory plate; 3, ectomesoderm; 4, eye; 5, prototroch; 6, mouth; 7, stomodaeum; 8, stomach; 9, proctodaeum; 10, anus; 11, statocyst; 12, archinephridium, consisting of one solenocyte; 13, mesoderm bands; 14, blastocoel.

strongly supported by the discovery by Semper in 1859 in the rice fields of the Philippines of a rotifer which he named *Trochosphaera* and which through its inflated spherical form and equatorial ciliary girdle bears considerable superficial resemblance to a trochophore larva. Time has detracted from the rotifer part of the trochophore theory, for those rotifers whose ciliary arrangements most suggest the girdles of the trochophore are now regarded as specialized types and the primitive ciliary apparatus of the rotifers has not much likeness to the trochophore girdles. Further the rotifer *Trochosphaera*, which has been refound and restudied in various localities, is now known to be merely an aberrant type of no especial evolutionary significance. Nevertheless, while discarding the

rotifer part of the trochophore theory, one must admit the general soundness of Hatschek's view that the trochophore is about at the structural level of a rotifer, i.e., is of the pseudocoelomate grade of structure. The fact further that nearly identical trochophores occur in two phyla in which the adults are anatomically very different, i.e., the annelids and the mollusks, suggests that the trochophore is indeed a reminiscence of the common ancestor of the eucoelomate Protostomia and perhaps also

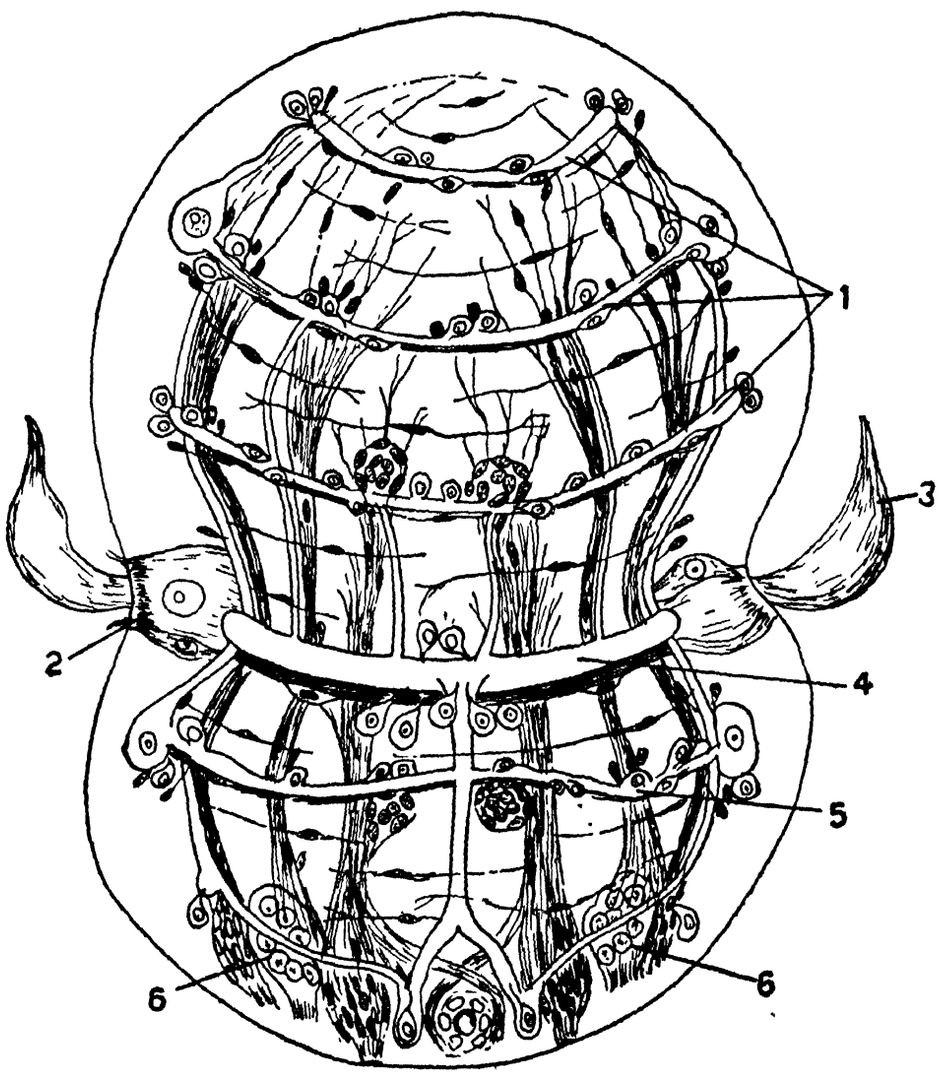

FIG. 5.—Trochophore of the annelid *Lopadorhynchus* (*after E. Meyer*, 1901), showing nervous system (blank) and muscular system (striated). The orientation of the larva is such that the apical sensory center does not show. 1, upper three nerve rings; 2, ciliary cell of the prototroch; 3, prototroch; 4, main nerve ring underlying the prototroch; 5, lower nerve ring; 6, mesoderm bands.

of the pseudocoelomate groups. However, the origin of the acoelomate Bilateria remains unaccounted for on this theory.

The ctenophore-trochophore theory, mentioned above, is a more recent and widely accepted version of the trochophore theory. It proposes to pass directly from a ctenophore-like ancestor to the trochozoon and so to bridge the gap between the radiate and bilateral animals. The chief ctenophore resemblances of the trochophore are: the apical nerve center with its attached sense organs, the radiating subectodermal nerves, often (but not always) eight in number, the occurrence of the "cross" in the cleavage pattern, and the origin of the prototroch from

four groups of ciliated cells. The apical nerve plate and sense organs are, however, also a feature of the planuloid ancestor, and the other resemblances are a necessary consequence of the quadripartite pattern characteristic of spiral cleavage. This quadripartite pattern is the result of the two meridional cleavages producing four blastomeres, each of which roughly forms one-fourth of the embryo. The argument therefore boils down to the question whether cleavage into four blastomeres is in fact reminiscent of a ctenophore ancestry. And this does not appear to be the case since the ctenophore egg goes through three meridional cleavages producing a wreath of eight blastomeres, and the details of its cleavage are not similar to the course of spiral cleavage. Further the nervous system of the developed trochophore with its longitudinal nerves connected by circular nerves is more like that of the acoel flatworms (which often also have eight longitudinal nerve trunks) than it is like that of a ctenophore. The ctenophore-trochophore theory is therefore rejected on these grounds and those previously mentioned.

A main difficulty in the path of the trochophore theory and its variants has been to allocate the acoelomate groups, for these can no longer be disregarded as degraded from higher bilateral phyla. This difficulty is here met by the interpolation in the phylogeny of an acoeloid grade of ancestor from which the flatworms are readily derived. The phylogenetic series here proposed is then: planuloid ancestor–acoeloid ancestor–trochozoon (pseudocoelomate grade). The gap from the acoeloid ancestor to the trochozoon is probably too large and may need to be filled by a type with a digestive tract but no anus, resembling stages seen in the development of polyclads (Fig. 2*E*).

An attitude of conservatism should always be maintained in regard to the evaluation of larval types. A larva is a developmental stage that leads a free existence. Larvae are practically limited to marine animals. The main reasons given for this (Needham, 1930) are: that larvae are too delicate to withstand the much wider range of environmental factors in fresh water than in the sea; that they would be swept away by currents; and that fresh water is poor in the salts needed by many larvae. It results that animals, to reproduce successfully in fresh water, must produce larger and fewer eggs, better provided with food and salts than their marine relatives; the eggs must be protected with shells, jelly, etc.; must be fastened to objects or develop inside the mother; and the young animal must hatch in a fully developed condition. Consequently, the development of fresh-water animals is generally highly modified and furnishes poor material for phylogenetic speculations. It is therefore difficult to work out the relationships of groups of animals which are predominantly fresh-water. Even among related marine groups, some may have free larvae and others not, without apparent reason. In

such cases the question arises which type of development is the more primitive. Again as larvae must fend for themselves and find food, they are very apt to display adaptive modifications which are without phylogenetic significance. Pelagic larvae tend to present common characters adapted to pelagic life, as transparency and lightness of body, swimming apparatus mostly in the form of ciliated bands, lobes and projections for buoyancy, and a food-catching mechanism, mostly of the mucous-ciliary type. Evidently great caution must be exercised in the interpretation of larvae, and most weight should be placed on characters not common to pelagic animals. In the case of the trochophore larva, the most salient features are the form of the nervous system, the presence of an anus, and the occurrence of primitive nephridia. These suggest an ancestral form higher than a flatworm and lower than an annelid.

The foregoing analysis carries the line of evolution from the radiates to and through the protostomous Bilateria. The relation of the Deuterostomia to this line of ascent remains very dubious, and this situation casts much doubt on the generally accepted ideas of the original modes of origin of mesoderm and coelom.

V. MODES OF ORIGIN OF THE MESODERM

The term mesoderm is rather loosely applied to all cells, cell layers, or cell masses which occur in the embryo between the ectoderm and the entoderm. The mesoderm is also spoken of as the third germ layer. As already noted, there are two kinds of mesoderm which seem to be phylogenetically distinct, the ectomesoderm and the entomesoderm. The ectomesoderm exists in both the Radiata and the Protostomia and is undoubtedly the oldest form of mesoderm. It is always mesenchymal and typically consists of inwandered ectodermal cells, in spiral cleavage of cells descended from the second and third quartets of micromeres. Ectomesoderm appears to be absent in the Deuterostomia. The Protostomia presumably inherited the ectomesoderm from a radiate ancestor, and their entomesoderm is a later development originating in the evolution of the Protostomia from a radiate ancestor.

The entomesoderm, the "true" or definite mesoderm, includes all mesoderm which arises from or with the entoderm. It may form as mesenchyme or as bands, plates, or sacs, more or less epithelial in character. The attempt of the Hertwigs (1882) to draw a sharp distinction between entomesoderm of mesenchymal origin and that of epithelial origin (mesothelium) was mistaken. The entomesoderm may arise by either method, and mesoderm which begins as epithelium may later become mesenchymal or vice versa. The time of origin of the entomesoderm is also variable. The following modes of formation of the entomesoderm occur among the Bilateria.

1. Teloblastic Method.—As already noted, this method is associated with spiral cleavage. The cell 4*d* gives off the two teloblasts or primordial mesoderm cells which pass into the blastocoel and there proliferate on each side a mesoderm band (Fig. 3*F*, *G*). The fact that some of the offspring of 4*d* are entoderm and participate in the gut wall is taken to establish the entodermal nature of the mesoderm so formed. This is also indicated by the purely entodermal character of the sister cells of 4*d*.

2. Derived Mesoderm-band Method.—In arthropods the entomesoderm also comes from paired bands, but the latter do not originate from teloblasts. They come from a mass of cells arising around the blastopore. Since the later development of these bands is very similar to that in annelids, from which arthropods are believed to have evolved, the entomesoderm of arthropods is regarded as originating by a modified teloblastic method.

3. Enterocoelous Method.—The mesoderm is formed in whole or in part by the outpouching of the archenteron wall as one or more pouches (Fig. 6*A*). This is an epithelial mode of entomesoderm formation. It is characteristic of the Deuterostomia, i.e., the Chaetognatha, Echinodermata, and lower Chordata, but also occurs in the Brachiopoda.

4. Lamellar Method.—The mesoderm grows out as a flattened stratum of cells from around the blastopore and is more or less mesenchymal in character. This manner of mesoderm formation is correlated with meroblastic development and is best seen in vertebrates where it is commonly regarded as a modified enterocoelous process.

5. Mesenchymal Method.—The formation of entomesoderm by inwandering of entoderm cells (Fig. 6*B*) en masse or more or less singly is common and may be combined with other modes of mesoderm production. Since in fact all methods of mesoderm origin except the enterocoelous are more or less mesenchymal, no very sharp line can be drawn between them.

With regard to the theoretical interpretation of the modes of entomesoderm formation, the same question arises as with regard to entoderm formation, i.e., was the epithelial (enterocoelous) or the mesenchymal method the primitive one? The enterocoelous origin by evagination from the archenteron has been widely accepted as primitive and all others as derived. This view, however, rests not upon direct evidence but on a phylogenetic speculation to the effect that the archenteral evaginations of the Deuterostomia are identical with the gastric pockets of a coelenterate. Adherents of the enterocoelous theory regard the teloblasts as precocious archenteral pockets reduced to single cells.

There are serious objections to the idea of the primary nature of the enterocoelous method of entomesoderm formation. This method is characteristic of the Deuterostomia whose relation to the Radiata cannot

be traced. The line of ascent obviously leads from the Radiata to the Protostomia, and hence it is more logical to seek the original mode of entomesoderm formation among the latter. The derivation of the teloblastic method from the enterocoelous is not very convincing. Further,

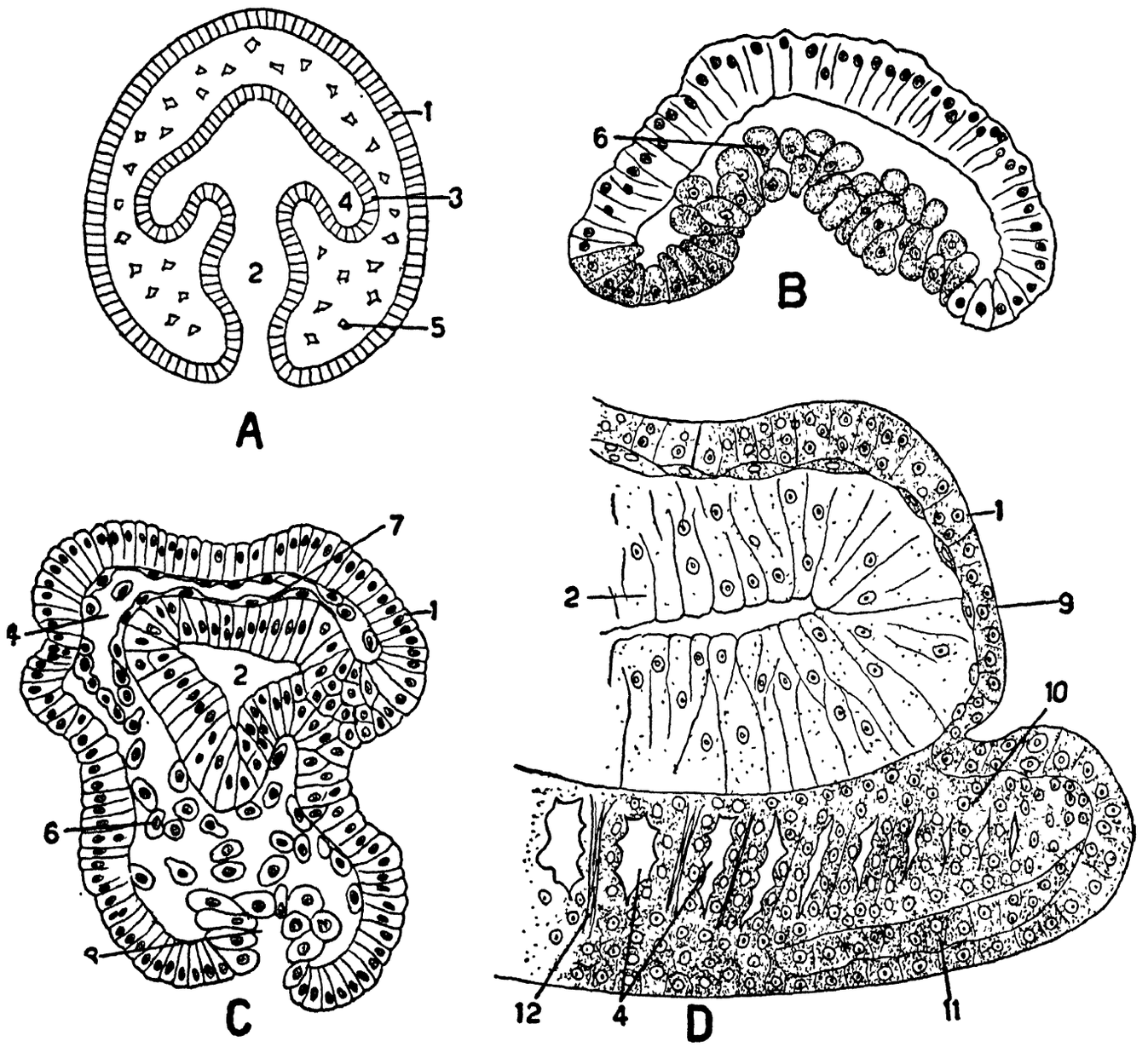

FIG. 6.—Origin of mesoderm and coelom. *A*. Diagram of the formation of the coelomic sacs by the enterocoelous method in an echinoderm. *B*. Formation of the mesoderm by ingression from the invaginating entoderm in *Phoronis;* entoderm and mesoderm stippled. *C*. Formation of the coelom in *Phoronis* by arrangement of mesoderm cells; note formation of protonephridium by an ectodermal invagination. (*B*, *C*, *after Ikeda*, 1901.) *D*. Embryo of an earthworm, parasagittal section through the rear end, showing the mesoderm band breaking up into segments in each of which a coelomic split is appearing (*after Wilson*, 1889). 1, ectoderm; 2, archenteron; 3, mesoderm sac; 4, coelom; 5, mesenchyme cells; 6, mesoderm cells; 7, peritoneum; 8, ectoderm invagination to form protonephridia; 9, future proctodaeum; 10, mesoderm band; 11, nephridial cord to form metanephridia separating from mesoderm band; 12, septum.

while the Protostomia show no reminiscence of a preceding enteroco method, the chief enterocoelous phylum, the Echinodermata, exhibits a considerable formation of mesoderm by a mesenchymal method prior to the evagination of the archenteron sacs. On the other hand, the teloblastic method can hardly be regarded as primitive, and in fact the

determinate mode of development seems specialized and shortened from the indeterminate type; and teloblast formation is more plausibly derived from an ancestral general inwandering than it is from the enterocoelous method. It seems most logical to seek for the original mode of entomesoderm formation among the most primitive Protostomia, namely, the turbellarian order Acoela. In this group, the available embryological evidence indicates that the entoderm and the entomesoderm are not distinctly separated but together form an interior mass which originates by inwandering at the blastopore. The evidence thus seems to favor some sort of mesenchymal inwandering as the original method. The entomesodermal inwandering differs from the ectomesodermal one in that it is limited to the region around the blastopore or where the blastopore will form. This association of the entomesoderm with the blastopore is general throughout the protostomous Bilateria, and in fact it may well be that entomesoderm formation is a phenomenon of the blastopore rather than of the entoderm. The relation of entomesoderm to the blastopore is difficult to explain morphologically but physiologically may be related to the known high metabolic activity of the blastopore rim. If, as here suggested, mesenchymal inwandering from around the blastopore was the original mode of entomesoderm formation, the whole process of mesoderm production becomes more logical and understandable; for then the giving off of ectomesoderm and entomesoderm would constitute two stages of the same process. That this view may be the correct one is further evidenced by the fact that not infrequently the definitive mesoderm is a combination of tissues of ecto- and entomesodermal origin (e.g., body-wall musculature of some annelids, E. Meyer, 1901); and in the snail *Paludina*, entomesoderm formation is secondarily suppressed and the whole of the adult mesoderm is of ectomesodermal origin (Dautert, 1929).

VI. BODY CAVITIES OF THE BILATERIA

The body cavities of animals are of several sorts, and it is necessary to distinguish clearly between them. The first cavity to appear is that of the blastula, the *blastocoel* or *primary body cavity*. With the formation of the archenteron, the blastocoel may be completely obliterated by the contact of entoderm with ectoderm or by the accumulation of mesogloea or mesenchyme between them. This happens in the radiate phyla where the digestive cavity is the only body space of the adult.

In the bilateral phyla several things may happen. The space between ectoderm and entoderm may become filled up with mesoderm in the form of muscle fibers and mesenchyme. This is the case in the phyla Platyhelminthes and Rhynchocoela in which again the digestive cavity remains the sole internal space. Such animals may be termed *acoelomate*, i.e.,

without a body cavity (Fig. 7*A*). In other groups, the original blastocoel remains as a considerable space between digestive tract and body wall. Such a condition obtains in the acanthocephalan worms, nematodes, rotifers, entoprocts, and related forms where a large cavity, known by its embryonic history to be a persistent blastocoel, exists between gut and body wall. Such a cavity will be designated a *pseudocoel*[1] or false coelom, and animals so constructed will be spoken of throughout this treatise as *pseudocoelomate* (Fig. 7*B*).

The true *coelom* or *secondary body cavity* is a cavity in the entomesoderm, and its occurrence is therefore absolutely dependent on the formation of entomesoderm. It has essentially the same different ways of origin as the entomesoderm, three ways.

1. Schizocoel.—In the teloblastic, derived teloblastic, and lamellar modes of mesoderm formation, the coelom arises as a split inside the mesodermic bands, plates, or masses (Fig. 6*D*). The split expands until the mesoderm comes in contact with the body wall on one side and the gut wall on the other.

2. Enterocoel.—In the enterocoelous method of mesoderm formation, the mesodermal sacs evaginated from the archenteron become cut off and lie in the blastocoel. Their cavity is the coelom, their walls the mesoderm. These sacs expand until they touch the body and gut wall, and the end result is therefore the same as by the schizocoelous method.

3. Mesenchymal Coelom.—The mesenchyme may rearrange itself so as to enclose a space which is then a true coelom since it is bounded on all sides by mesoderm. This method is said to occur only in the worm *Phoronis* (Fig. 6*C*).

Certain terms are applicable to all coelomate animals. That portion of the mesoderm which adheres to the inner surface of the body wall is called the *somatic* or *parietal* mesoderm. From it differentiate the muscle fibers and connective tissue of the body wall. That portion which adheres to the outer surface of the gut and other viscera is termed the *splanchnic* mesoderm and is the source of the muscle fibers and connective tissue of the viscera. The mesoderm cells next the coelomic cavity arrange to an epithelium called the coelomic lining or *peritoneum*, and this is termed *parietal* where it lines the inside of the body wall and *visceral* where it clothes the digestive system or other organs. Because of the way in which the coelom arises, every organ that is not embedded in the body wall or gut wall becomes necessarily covered by peritoneum. If an organ does not project into the coelom, the peritoneum clothes that sur-

[1] This is not the original usage of the word pseudocoel. This term was employed by the Hertwigs in 1882 in their classical article Die Cölomtheorie as a name for mesenchymal spaces; they confused under one name pseudocoel, haemocoel, and schizocoel.

face of the organ which faces the coelom. Such organs are said to be *retroperitoneal.* If an organ projects into the coelom, it is necessarily sheathed by a layer of peritoneum and is connected to other parts by a sheet composed chiefly of a double layer of peritoneum and called a *mesentery.* As the coelom expands, the splanchnic walls of the mesoderm meet above and below the digestive tract to form the *dorsal* and *ventral* mesenteries of that tract (Fig. 7*C*). The adult relations of coelom and mesenteries and the parts formed by the mesoderm are identical in schizocoelous and enterocoelous forms. Naturally the expansion of the mesoderm completely obliterates the blastocoel.

A true coelom is thus defined as a space between digestive tract and body wall which is bounded on all sides by tissue of entomesodermal origin and lined by peritoneum. Throughout this treatise the word coelom will be used to designate only a true coelom.

It is obvious from the foregoing that the nature of a body space can be determined only by the study of its embryonic history. The embryology of invertebrates is inadequately known, but according to available information, the Bilateria can be arranged as follows with regard to body spaces. These groupings do not, however, entirely correspond to taxonomic relationships.

1. Acoelomate phyla, without body space other than the digestive cavity; mesenchyme and muscle fibers fill region between digestive tube and epidermis (Fig. 7*A*). Phyla Platyhelminthes and Rhynchocoela.

2. Pseudocoelomate phyla, with a persistent pseudocoel (= blastocoel) between digestive tube and body wall (Fig. 7*B*). Phyla Acanthocephala, Aschelminthes (Rotifera, Gastrotricha, Kinorhyncha, Priapulida, Nematoda, Nematomorpha), and Entoprocta.

3. Coelomate phyla, which have a true coelom (Fig. 7*C*).

a. Coelom an enterocoel. Includes the Deuterostomia (Chaetognatha, Echinodermata, Hemichordata, and Chordata). The Brachiopoda also form their coelom by the enterocoelous method.

b. Coelom a schizocoel. Here belong the remaining phyla of the Protostomia, including the Phoronida, which latter form their coelom by a variant of the typical schizocoelous method (Fig. 6*C*).

Some phylogeneticists maintain that all Bilateria should be classified as coelomate animals since, so they say, they are derived from coelomate ancestors. The acoelomate phyla are said by these zoologists to have lost the coelom through invasion by mesenchyme and the pseudocoelomate groups to have retained an embryonic condition. The former statement is certainly untrue, and the latter lacks supporting evidence.

The value of the coelom in the animal economy is to be sought along two lines. First, the coelom frees the digestive tract and other organs from their previous encirclement by mesenchyme and gives them space

and freedom for further differentiation and greater activity. The digestive tract no longer need strive for increased surface by lateral branchings but instead elongates and can secure more absorptive surface by coiling. It has also now become provided with a muscular wall which facilitates grinding and passage of food. The second and possibly chief function of the coelom is urogenital. The coelom furnishes a space in which

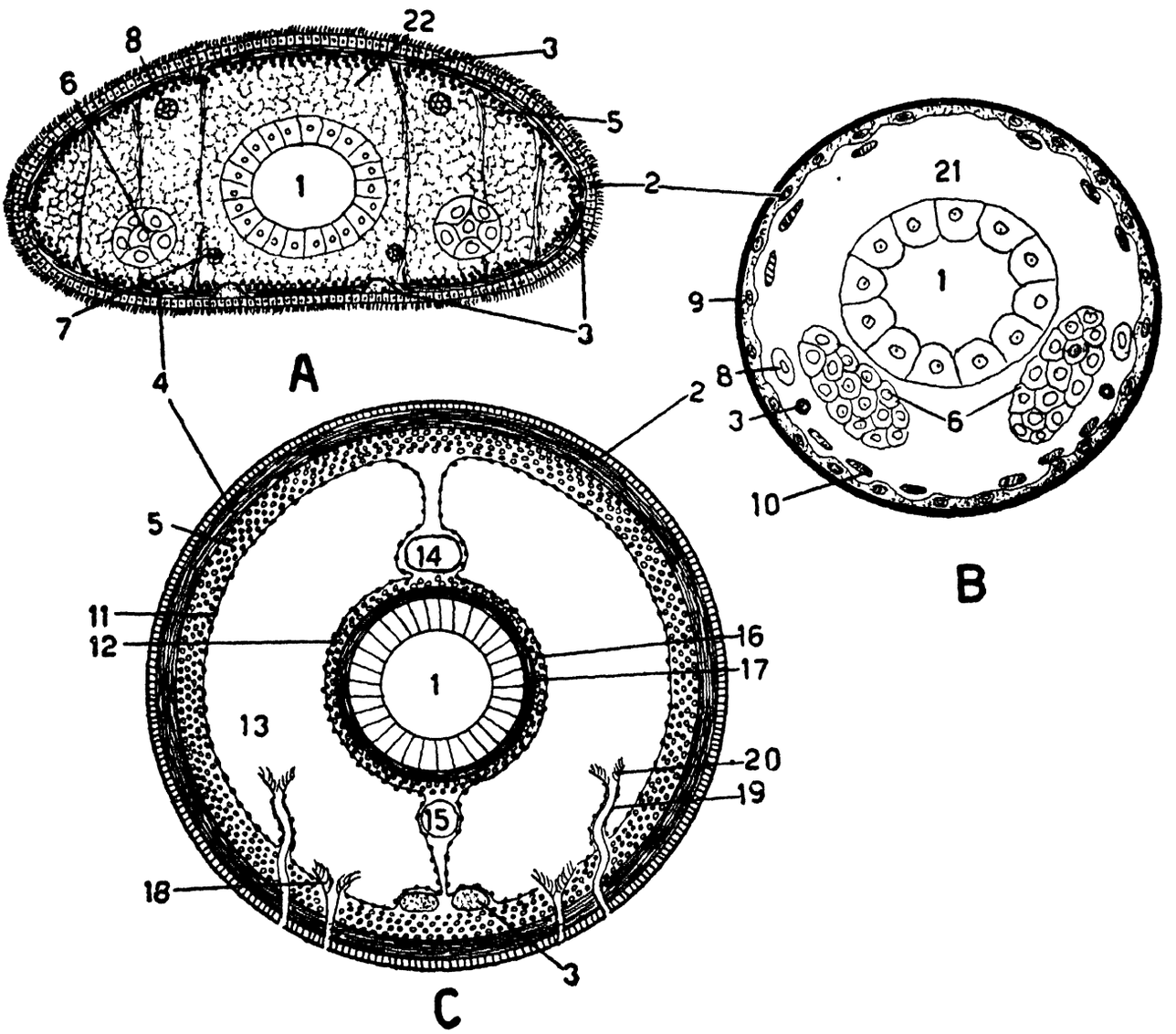

FIG. 7.—Diagrammatic cross sections of grades of structure. *A*. Acoelomate grade. *B*. Pseudocoelomate grade. *C*. Eucoelomate grade. 1, intestine; 2, epidermis; 3, nerve cords; 4, circular muscle layer; 5, longitudinal muscle layer; 6, gonad; 7, gonoduct; 8, protonephridium; 9, cuticle; 10, muscle bands; 11, parietal peritoneum; 12, visceral peritoneum; 13; coelom; 14, dorsal blood vessel; 15, ventral blood vessel; 16, longitudinal muscle layer of gut; 17, circular muscle layer of gut; 18, gonostome; 19, metanephridium; 20, nephrostome; 21, pseudocoel; 22, parenchyma.

nitrogenous wastes and excess water can accumulate and from which they can be discharged by way of excretory ducts; in fact, connection with the exterior by means of excretory ducts is a characteristic feature of the coelom. Usually also gonoducts for the discharge of the sex cells connect the coelom with the exterior. In coelomate animals, the gonads project into the coelom, and this is probably an important relationship since thereby ample space is provided for the enlargement of eggs and hence the production of large-yolked eggs.

Speculation as to the primitive mode of coelom formation necessarily follows the same trends as with regard to entomesoderm formation. The enterocoelous method is commonly accepted as the original one. Arguments against this view were already given. Here it may be repeated that the schizocoelous phyla are much more directly related to the Radiata than are the enterocoelous ones, that the relations of the latter to the other Bilateria are obscure, and that it appears more logical to seek for the original method of coelom formation among the Protostomia. The indications are that the schizocoelous method was the original one.

The question just discussed is intimately related to the further question of the phylogenetic significance of the coelom. On this matter there are three principal theories.

1. Enterocoel Theory.—This theory accepts the enterocoelous origin of the coelom as the primitive method and regards the mesodermal outpouchings as identical phylogenetically with the gastric pockets of the Scyphozoa and Anthozoa (Sedgwick, 1884). The bilateral ancestor is assumed to have had gastric pockets which became constricted off as coelomic sacs. As further evidence it is cited that in the Radiata the gonads often occur in the walls of the gastric pockets and in coelomate animals they are correspondingly located in the coelomic wall. The enterocoel theory has met with much favor, but cogent arguments can be raised against it. First, gastric pockets occur in the more highly organized coelenterates which do not seem suitable as ancestral types. Second, the gastric pockets of coelenterates do *not* arise as evaginations of the entoderm but very differently by ingrowth of septa from the body wall. Third, although the gonads are in fact located in the walls of the pockets, the sex cells themselves are usually of interstitial, not entodermal, origin, and indeed it seems that the sex cells originally were mesenchyme cells. Finally, conditions in the most primitive Bilateria do not support the enterocoel theory of either mesoderm or coelom formation.

2. Gonocoel Theory.—This, the most popular theory of the coelom, regards the coelom as the cavity of an expanded gonad. This idea was first expressed by Hatschek (1878) but was given its first exposition by Bergh (1885), who compared the segmented coelom of annelids with the linear series of gonads of flatworms and nemertines. The theory was further expounded by Lang (1881, 1904) and especially by E. Meyer (1890, 1901); both authors were led to acceptance of the theory by their studies of turbellarian and annelidan anatomy. The theory received much impetus from the finding by Lang of a marine planarian [*Procerodes lobata*, called by Lang (1881) *Gunda segmentina*], in which, as not uncommonly in marine planarians, the testes alternate with the intestinal branches and form a neat longitudinal row on each side. If now the

intestinal branches were to be withdrawn and the gonads expand so as to touch each other, the row of gonads on each side would resemble the row of coelomic sacs of an annelid (Fig. 8). This theory, like the previous one, also accounts for the origin or apparent origin of the sex cells from the coelomic wall since this would necessarily be the case if the coelomic sac is nothing but an expanded gonad. The opening of the gonoducts into

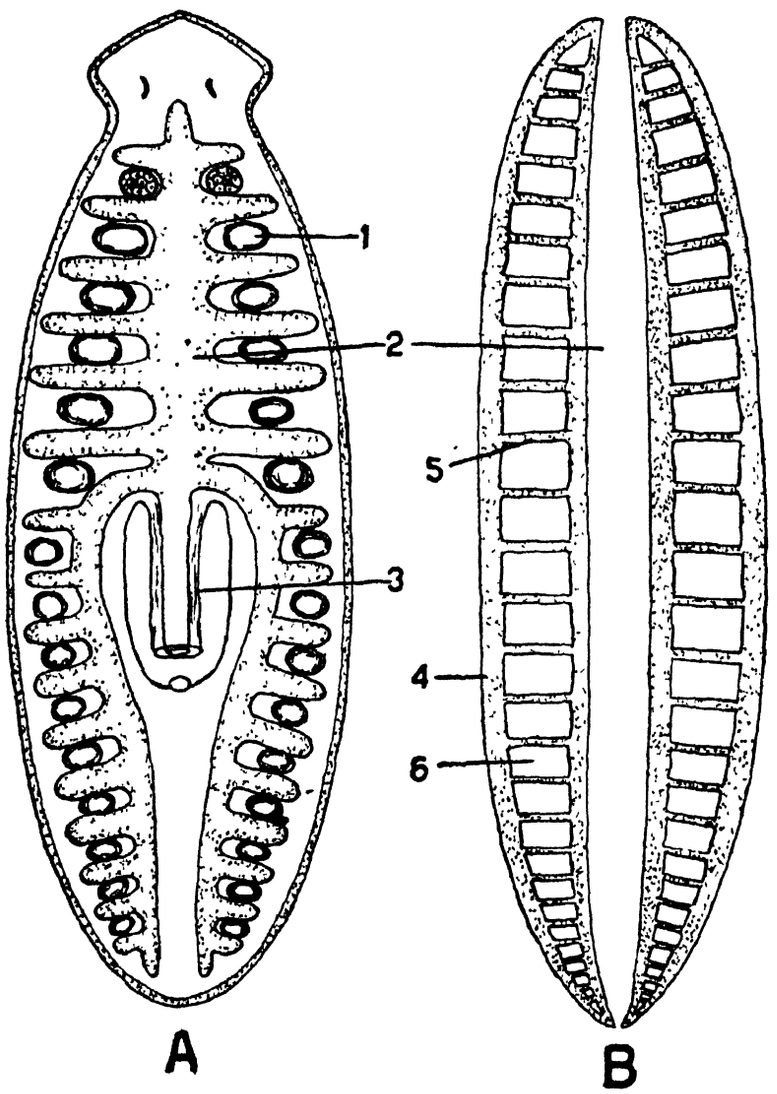

FIG. 8.—Diagrams to illustrate the gonocoel theory of the coelom. *A*. Triclad flatworm with gonads alternating with intestinal branches. *B*. Annelid with gonads expanded to form cubical coelomic sacs that fuse to body and intestinal walls. 1, gonads; 2, intestine; 3, pharynx; 4, body wall; 5, septum; 6, coelom.

the coelom is also explained. An extensive discussion of the gonocoel theory is given by Lang (1904).

The chief defect of the gonocoel theory, in the author's opinion, is that it links coelom formation with segmentation. The theory is based primarily on the occurrence of gonads in an anteroposterior row in nemertines and flatworms and hence can account only for a segmented coelom such as that of annelids (Fig. 8). It necessitates the assumption that all coelomate animals have passed through a segmented stage. But the majority of the coelomate phyla are not segmented, and there is no evidence that they came from segmented ancestors. Another difficulty of the theory is that it entails an independent origin of entomesoderm and

coelom, and this is contrary to all the facts of embryology. This difficulty can be met only by supposing that all the mesoderm cells were originally sex cells. This conclusion has indeed been accepted by the more ardent proponents of the gonocoel theory, but it too is contrary to the facts which indicate that the sex cells of the lower Metazoa are derived from a generalized connective tissue which has many other functions as well. As a further criticism of the gonocoel theory, it is by no means clear that the sex cells actually originate from the coelomic lining in coelomate animals, for in many forms there has been demonstrated a "germ track" or a tracing back of the sex cells to certain cells of embryonic stages. In such forms, the sex cells later wander into the gonads, and indeed it seems probable that the general association of the gonads with the coelom is of secondary nature. Finally it may be questioned that the linear arrangement of the gonads on which the gonocoel theory was based is of real significance. In these lower worms the gonads develop after the intestinal branches have formed, and there is no other room for them except the regions between the intestinal branches. If the gonads are small, a number of them will occur between successive branches; but if they are large, as is the case in Lang's famous marine planarian, then there is room for only one between successive intestinal diverticula. There then results the linear arrangement which so excited earlier zoologists but to which no importance is now assigned by students of planarians.

3. Nephrocoel Theory.—On the basis that the chief function of the coelom is excretory, Ziegler (1898) proposed that the coelom represents the expanded inner end of a nephridium. This theory accounts for the constant association of excretory ducts with the coelom but in general lacks supporting facts. Some coelomate groups, as the echinoderms, do not have excretory organs.

4. Schizocoel Theory.—This fourth possibility has occasionally been mentioned in the literature. If a mesenchymal origin for the mesoderm is accepted as primitive, then it necessarily follows that the coelom was originally formed by the schizocoelous method. On this view the coelom is a new formation, not related in any way to the gonads of the lower Bilateria or the entodermal pouches of the Radiata, and neither entomesoderm nor coelom had any antecedents in lower forms. It seems probable that the appearance of spaces or splits in the mesoderm leading to coelom formation resulted from the accumulation of fluid, possibly of excretory nature.[1] As concerns the relation of the sex cells to the coelom,

[1] The schizocoel theory therefore leans somewhat toward Faussek's version (1899) of the nephrocoel theory. The coelom is not regarded as an expanded nephridial organ but as originally an excretory space for the accumulation of excretory fluid. With such space the already present nephridial tubules become associated.

it may be said that the sex cells seem from the start to be independent of any of the germ layers. The archaeocytes of sponges and the interstitial cells of coelenterates classify as primitive mesenchyme cells. Also among the lower Bilateria the sex cells are of mesenchymal origin. The sex cells tend to become associated with available cavities for discharge to the exterior, in the radiates, with the digestive cavity, in coelomate animals, with the coelom.

VII. SEGMENTATION

Metamerism or *segmentation* is the division of the body along the anteroposterior axis into a serial succession of sections, each of which contains identical or similar representatives of all the organ-systems of the body. The sections are termed *segments* or *metameres* and are delimited externally by constrictions of the body wall. Each segment primitively bears externally a pair of appendages, when such are present, and contains a pair of nerve ganglia, a pair of nephridia, a pair of gonads, paired blood vessels and nerves, and a portion of the digestive and muscular systems. In short all parts which do not run the length of the animal are serially repeated at regular intervals along the axis, and it is this repetition which constitutes the essence of metamerism. In an ideally segmented animal, all the segments are identical; such a condition is termed *homonomous*. No such animal exists since one or more head segments and the anal segment necessarily differ from the others, but the polychaete annelids approach the ideal. In most segmented animals, however, the segmentation is *heteronomous*, i.e., has undergone local alterations through loss or fusion of segments, emphasis of certain organs in some segments, loss of organs from others, migrations of organs to other than the original segments, etc. Such alterations commonly begin anteriorly and proceed posteriorly so that the posterior region of the animal usually retains the more primitive condition. Commonly the head of segmented animals represents several fused segments with emphasis on nervous structures and loss of representatives of other systems. Primitively the number of segments is large and indefinite and becomes limited to a definite, relatively small number in forms with a high degree of heteronomous segmentation.

The foregoing remarks apply to *true* or *mesodermal* segmentation. There appears to be another kind of segmentation among invertebrates, which will be termed *superficial* segmentation. This begins in the cuticle and may proceed inward to a limited extent; it involves the cuticle, often the body-wall musculature, and sometimes the nervous system but not more internally located systems. It is manifested in the Acanthocephala and many of the Aschelminthes. On the other hand mesodermal segmentation appears to be fundamentally a phenomenon of the mesoderm

and proceeds from the interior outward, so that the external constrictions of the body wall follow the internal segmentation and presumably represent lines of muscle attachments. Mesodermal segmentation appears to have arisen independently three times in the animal kingdom, in the annelid-arthropod line, in the chordate line, and in the tapeworms, which the author, contrary to usual views, considers to be segmented. Hereafter, whenever the word segmentation is used without qualification, it is to be understood that true or mesodermal segmentation is meant.

In most cases of mesodermal segmentation, the segments form in an anteroposterior sequence so that the first segment is the oldest, the last the youngest; and new segments arise in a growing zone in front of the terminal piece bearing the anus. In tapeworms, however, the opposite condition obtains, for the last segment is the oldest, the first the youngest, and new segments develop in a growing zone in the "neck" region. Some zoologists have attempted to explain this difference by postulating that the "head" (scolex) of tapeworms is really the rear end; but modern studies on tapeworm development prove that the scolex is in fact the anterior end. Hence it is evident that tapeworm segmentation has arisen independently of that of annelids and arthropods, and this would indeed be a necessary conclusion from other lines of evidence. Zoologists usually claim that tapeworms do not have "true" segmentation (without defining what they mean by true segmentation); but the author sees no way of defining segmentation that would exclude tapeworms, unless the region of segment formation enters into the definition. As the region of segment formation appears to the author a minor point, the tapeworms are here regarded as truly segmented animals. Although the mode of formation of segments is identical in annelids, arthropods, and chordates, the last group is not now regarded as directly related to the other two, and hence segmentation must be supposed to have originated independently in the chordates.

There have been several theories of the phylogenetic origin of mesodermal segmentation. They revolve mostly around the question whether the repetition of organs is primary and the segmentation of the mesoderm secondary or whether the organs are serially repeated because the mesoderm from which they develop became segmented. In this connection it may be stated that a tendency for organs to spread throughout the available space is a primitive character and the sharp localization of an organ a more specialized condition. On this general principle it seems a priori probable that the repetition of organs preceded segmentation. The following are the chief theories of segmentation (see also Hatschek, 1888; Lang, 1904).

1. Corm or Fission Theory.—This idea, the most widely accepted of the various explanations of segmentation, states that a segmented animal

is really a chain of zooids resulting from incomplete fissions, and seeks the cause of segmentation in asexual reproduction. The number of animals that form such chains of zooids is few, and in none of them (except the scyphistoma of jellyfish) does the process resemble the segmentation of a segmented animal. In zooid formation, a fission plane appears near the middle of the animal, dividing it into anterior and posterior zooids; in each zooid a new fission plane develops, dividing this again into anterior and posterior zooids; and so on (Fig. 9). In the resulting chain of zooids, the successive zooids are not at all serially arranged with respect to age and the youngest zooid may be anywhere in the chain. In fact, the strobilization of a scyphozoan scyphistoma (P–C, page 522) presents the only analogy between asexual reproduction and segment formation; the ephyrae arise in oral-aboral succession in the same way that segments form in an annelid. Strobilation, however, seems to be an adaptation to a sessile mode of life, and it is impossible to conceive of a free-swimming animal reproducing in this manner, since it would lose its head at each fission. Another of the great difficulties of the corm theory, never satisfactorily answered, is to homologize the head and anal segments with the other segments. Hence the corm theory, although at first sight the most plausible, meets insuperable difficulties.

2. Pseudometamerism.—As mentioned above, primitive animals exhibit a tendency toward repetition of parts and the spreading of systems throughout the body, as shown by the branching intestine, numerous gonads, etc., of lower forms. In an elongated worm-shaped body, this tendency would lead to anteroposterior repetition of parts such as is a prominent feature of flatworms. If such a body broke up between head and posterior end into segments, a segmented animal would result. Some theorists assume that such a breaking up was caused by the swelling of the gonads at sexual maturity. The enlarged gonads would impede locomotion, and body bendings would tend to become localized at the regions between the gonads where constrictions leading to a segmented condition might form.

3. Locomotory Metamerism.—This idea is similar to the foregoing, ascribing metamerism to the breaking up of the body as a result of serpentine swimming movements. It differs from pseudometamerism in that it postulates the breaking up of gonads and other organs as a secondary result of muscular segmentation.

4. Theory of Cyclomerism.—This theory may be expressed by the aphorism (Lang, 1904) that the metamerism of the Bilateria is directly derived from the cyclomerism (radial arrangement of parts) of the Radiata. It will be perceived that this hypothesis is a corollary of the enterocoelous theory of mesoderm and coelom formation. The mesodermal segments are considered to be gastric pouches that show a linear

instead of a circular arrangement. Now there is but one coelenterate group in which the mode of formation of the septa can be homologized with segment formation, the Ceriantharia. It is generally agreed that the oral surface of coelenterates is the ventral surface of the Bilateria, that the sagittal planes correspond, and that the "dorsal" end of the sagittal plane of coelenterates is the anterior end of this plane in Bilateria. If one then orients a *Cerianthus* in this manner, it is seen that new septa are formed in couples at the "posterior" end as in segmented animals (see P–C, page 628, Fig. 206*B*) and that (omitting the three most dorsal couples) the first metasepta are the oldest and the others decrease in age "posteriorly." Acceptance of the cyclomerism theory entails the following large assumptions: that a cerianthid-like anthozoan was the ancestor of all the Bilateria, that the mesoderm and coelom are primitively enterocoelous and represent the gastrovascular compartments of anthozoans, and that the original Bilateria were segmented and coelomate and these characters have been lost from many groups. What are believed to be cogent arguments have already been advanced against such ideas, and the theory seems to the author wholly unacceptable.

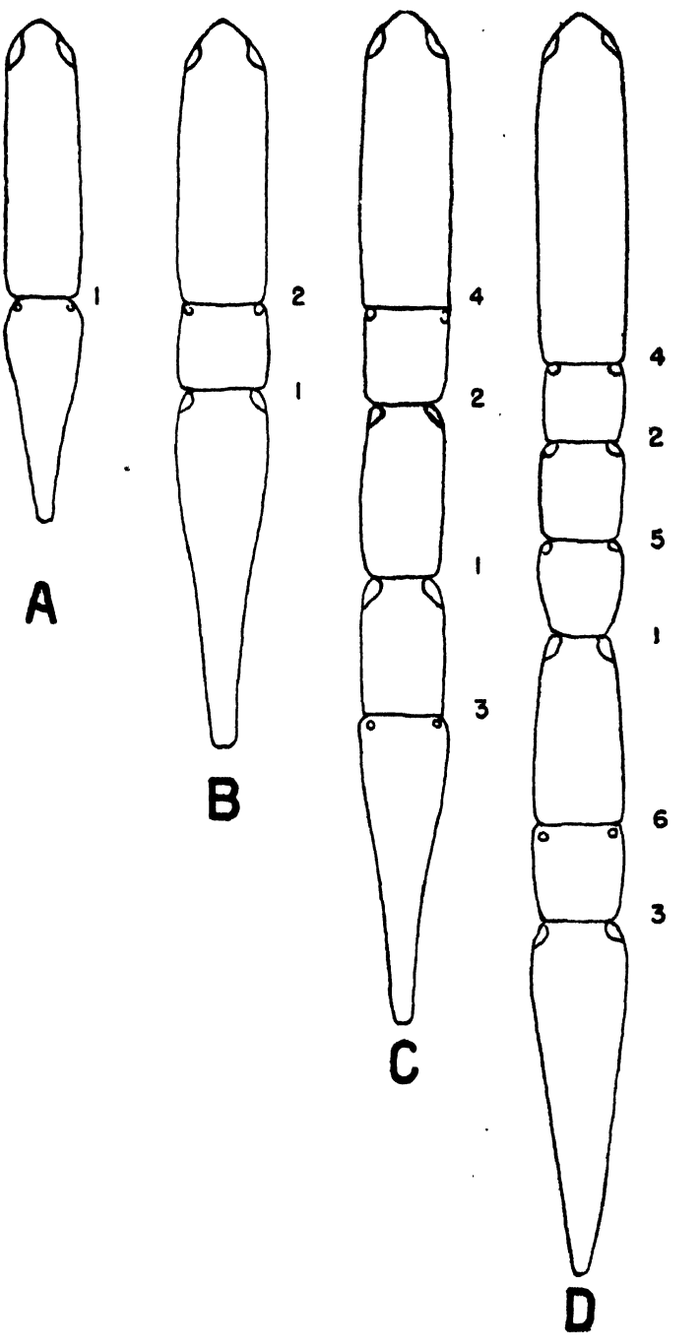

FIG. 9.—Process of fission to form a chain of zooids in the rhabdocoel flatworm *Stenostomum* (*after Child*, 1941, *Patterns and problems of development, courtesy University of Chicago Press*). *A*. First fission plane dividing worm into two zooids. *B*. Second fission plane has formed in anterior zooid. *C*. Third fission plane has formed in posterior zooid, anterior zooid has another plane. *D*. Both zooids have additional planes. 1–6, order of formation of fission planes.

Of the various theories of segmentation, a combination of pseudometamerism and locomotory metamerism appears most plausible, namely, that the organs were already scattered before segmentation occurred and that the impetus to the segmentary subdivision of the body came from the body musculature.

VIII. THE ORGAN-SYSTEMS OF THE BILATERIA

The fact that the various organ-systems present many differences in morphological detail among the bilateral groups has resulted in a confused terminology. With each phylum one is apt to encounter a new set of names for the various parts of the same organ-system. While this difficulty cannot be altogether eliminated because of the bewildering diversity of form which any one system can manifest, an effort will be made toward a more uniform terminology than is now encountered in zoological works.

An organ is a tissue complex that has definite form and serves some specific function. An organ-system is the sum of the organs that serve one function.

1. Integument.—The integument or body covering consists in invertebrates of a single-layered epithelium plus secreted materials to the outer side of this epithelium. The covering epithelium will be uniformly termed *epidermis* throughout this treatise. It is a continuance of the embryonic ectoderm and in invertebrates consists of a flattened to columnar simple epithelium, cellular or syncytial, and never stratified, although sometimes small cells are intercalated between the bases of the other cells. Gland cells and sensory structures are often interspersed among the regular epithelial cells, and often the epidermis is ciliated. A delicate ciliated epidermis is a primitive character and is suitable only for an aquatic habitat. For better protection and for adaptation to land habitats, invertebrates must develop a more resistant epidermis. Mucus secretion is often adopted as a protective device, but a more efficient method is the secretion by the epidermis of resistant layers which in invertebrates are always noncellular. The most usual of such secretions is a thin or thick membrane secreted on the exposed surface of the epidermis and known as a *cuticle*. The cuticle is commonly protein in nature or a combination of protein and chitin and is often of complicated structural and chemical composition. The cuticle may be sufficiently thick and firm to constitute an encasement or *lorica* for the animal. Sufficiently thickened and hardened epidermal secretions come under the general name of *exoskeleton*. In invertebrates the exoskeleton takes the form of calcareous shells as in mollusks and brachiopods, or chitin impregnated with calcium carbonate as in crustaceans, or other chitin mixtures.

Among invertebrates the tissues beneath the epidermis do not participate in the integument as they do in vertebrates, and therefore invertebrates do not possess a "skin" separable from the muscular layers of the body wall.

2. Endoskeleton.—Hard supporting parts formed in and by the mesoderm are termed endoskeleton. The spicules of sponges and of alcyonar-

ians classify as endoskeleton. Among the Bilateria, endoskeleton is extensively developed only in the Echinodermata, where it takes the form of calcareous spicules, rods, and plates. The cephalopod mollusks also possess endoskeleton in the form of a cartilage-like encasement for the main nervous ganglia.

3. Muscular System.—Of the three types of locomotion occurring in animals (P–C, page 3), only the muscular is feasible for animals of any size and for the production of rapid energetic movements. The term muscular system is usually understood to refer only to the musculature of the body wall by which locomotion is effected and does not include the muscles of the intestinal wall or other viscera. Primitively, the muscular system consists of a sheath of circular and longitudinal layers, lying beneath the epidermis. This condition more or less obtains in the lower Bilateria, with such minor changes as thickening of the layers, especially the longitudinal one; addition of more layers, sometimes diagonal in direction; interspersion of the muscle layers with connective tissue; and division, particularly of the longitudinal layer, into bands. Muscle layers close to the epidermis are called the *subepidermal* musculature; fibers which course through body tissues form the *mesenchymal* musculature; and in coelomate animals where the body wall is definitely separated from the intestinal wall, the musculature becomes the *body-wall* musculature. No great advance in efficiency of the muscular system is possible until the development of hard parts, i.e., either an exo- or an endoskeleton, to which the muscles can attach. When this happens, the muscle layers break up into individual *muscles*, i.e., bundles of muscle fibers molded into a definite shape and attached to hard parts by connective tissue which may form a cord or band termed a *tendon*. Such muscles enable an animal to execute far more rapid, precise, and varied movements than does the simple sheath system.

4. Nervous System.—The nervous system is specialized for rapid conduction and thus constitutes the chief mechanism in the body for communication between parts and for the coordination and correlation of activities. It is made up of nerve cells, also called *ganglion* cells, with a small amount of supporting tissue. A nerve cell has an enlarged portion, the *cell body*, containing the nucleus, and one or more elongated branches, the *neurites*, extending out from the cell body. There are two general types of nervous system, the *diffuse* and the *concentrated*. The diffuse system is the original and more primitive type; it consists of nerve cells and neurites distributed throughout the body, usually within or just beneath the epidermis, as a sort of network. It was formerly believed that the neurites in the diffuse type were actually fused to make continuous pathways, but it now seems established that the diffuse system, like the concentrated, is *synaptic* (P–C, page 397), i.e., the ends of the neurites

are in contact but not fused. In the diffuse system there are no nerves in the proper sense of this term as all the nervous strands contain nerve cell bodies as well as neurites. The diffuse system is also characterized by a lack of polarization since the neurites are not differentiated into axones and dendrites and functional impulses proceed along them in either direction. A diffuse nervous system is found in cnidarians, ctenophores, echinoderms, and flatworms.

The diffuse nervous system is more or less correlated with radial symmetry, and the manner in which such a radial system becomes bilateral has already been indicated. The nerve plexus concentrates into a limited number of meridional strands running from an aboral center. With the assumption of bilaterality, the aboral center shifts forward becoming the brain, and the meridional strands become longitudinal nerve cords (Fig. 2). Such a condition is seen in the lower orders of flatworms, the Acoela and Polycladida. Soon, however, the two ventral strands thicken and take precedence over the others, and later the others are eliminated so that the main nervous system behind the head consists of the two *ventral nerve cords,* as in many flatworms, annelids, arthropods, and some mollusks. The connections between the longitudinal strands, originally net-like, become more or less transverse; and when the longitudinal cords are reduced to two the transverse connections between them are reminiscent of the rungs of a ladder, whence this form of nervous system is called the *ladder type.* It is evident that the ladder type of nervous system is not an original or fundamental type but simply one of various possible derivatives from the primitive radial type which might be called "barrel" type, as the numerous longitudinal strands are like the staves of a barrel. As a further evolution of the ladder type, the two ventral cords may approximate so closely as to appear to be a single cord.

Concomitantly the nervous system tends to recede further into the interior, to the inner side of the muscle layers, and the nerve cell bodies tend to concentrate into masses known as *ganglia.* There thus arises the *concentrated* or *ganglionic* nervous system in which (in its final form) all the nerve cell bodies are located in ganglia while the nervous strands outside the ganglia are true *nerves* composed only of neurites. However, a complete absence of nerve cell bodies from the nerves is to be seen among invertebrates only in arthropods and higher mollusks. The ganglia and the direct connections between them known as *connectives* or *commissures* constitute the *central* nervous system while the nerves distributed throughout the body are the *peripheral* nervous system. There is also in annelids, mollusks, and arthropods a special part of the nervous system supplying the digestive tract, particularly its anterior portion. This is variously known as the *stomodaeal, stomatogastric,* or *sympathetic* nervous

system. It seems best to designate this simply as the *enteric* nervous system. The concentrated type of nervous system is *polarized*, i.e., conduction is functionally effective only in one direction along the neurites. The neurites become differentiated into an *axone* in which effective impulses pass away from the cell body and one to several *dendrites* in which they run to the cell body.

With the concentration of the nerve cell bodies into ganglia, the main nerve center comes to form a *brain*, composed of ganglionic masses, usually two in number, termed the *cerebral ganglia*, also *suprapharyngeal* or *supraesophageal ganglia*, from their position above the anterior part of the digestive tract. As these terms are cumbersome and as the part of the digestive tract concerned varies in different groups, it seems best to adhere to the one name, cerebral ganglia. From the dorsal position of the nerve center and the manner of evolution of the nervous system from a radial pattern it follows that the longitudinal trunks supplying the ventral region of the body must necessarily pass to either side of the anterior part of the digestive tract to reach that region. This embracing of the anterior part of the digestive tract by nerve cords is a characteristic feature of the nervous system of most of the bilateral invertebrates. These embracing cords will be termed the *circumenteric connectives* to avoid such awkward expressions as the usual names, *circumesophageal* or *circumpharyngeal connectives*, which are often in addition misnomers as some other part of the digestive tract may be concerned. In some groups, as nematodes, the nerve center consists of a ganglionated ring around the digestive tract, and this will be called the *circumenteric nerve ring*. The main longitudinal trunks of the nervous system are designated by their position as *dorsal*, *lateral*, *ventral cords*, etc. As already noted, the ventral cords are often the most prominent or the only longitudinal cords. In segmented groups each ventral cord has primitively a ganglionic enlargement in the middle of each segment, but often the number is less through fusion of ganglia. Usually the first pair of ganglia of the ventral cords is enlarged or of composite nature and is then designated by a special name, commonly *subesophageal* or *subpharyngeal* ganglia. Here again the simpler term *subenteric* ganglion is suggested.

The central nervous system of invertebrates differs from that of vertebrates in that it is always solid, not hollow as in the latter. The invertebrate nervous system like that of vertebrates is of ectodermal origin.

5. Sensory System.—Sensory cells and sensory organs are specializations which are peculiarly sensitive to environmental conditions and notify the organism of alterations in these conditions. They are designated by the general name of *receptors* which term may be prefixed by a root indicative of the environmental condition concerned. Receptors are most abundant and most differentiated at the body surface where they

respond to external factors, but they also exist in internal organs where they register various visceral conditions. As previously explained (P–C, page 279), sensory cells are of two sorts: *sensory nerve cells* or *neurosensory cells* which are really nerve cells with a neurite running into the interior, and nonnervous sensory cells which are modified epithelial cells and must be supplied by fibers from the nervous system. The sensory cells of invertebrates are *all* of the neurosensory type, and sensory organs consist of aggregations of such neurosensory cells plus associated cells of other types. Neurosensory cells despite innumerable variations in detail present a general morphological similarity. The rounded cell body containing the nucleus is situated in or just below the epidermis, sends to the surface a slender process which terminates in one to several projecting points, bristles, or flagella-like hairs, and sends into the interior a branching nerve fiber which connects with the nervous system or may end directly on an effector (Fig. 10*F*). If such a neurosensory cell withdraws sufficiently into the interior, it becomes a sensory ganglion cell of the nervous system with free nerve endings at the surface; this is supposed to be the phylogenetic origin of the sensory cells of ganglia. Free sensory nerve endings have been described for various invertebrates, although relatively uncommon.

A sensory organ or *sensilla* (plural, sensillae) is in invertebrates a cluster of neurosensory cells plus one or more kinds of other cells, which may be pigment cells, gland cells, or supporting and protective cells.

The external factors which stimulate sensory cells may be classified as mechanical, chemical, thermal, and photic. Mechanical stimuli may be subdivided into contact, gravity, sound waves, and water currents. Receptors for contact stimuli, such as touch and pressure, are termed in general *tangoreceptors* and usually consist of single neurosensory cells of the type described above. They are of wide distribution in invertebrates although certain parts, such as palps, tentacles, and antennae, are generally more thickly supplied with tangoreceptors than are other parts. *Static* organs for the perception of the direction of gravity by means of which the animal maintains a certain position and returns to that position when disturbed consist fundamentally of a mineral mass (*statolith*) or bunch of granules (*statoconia*) which rest upon the hairs of neurosensory cells. Any change in the position of the animal moves the statolith or statoconia so that different hairs are stimulated and the animal is made aware of the change of orientation. The more advanced types of static apparatus are enclosed in a vesicle, and the whole structure is then termed a *statocyst* (Fig. 10*A*). In the Bilateria, statocysts are found in the acoel and a few other flatworms, a few nemertine and polychaete worms, some holothurians, most mollusks, and many crustaceans. Many invertebrates detect the direction of water currents (*rheotactic* response), and

special *rheoreceptors* have been described in some forms. While tangoreceptors in general probably also serve to detect vibratory stimuli in terrestrial invertebrates, specific organs sensitive to vibration, known as *scolopophorous* organs, occur in insects and a few other arthropods. The essential feature of these organs is a special type of elongated neurosensory cell whose thickened distal tip, termed the *scolops*, is embraced by accessory cells. The whole unit, called a scolopophore, is under tension, being fastened at both ends (Fig. 10*E*). The more complicated types of scolopophorous organs consist of a number of scolopophores plus various accessory parts, particularly one or two thin tensed integumental membranes, known as *tympanic membranes*. Such *tympanal* organs, also called *chordotonal* organs, occur on the legs, thorax, and abdomen of various insects and are *phonoreceptors* or organs of hearing, in the vertebrate sense, although generally responding to sound waves of higher frequency than does the vertebrate ear.

Chemoreceptors for the detection of food and other substances in the medium are of wide occurrence in invertebrates and are strewn all over the body or more or less limited to the anterior end. They are morphologically similar to tangoreceptors. Often patches of chemoreceptors are sunk into pits or grooves to which cilia direct water currents, or they may be mounted on papillae or other projections.

Light perception is often evinced by the entire invertebrate body, although it has not been possible in most cases to identify the sensory cells or endings concerned. Besides this general responsiveness to light, most invertebrates are provided with specific *photoreceptors*, which may consist of single neurosensory cells but are usually compounded structures termed *ocelli* or *eyes*, consisting of neurosensory cells, pigment cells, supporting or other kinds of cells, and often light-refracting structures. The photosensitive neurosensory cell, called a *retinal* cell, may not differ from the general run of receptor cells but often shows characteristic differentiations, especially a striated border or other fibrillar structures. Pigment is a constant feature of photoreceptors; it may be situated in the retinal cells themselves but more often occurs in special pigment cells. The purpose of the pigment is to shut off light except that parallel to the long axis of the retinal cells. The light-refractive bodies found in eyes are of various sorts and origins. Often the cuticle is thickened to a biconvex shape or invaginated as a spherical body; these cuticular accessories are known as *lenses*. Instead or also there may be a gelatinous mass termed the *vitreous body* secreted by cells of the eye, or refractive bodies formed by the fusion of transparent cells.

Eyes are of three general grades of structure: *pigment-spot ocelli*, *pigment-cup ocelli*, and *vesicular ocelli*. The first consists of a spot flush with the surface composed of intermingled retinal and pigment or sup-

porting cells. Next this spot invaginates to form a cup or pit, the cavity of which may contain a refractive body. By the closure of the cup, the vesicular eye results; this is usually of complicated structure with one or more refractive bodies (Fig. 10 *B–D*).

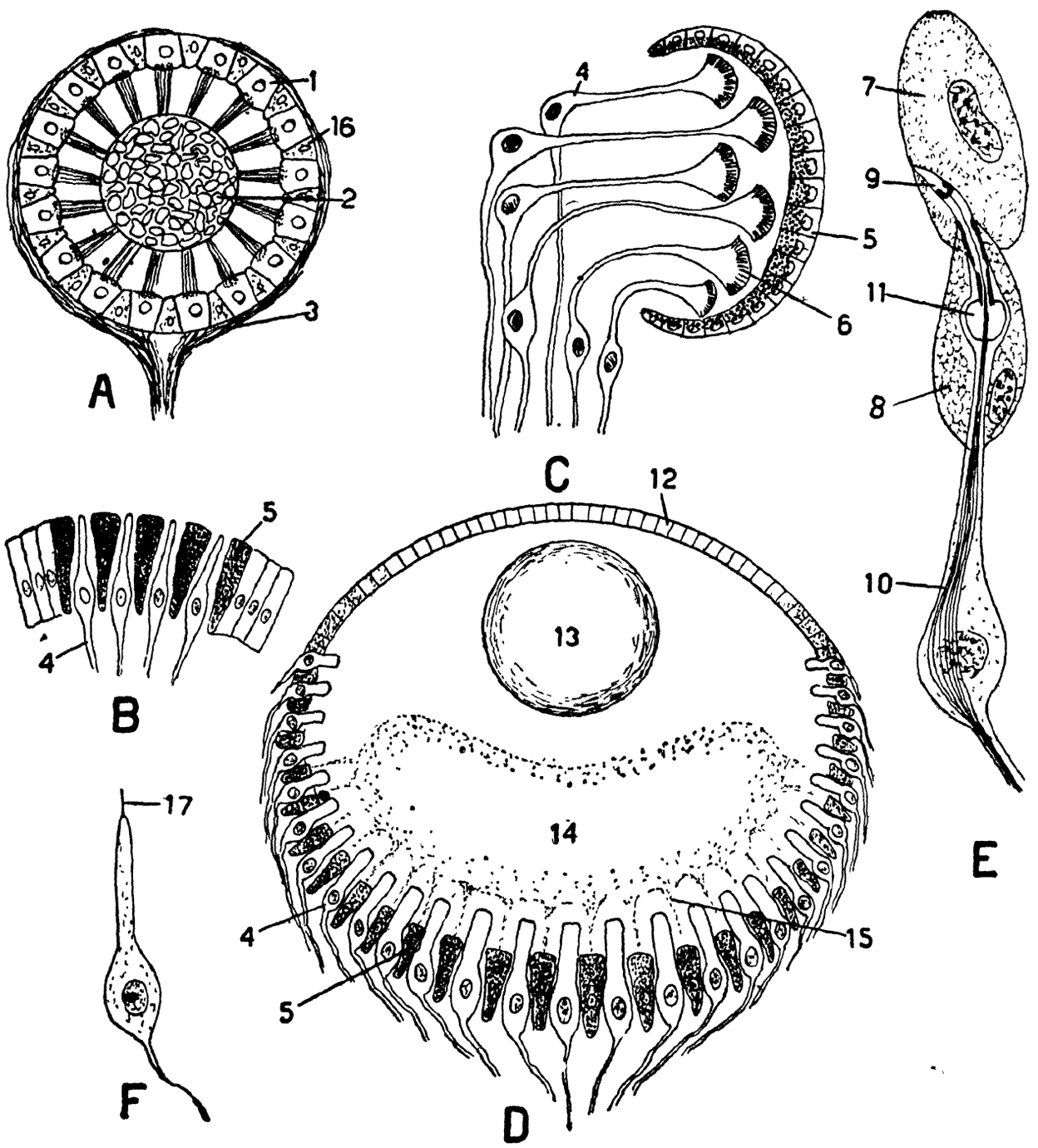

FIG. 10.—Sensory organs. *A*. Diagram of a statocyst. *B*. Diagram of a pigment-spot ocellus. *C*. Diagram of pigment-cup ocellus of the inverse type (*based on Hesse*, 1897). *D*. Diagram of a vesicular ocellus, converse type. *E*. A scolopophore (*after Schwabe*, 1906). *F*. Generalized neurosensory cell. 1, neurosensory cells with sensory bristles; 2, statoconia; 3, nerve fibers; 4, retinal cells; 5, pigment cell; 6, rod border; 7, cap cell; 8, cover cell; 9, peg; 10, neurosensory cell containing bundle of neurofibrils; 11, vacuole; 12, cornea; 13, lens; 14, vitreous body; 15, secretion strands; 16, supporting cell; 17, sensory bristle.

Eyes in which the retinal cells are oriented in the normal position, i.e., with their distal ends facing the exterior, are termed *converse* eyes. Those in which the free ends of the retinal cells face the interior of the cup or vesicle are spoken of as *inverse* eyes. Both types of eyes occur throughout

the Bilateria often within the same phylum, and inverse retinal cells may occur in eyes of relatively simple construction.

6. Digestive System.—The digestive system or digestive tract consists in its most primitive form, exemplified in the Hydrozoa, of an entoderm tube, the archenteron of embryonic stages, opening only by the mouth. A tendency to increase the digestive and absorptive surface by branching is early exhibited. There also soon becomes added to the original tube an ectodermal invagination at the mouth end, the *stomodaeum*. As the first part of the digestive tract usually serves, not for digestion, but for swallowing prey, often still alive and capable of inflicting injury, the formation of this region from hardened protective epidermis is readily understood. The stomodaeum early becomes invested with muscular coats as an aid to swallowing, thus constituting in whole or part the *pharynx* of adult anatomy. Anthozoans, ctenophores, and flatworms remain at this stage in which the digestive tract consists of a more or less muscular pharynx and a branched intestinal tube. In the next stage, the digestive tube develops a posterior opening, the *anus*, defined above (page 3), usually by way of another ectodermal invagination, the *proctodaeum*. Thus in the higher Bilateria only the middle region of the digestive tract, or *midgut*, has an entodermal lining. The relative contributions of stomodaeum, midgut, and proctodaeum to the adult digestive system vary greatly in different phyla, and the parts formed from them also exhibit so much variation that a uniform terminology is difficult if not impossible.

In most Bilateria, the digestive tract becomes freed from the body wall (except of course at the two ends) by the formation of either a pseudocoel or a coelom, and thereafter tends to achieve increased surface by coiling rather than by lateral branching. In pseudocoelomate animals, the digestive tract still consists chiefly of a single epithelial layer; but in coelomate animals, the splanchnic mesoderm attaches to the epithelium and develops muscular and connective tissue layers. The wall of the digestive tract thus becomes firm, muscular, and many-layered, and capable of carrying on peristaltic movements. Those portions of the digestive tract in which grasping, mastication, grinding, or mixing of the food with digestive juices occur have the strongest musculature.

The following are the chief parts of the digestive system. The *mouth* is primitively situated at about the middle of the ventral surface but shifts anteriorly in most Bilateria. In the Protostomia it is a direct continuation of the blastopore or the anterior part of the elongated blastopore or forms where the blastopore closed; in the Deuterostomia it appears to be a new formation. The mouth may be provided with protrusions termed *lips*. The mouth generally leads into a nonmuscular *buccal tube* or *capsule* (also called *oral cavity*, *buccal cavity*, *vestibule*, and other names), and this is usually succeeded by a muscular *pharynx*

employed chiefly in grasping and swallowing food. The cavities of these parts are termed *buccal* and *pharyngeal cavity*, respectively. Both usually receive secretions from unicellular glands in or attached to their walls or from definite compound *buccal* or *pharyngeal glands* opening into their cavities by ducts. The pharynx is often provided with teeth, jaws, or other hard structures for gripping prey. It may be projectable to the exterior either by direct muscular elongation, *protrusible* pharynx, or by turning inside out, *eversible* pharynx[1] (Fig. 11).

When the digestive tube following the pharynx is of similar form throughout its length, it is called simply *intestine*. Often, however, the

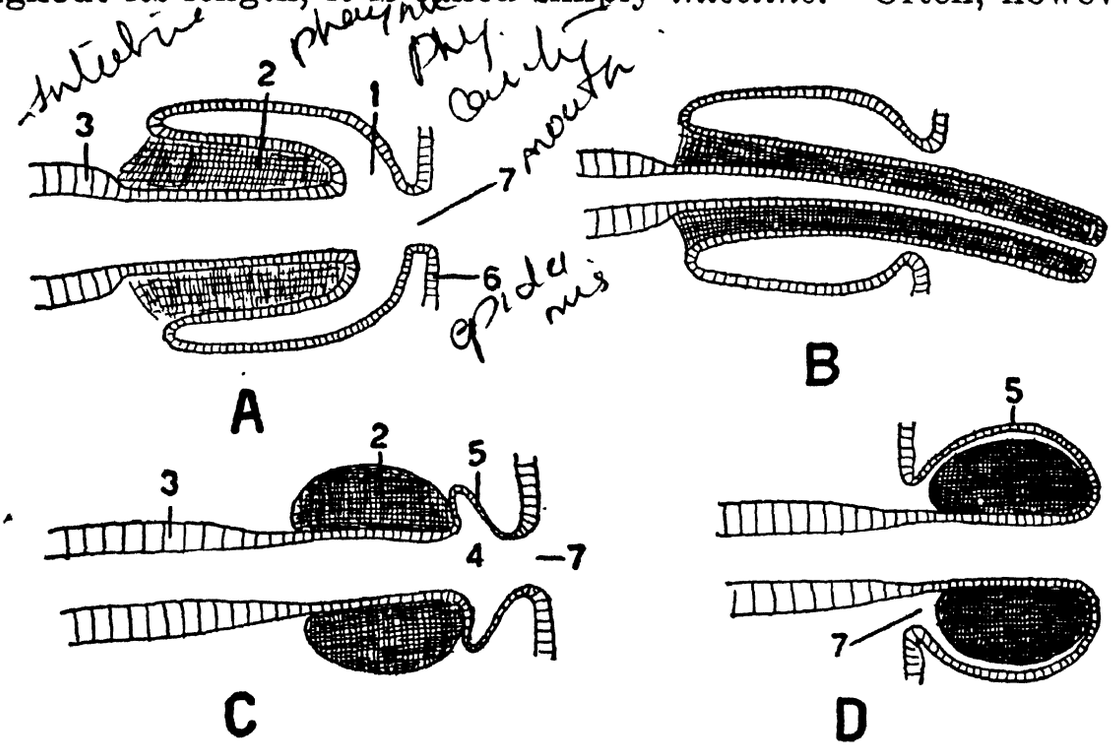

FIG. 11.—Diagrams of protrusible and eversible types of pharynx. *A*. Protrusible type at rest. *B*. Same, protruded by simple elongation. *C*. Eversible type at rest. *D*. Same everted by turning inside out of buccal capsule. 1, pharyngeal cavity; 2, pharynx; 3, intestine; 4, buccal cavity; 5, buccal capsule; 6, epidermis; 7, mouth.

pharynx is succeeded by a narrowed, scarcely muscular tube, the *esophagus*, and this leads to an enlarged region, the *stomach*. An expansion of the esophagus called *crop*, serving as a food reservoir, may precede the stomach. When the stomach is especially adapted for grinding food it is often called *gizzard*, but this term may be indiscriminately applied to any part of the digestive tract specialized for food grinding. Behind the stomach, the digestive tract continues to the anus as a narrowed tube, the *intestine*, which in invertebrates is not divisible into small and large intestine. The terminal portion of the intestine when different from the rest may be called *rectum*, and if it receives the urogenital ducts the term *cloaca* is applied. Large glands, here called simply *digestive glands*, open into the stomach in some invertebrates, particularly mollusks and crus-

[1] The protruded or eversed pharynx is often called *proboscis*, but this name is also used in so many other connections that it will be avoided here.

taceans. Any hollow diverticulum from the digestive tract is usually termed a *caecum* (plural, *caeca*).

7. Respiratory System.—Small animals with a soft epidermis can obtain sufficient respiratory exchange by diffusion through the surface. With increase in size or hardening of the surface, devices for securing a more rapid and greater exchange of respiratory gases are necessary. Such devices may be physiological, consisting of respiratory movements, such as body undulations, for wafting fresh water over the animal; but they are commonly morphological and then constitute a more or less developed respiratory system. The essential features of a respiratory organ are thin walls through which diffusion can take place readily and a large amount of surface exposed to the surrounding medium. Hence such an organ is a thin-walled structure, much folded, branched, or lobed to increase surface, and either evaginated to the outside or invaginated to the interior. The respiratory system consists of one to many such organs, often serially arranged. The evaginations are known as *gills* and in invertebrates are filamentous, lamellar, branched, or feathery structures composed of delicate thin integument enclosing a small amount of other tissue. Gills are adaptations for breathing oxygen dissolved in water and are therefore either freely exposed on the exterior of the animal or, if protected, are situated in the path of water currents. Animals with gills usually exhibit rhythmic respiratory movements or else have a mechanism for pumping water over the gills. Gills may occur in animals which lack a circulatory system and then serve simply to increase the amount of surface exposed to the water, but usually they are richly supplied with blood which conveys the respiratory gases to and from the gills. The chief invertebrates with gills are annelids, mollusks, and the lower arthropods. Invaginations into the interior are usually known as *lungs* and are adaptations for breathing air directly. Lungs are limited to air-breathing vertebrates; among invertebrates a structure analogous to the vertebrate lung occurs only in the pulmonate snails where it consists of a very vascular sac of invaginated integument. Unique among respiratory systems is the *tracheal* system of insects and some other arthropods composed of integument invaginated as a branching set of air tubes permeating the entire body. In this system air is brought directly to the body cells by the tracheal tubes, whereas in other respiratory systems the respiratory gases are conveyed to and from gills or lungs by way of a circulatory system. The tracheal system is an adaptation to aerial life, and air is pumped in and out of the tracheal tubes by respiratory movements; but the system can be utilized for aquatic life by means of tracheal gills, which are gills containing tracheal tubes instead of blood vessels. The tracheal system can also imitate lungs in the way of invaginated integumental sacs whose walls are liberally supplied with tracheae.

8. Circulatory System.—In the smaller and simpler invertebrates some degree of circulation of body fluids is undoubtedly brought about by general body movements and by ciliary currents. But as animals increase in size and complexity a definite circulatory system is needed to distribute the products of digestion throughout the body, to transport the respiratory gases to and from the respiratory system, and to convey the nongaseous metabolic wastes to the excretory organs. The *circulatory* or *blood-vascular* system consists of a set of branching tubes, the *blood vessels*, filled with a fluid, the *blood*, which carries food and oxygen to the body cells and takes away carbon dioxide and other metabolic end products. The blood must necessarily circulate, and this is accomplished by the specialization of part of the circulatory system as a contractile mechanism along which a wave of contraction runs at regular intervals forcing the blood in the direction of the wave. The blood thus makes a continuous circuit through the body returning to the starting point; as it passes through the gills or lungs it receives oxygen and gives up carbon dioxide; as it flows in the walls of the digestive tract it takes up the products of digestion; in the excretory system it gives up metabolic end products; and it brings food and oxygen to all the body cells, receiving from them metabolic wastes. The exchange of materials so far as known takes place by simple diffusion through the thin walls of the finer blood vessels (*capillaries*) or blood spaces (*sinuses*), or else the tissues are directly exposed to the blood.

In lower Bilateria, some of the blood vessels, particularly the middorsal vessel, serve as the contractile mechanism; but in the higher forms, a very muscular organ, the *heart*, is developed to propel the blood. In invertebrates the heart is situated in the middorsal line and represents a specialization of the middorsal blood vessel. As the heart must undergo vigorous contractions, it is always situated in a space which is commonly a portion of the coelom termed *pericardial cavity*. The heart may consist of one or two *auricles* which receive the returning blood and a muscular *ventricle* which pumps it out; but among invertebrates such division does not necessarily occur. *Accessory* hearts may be present. As in vertebrates, the vessels which carry the blood away from the heart are termed *arteries*, and those which return blood to the heart are called *veins*. Blood-containing spaces without definite walls are named *sinuses* when large or *lacunae* when small.

Among the invertebrates there are two types of circulatory system, the *closed* and the *open* or *lacunar* system. In the closed system the blood is always confined in definite blood vessels, tubes with definite walls. These vessels subdivide into finer and finer braches and ultimately into the microscopic *capillaries* which connect the arteries and veins and through which exchange of materials between the blood and the body cells

occurs. In the open system there are no small blood vessels or capillaries, but the arteries soon lose their walls and open out into lacunae and sinuses from which the blood slowly works its way into the open ends of veins. An open system is found in mollusks and arthropods in which groups the blood spaces have so expanded as to crowd the coelom almost out of existence. The organs of these animals thus lie directly in a blood-filled space, the *haemocoel*, while the true coelom is restricted to a few small cavities. This process of encroachment of the haemocoel on the coelom was first elucidated by Lankester (1888) who termed it *phlebedesis* (1900).

The fluid which is carried inside the blood vessels is termed the blood; it consists of a nutrient fluid, the *plasma* or *lymph*, and various kinds of free cells floating in the plasma. In invertebrate blood there are relatively few cells as compared with vertebrate blood, and these are mostly similar in appearance to vertebrate white blood corpuscles. Red cells similar to vertebrate red blood corpuscles occur in the blood of nemertines and in the coelomic fluid of sipunculids and some polychaetes, but in invertebrates the red coloring matter of the blood (when present) is usually free in the plasma, not contained in cells.

The blood usually contains a special oxygen-carrying substance which unites readily with oxygen when the oxygen pressure is high, as in the respiratory organ, and gives up oxygen readily when the oxygen pressure is low, as in the body cells. This substance is a chromoprotein (colored protein) containing a metal, usually iron or copper; the iron-containing protein is called *haemoglobin*, the copper-containing one, *haemocyanin*. These differ in chemical construction in different species, so that actually there are a vast number of haemoglobins and haemocyanins. Haemoglobins constitute the red coloring matter of vertebrate blood and in vertebrates are contained inside cells which are therefore called red blood corpuscles. The blood of a number of invertebrates contains a haemoglobin and is therefore red, but as stated above the haemoglobin is seldom contained in cells. Haemocyanins are bluish when loaded with oxygen; they are found in the blood of mollusks and crustaceans.

The fluid which fills body and tissue spaces outside of the circulatory system is called in invertebrates by various names, as *lymph*, *haemolymph*, and *coelomic fluid*. It will here be termed uniformly the lymph. In invertebrates this does not run in definite channels as in vertebrates; in short, there is no lymphatic system, but the lymph is undoubtedly moved about by body motions and ciliary action. The lymph contains various types of cells identical with those which occur in the blood of the same animal.

A high degree of correlation exists between the circulatory and respiratory systems. Where the respiratory organs are sharply localized, the

circulatory system is commonly well developed; and where the respiratory system is diffused throughout the body, as is the case with the tracheal system of insects, the circulatory system shows a marked retrogression.

9. Excretory System.—There are scarcely any more vexed questions in comparative anatomy than the homology of the excretory system in the various phyla and the relations of the excretory and genital ducts. No final decision can be reached on these matters at present.

The function of the excretory system is the regulation of water content and the elimination of unusable metabolic products, especially nitrogenous ones. The essential features of an excretory organ are therefore: a mechanism for filtering water, secretory cells for concentrating nitrogenous substances, and a means of producing a flow of the excretory fluid to the exterior. The last is usually ciliary. In general, excretory organs do not manufacture the substances in the excretory fluid; they obtain them from the lymph or blood. After decades of argument as to whether they separate these substances from the lymph or blood by physical means (such as diffusion) or by active secretory processes on the part of the cells of the excretory organ, it now appears that both processes are involved. There may be a resorption of water and other substances from the excretory fluid before it is discharged.

The morphological unit of the excretory system is a tubule, termed in invertebrates a *nephridial tubule* or more briefly a *nephridium*. This tubule consists of a single-layered epithelium, the cells of which possess special secretory powers. In invertebrates the nephridial tubules are discrete; in short, they are not massed together to form a kidney as they are in vertebrates. An invertebrate may have one to many pairs of nephridia; in coelomate segmented invertebrates there is theoretically one pair to each segment, but actually nephridia are nearly always lacking from some segments, especially the most anterior ones and the genital segments.

Leaving out of account the peculiar excretory tubules of insects (and some other arthropods) which are outgrowths of the digestive tract, there are in invertebrates two main kinds of nephridia, *protonephridia* with closed inner ends and *metanephridia* with open inner ends. There are further two kinds of protonephridia, those with *flame bulbs* and those with *solenocytes*. The phylogenetic relationship between the main kinds of nephridia constitutes one of the difficult questions already mentioned.

Protonephridia with flame bulbs (Fig. 12*A*) are branched tubules whose finer twigs are closed terminally by an apparatus here called a flame bulb. A flame bulb (Fig. 12*B*) is a cup-shaped mass of protoplasm bearing a tuft of cilia which projects into the cavity of the cup. The undulations of the ciliary tuft are suggestive of a flickering flame and create a water current moving distally in the tubule. Flame bulbs are

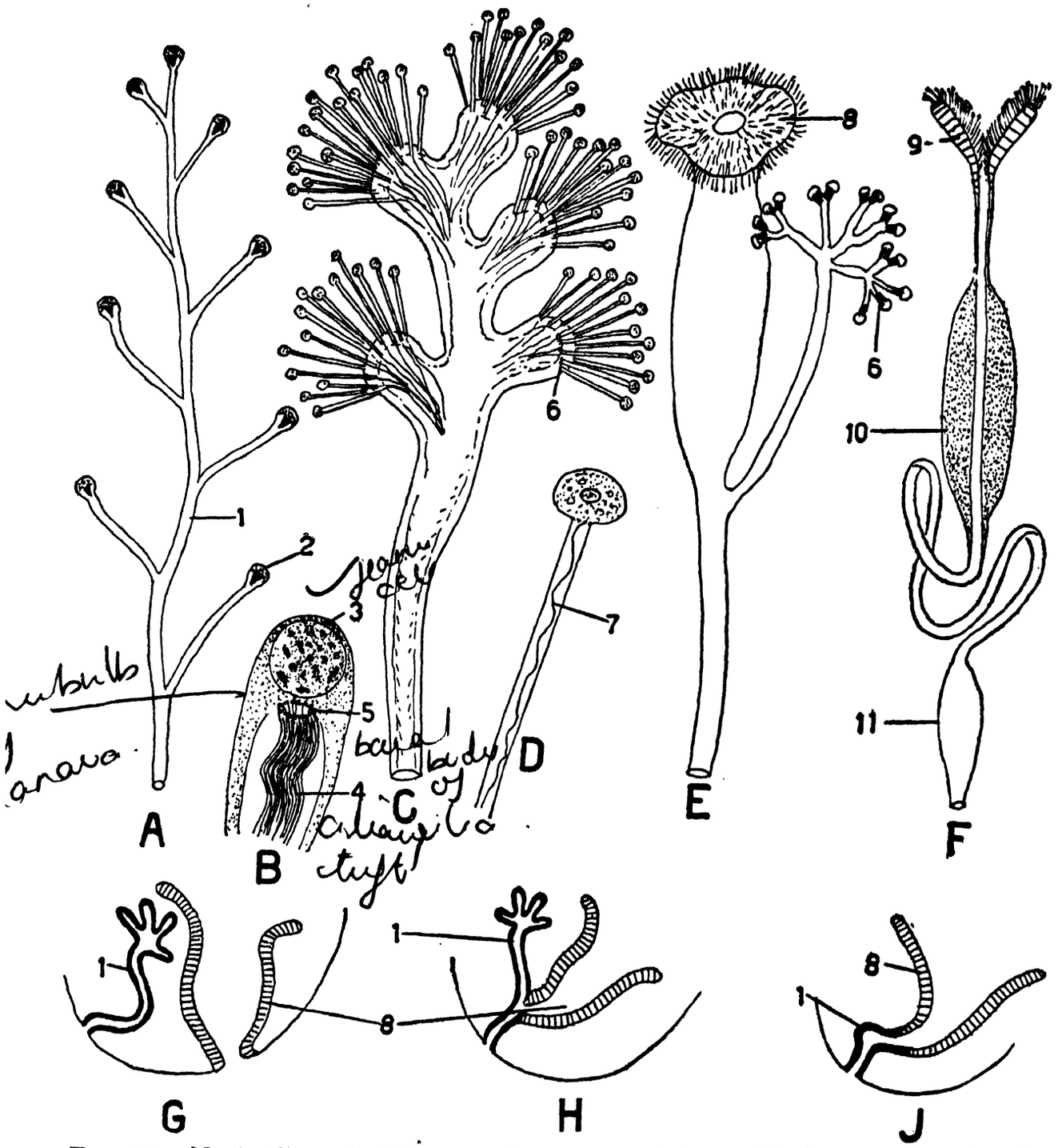

FIG. 12.—Nephridia. *A.* Diagram of a protonephrium with flame bulbs. *B.* Flame bulb of a planarian (*after Willey and Kirschner*, 1938). *C.* Scheme of a protonephridium with solenocytes. *D.* A solenocyte. *E.* A nephromixium, consisting of a gonostome attached to a protonephridium (*based on Goodrich*, 1900). *F.* Diagram of a metanephridium. *G–J*, Diagrams of the formation of a nephromixium simulating a metanephridium (*after Goodrich*, 1900). *G.* Primitive condition, coelomic cavity has a protonephridium and a gonostome. *H.* Gonostome has fused to the protonephridium. *J.* Part of the protonephridium has degenerated, leaving gonostome attached to protonephridial tube, and the whole simulates a metanephridium. 1, protonephridial tubule; 2, flame bulb; 3, flame cell; 4, ciliary tuft; 5, basal bodies of cilia; 6, cluster of solenocytes; 7, flagellum; 8, gonostome; 9, nephrostome; 10, glandular region; 11, bladder.

usually single cells and hence are usually called *flame cells;* but as cases are known in which one cell is subdivided into many flame bulbs and others in which the flame bulb is multinucleate, it seems best to abandon the term flame cell. Protonephridia with flame bulbs are general throughout the acoelomate and pseudocoelomate Bilateria, although not every group in these phyla possesses them, and their occurrence may be

taken to indicate some relationship, however remote, between these assemblages.

Protonephridia with solenocytes (Fig. 12*C*) are closed nephridial tubules which bear one or more cells termed solenocytes; these are long tubular cells with a long flagellum springing from the protoplasmic mass at the end of the tube and playing in the tube (Fig. 12*D*). Solenocytic protonephridia occur in the trochophore and related larvae and in the adults of kinorhynchs, priapulids, some polychaetes, and *Amphioxus*.

Metanephridia are nephridial tubules whose inner end opens into the coelom by way of a ciliated funnel, the *nephridiostome* or, more briefly, *nephrostome* (Fig. 12*F*). Metanephridia are necessarily limited to coelomate animals and are found throughout the coelomate Protostomia except insects and some other arthropods. The invertebrate Deuterostomia in general lack excretory organs.

Both protonephridia and metanephridia open to the exterior by one or more pores, the *nephridiopores*. The terminal portion of a nephridial tubule either with or without junction with its partner may enlarge to a contractile sac or *bladder*. It is not uncommon for the nephridial tubules to open into the digestive tract or the genital system, and in such cases separate nephridiopores are, of course, lacking.

The first question for consideration is the relationship of the two kinds of protonephridia. The development of protonephridia with flame bulbs is poorly known; the scanty available evidence indicates an ectodermal origin from cells of one of the first three quartets of micromeres. The development of protonephridia with solenocytes is not known in those invertebrates which possess them in the adult stage but has been followed by several authors in the trochophore larva. The archinephridia of the trochophore are in fact protonephridia with solenocytes (Fig. 4). These develop from ectoderm cells of the third quartet of micromeres (Shearer, 1911). As far as the evidence goes, therefore, the two kinds of protonephridia appear to be variants of the same organ. There is, in fact, little morphological distinction between them and types transitional between solenocytes and flame bulbs occur, as in gastrotrichs.

The second question is the relation of the protonephridia to the metanephridia. According to the classical and widely accepted view of Goodrich (1900), all types of invertebrate nephridia (except nephromixia, see below) are homologous and the nephrostome is merely the opened proximal end of a protonephridium. Thus the relation of the nephrostome to the coelom is secondary. An important part of the Goodrich theory, however, is that there are *genuine primary* coelomic funnels which alone merit the name *coelomostome* and that these connect to the exterior by genuine coelomic ducts or *coelomoducts*. Coelomostome plus coelomoduct constitute the *genital duct* of a coelomate invertebrate. It will be

perceived that this idea is a corollary of the gonocoel theory of the origin of the coelom. The Goodrich theory, strongly supported by Lankester, thus admits of but two kinds of ducts from a coelomic cavity, the nephridium and the gonoduct. The nephridium is of ectodermal origin, growing in from the exterior and secondarily connecting with the coelom; hence it is not of the nature of a coelomoduct. The gonoduct is of mesodermal origin, growing from the interior toward the exterior; and it is the true coelomoduct with a true coelomostome (gonostome). Since a coelomic cavity is an expanded gonad it can have but one coelomic duct, and this is the original gonoduct. So runs the Goodrich theory.

It was discovered by Goodrich (1897) and verified by A. Meyer (1926) that in some of the lower polychaetes provided with solenocytes, the coelomostome (= gonostome or genital funnel) may fuse with the protonephridial tubule, forming a *nephromixium* (Fig. 12*E*), which then has both excretory and genital functions. It was further found that the solenocytic part of this nephromixium may degenerate, so that a tubule provided with a coelomic funnel and hence indistinguishable from a metanephridium results (Fig. 12*G–J*). Consequently there seem to be among these few polychaetes two kinds of metanephridia, true ones with their own funnel, and compounded ones formed of the fusion of a coelomostome (genital funnel) with a protonephridial tubule. The existence of such nephromixia appears beyond question. The following argument will concern only true metanephridia.

The development of the metanephridia of the annelids has been investigated by a number of workers, but there is some conflict in their accounts. Recent findings are in accord with the old results of Bergh (1899) to the effect that the entire metanephridium including the nephrostome originates from a single cell, the nephridioblast. According to some workers (Penners, 1923; A. Meyer, 1929; Vanderbroeck, 1934), the nephridioblast is of entomesodermal origin, being a cell of the mesoderm band. The nephridioblast proliferates a cord of cells that hollows out to become the metanephridium and forms a connection with the exterior distally, a ciliated funnel proximally. These findings directly contradict the Goodrich theory and indicate that metanephridia are not homologous with protonephridia but a new development in coelomate Protostomia; further that metanephridia are just as truly coelomoducts as are the genital ducts.

In 1945, shortly before his death, Goodrich published an extensive review on the literature of the nephridia and genital ducts that had appeared since his 1896 article. In this review, he reiterated his original position, accepting the gonocoel theory wholeheartedly, and avowing the identity and ectodermal or ectomesodermal origin of both proto- and metanephridia. He agreed with the above findings on the embryology of

the metanephridia but refused to accept the nephridioblast as a cell of the mesoderm band. In support of his position on this point, he quoted mainly the work of Bahl (1922) on the development of the nephridia of the earthworm *Pheretima.* Bahl plainly showed that the nephridia of *Pheretima* arise from two enlarged ectodermal cells on each side that are still in an ectodermal position after the mesoderm bands have begun to form coelomic cavities. Later these nephridioblasts pass into the interior between the ectoderm and the mesoderm bands and proliferate the nephric bands.

It appears impossible at present to decide whether or not protonephridia and metanephridia are variants of the same organ and therefore whether or not metanephridia classify as coelomoducts. The gonocoel theory and its corollaries are, however, definitely rejected.

10. Reproductive System.—This system consists of the sex glands or gonads, their ducts, the *gonoducts,* and various accessory parts. The gonads are usually numerous and distributed throughout the body in primitive forms, reduced to a single, sharply localized pair, or even to a single gonad, through loss of the partner, in more specialized members of a group. The scattered condition of the gonads is often spoken of as *follicular,* but this term is not very fortunate as the word follicle is also employed to mean a developing egg encircled by nutritive cells. When both testes and ovaries occur in the same individual, separately or combined into one gonad, the condition is spoken of as *hermaphroditism;* when in different individuals, it is called *gonochorism* or *dioeciousness.* A hermaphroditic animal may appear dioecious from the circumstance that ovaries and testes develop at different times in the annual cycle. When the testes develop first, the animal is said to be *protandrous;* when the ovaries precede, the term *protogynous* is applied. Hermaphroditism appears to be more primitive than gonochorism and to be associated with a sessile, sedentary, or parasitic life. The maturing of the gonads in a larval or juvenile animal is spoken of as *neoteny.* The gonads of the Bilateria are of mesodermal origin; the sex cells come from mesenchyme cells or cells of the coelomic lining (but see also page 27).

The male gonad is termed *testis* (plural, *testes*) and consists in general of single or clustered vesicles or tubules in which the spermatozoa develop. The main male duct will be called uniformly the *sperm duct* (usual name, *vas deferens*), and the minute ducts that in forms with numerous scattered testes connect these with the main sperm duct will be called *sperm ductules* (usual name, *vasa efferentia*). An animal usually has one pair of sperm ducts, regardless of the number of testes; or one duct in case of a single testis. When the sperm ducts unite prior to exit, the resulting duct will be called *common sperm duct.* That part of the common sperm duct that traverses the copulatory apparatus may be called *ejaculatory duct.* A

part of the male system serving as a reservoir for ripe sperm is termed *seminal vesicle.* When this is merely an expansion of the sperm duct, it will here be called *spermiducal vesicle,* and the expression seminal vesicle will be reserved for a muscular tubular or sacciform chamber appended to the male ducts or interpolated in their course. The separate ducts or common sperm duct may open directly to the exterior by a male gonopore, as is usually the case in animals that shed their sperm into the water; but in many Protostomia the terminal part of the common sperm duct traverses a more or less complicated *copulatory apparatus* serving to transfer the sperm directly into the body of the female. The essential part of the male copulatory apparatus is a *penis* or *cirrus.* The term penis is here restricted to a conical or cylindrical muscular projection that in use is simply lengthened by muscular action so that it can be protruded through the gonopore. The term cirrus will here be applied to a temporary projection that is formed by the turning inside out of the ejaculatory duct. Both penis and cirrus may be armed with spines, thorns, etc.; or the penis may consist essentially of a hard spine, then termed *penis stylet.* Various glands, sacs, or tubules may be appended to the penis or cirrus, and the whole then constitutes the copulatory apparatus. These accessory structures usually secrete substances essential to the life and health of the sperm.

In the act of *copulation* (sexual union), the sperm are typically injected into the female system by the insertion of the penis or cirrus into the female gonopore or the common gonopore. In hermaphroditic animals, this process is generally mutual, i.e., each copulant injects sperm into the partner. Many invertebrates, however, lack a copulatory organ but nevertheless are able to transfer sperm into the female by various devices, some of them incredibly bizarre. Thus the male spider exudes his sperm into a groove on the modified terminal joint of his second pair of appendages and inserts this into the female orifice. Some invertebrates employ *hypodermic impregnation* in which sperm are injected through the epidermis anywhere. The sperm may be done up in packets termed *spermatophores* that are deposited in or on the female.

The female gonad is called *ovary* and its duct *oviduct.* There is but one pair of oviducts or one duct in case of a single ovary; the two oviducts may unite to a *common oviduct* before reaching the female gonopore. When the ovaries are numerous small *oviductules* connect them with the main oviducts. An enlarged more or less modified portion of the oviduct in which the eggs accumulate and in which they may undergo more or less development is called *uterus.* The uterus may also be a tube or sac attached to the female system. Sacs in which the sperm received from the male are stored are termed *seminal receptacles* or *spermathecæ;* they may be diverticula of the female system or have no direct connection

with it. When the seminal receptacle harbors the sperm for only a short time, soon passing them elsewhere, it is called *copulatory bursa* (*bursa copulatrix*). Various glands or glandular diverticula may be present along the oviducts, common oviduct, or antrum, serving to secrete protective layers and coats for the eggs or adhesive materials for fastening them to objects.

Male and female gonopores in hermaphroditic species may be separate, one behind the other in the mid-ventral line, or there may be a common gonopore. The gonoducts may also open into the digestive tract, either near the mouth or near the anus, and in such case there are no distinct gonopores. The final part of either male or female system may consist of a chamber, the *antrum* (or *atrium*), that in turn leads to the gonopore. Parts of the reproductive system may have special external pores, distinct from the regular gonopores.

The comparative anatomy of the gonoducts and their relation to the nephridia have already been touched upon. In the acoelomate and pseudocoelomate Bilateria, the gonoducts are in continuity with the gonads and appear to have no phylogenetic relationship to the gonoducts of the coelomate forms. The gonoducts of coelomate animals appear to be coelomoducts and in general are not directly connected to the gonads but open into the coelom by ciliated funnels (gonostomes). The genital coelomoducts seem to be phylogenetically distinct from metanephridia. Coelomate animals may, however, lack gonoducts and use the nephridia for the discharge of sex cells. Or, as already noted, the gonostome may fuse to the nephridial structure to form a nephromixium which serves both excretory and genital purposes.

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CHAPTER X

THE ACOELOMATE BILATERIA—PHYLUM PLATYHELMINTHES

I. HISTORICAL

The phylum Platyhelminthes has had a long and devious history, chiefly because of persistent and recurrent attempts, evident even at the present time, to unite all vermiform animals under a phylum Vermes. Since there are many kinds of worms of very different morphology, naturally no two authors could agree upon the groups to be included in the Vermes and their relational arrangement, and throughout the nineteenth century the number of arrangements published was about equal to the number of interested zoologists. An exhaustive history of these attempts is given by Pagenstecher and Braun, 1879–1893. In the author's opinion, a phylum Vermes is an impossible conception. The mere fact that an animal is vermiform, i.e., many times longer than wide, can obviously be of no phylogenetic or systematic significance. Vermiform shapes as adaptive types are to be found in almost every invertebrate phylum.

The parasitic flatworms naturally attracted attention from ancient times. There is mention of parasitic worms, some probably tapeworms, in an Egyptian papyrus, dating from 1550 B.C., and tapeworms and bladder worms are recorded by various ancient writers. Linnaeus in the first edition (1735) of his *Systema Naturae* founded the ill-starred phylum Vermes, into which he threw all invertebrates except insects. In the 10th edition (1758), which forms the basis of scientific nomenclature, he recognized five orders of Vermes: Intestina, Mollusca, Testacea, Lithophyta, and Zoophyta; flukes and planarians fell under Intestina, tapeworms under Zoophyta. Pallas in 1766 first recognized the cestode nature of bladder worms and O. F. Müller (1773) added a new order Infusoria, which was a mixture of protozoans, rotifers, cercariae, and microscopic nematodes. These improvements were incorporated by Linnaeus in the 13th edition (1788) of the *Systema Naturae*, in which Lithophyta and Zoophyta were combined under the latter name, tapeworms were placed under Intestina, and Infusoria was made the lowest order of Vermes with much the same content as given by Müller. Goeze (1787) added much to the knowledge of tapeworms and Zeder's 1800 edition of Goeze's work gave the first natural grouping of parasitic worms under the common names of roundworms, hooked worms, flukes, tapeworms, and bladder worms. For these same groups scientific names were created by Rudolphi (1808–1810), namely, Nematoidea, Acanthocephala, Trematoda, Cestoidea, and Cystica. Lamarck had a better understanding of animal relationships than most of his predecessors and contemporaries and began the separation of the annelids and noninsectan arthropods from the lower worms, creating the name Annelida (1809). Later (1816) he placed the various groups of flatworms together under the name Vers molasses or soft worms. Cuvier, following Lamarck's leads, eliminated the phylum Vermes, placing protozoans, coelenterates, echinoderms, and the parasitic worms under the Radiata or Zoophyta. Under Radiata, the group Intestinaux or Entozoa included roundworms, flatworms, acanthocephalans, and nemertines. As a result of Cuvier's prestige, the phylum Vermes was submerged for some years and the parasitic worms plus the free-living flatworms were generally termed Helminthes or Entozoa. In

1831, Ehrenberg created the name Turbellaria but had a poor conception of the group, including in it annelids, nematodes, nemertines, and various free-living flatworms. In 1835 he limited the name Turbellaria to be practically equivalent to the present group Rhabdocoela. Leuckart in 1848 combined the flatworms with nemertines and leeches under the name Apodes, which he later (1854) altered to Platodes. The greatest advance at this time was made by C. Vogt (1851), who correctly recognized the leeches as annelids, placed the nematodes, gordiaceans, acanthocephalans, and gregarines under the class Nematelmia, and the true flatworms plus the nemertines under the class Platyelmia. Gegenbaur (1859), following Vogt's lead, presented a similar arrangement but altered Vogt's names to the etymologically better forms, Platyelminthes and Nemathelminthes. Gegenbaur's Platyelminthes comprised three groups: Turbellaria (including nemertines), Trematoda, and Cestoda. Gegenbaur also revived the phylum Vermes, under which he included, in addition to the Platyelminthes, Annulata, Oestelminthes (Sagitta), and Nemathelminthes (nematodes, gordiaceans). Ehlers (1864) also recognized the phylum Vermes, which he considered to comprise the classes Annelida, Gephyrea, Nematoda, Nemertina, Turbellaria, Trematoda, Acanthocephala, and Cestoda. Here for the first time the nemertines were separated from the Turbellaria. This separation was recognized by most later authors so that the phylum Platyelminthes was considered to consist of four classes, Turbellaria, Trematoda, Cestoda, and Nemertina, an arrangement still widely employed. It remained for Minot (1876) to appreciate the many differences between the nemertines and the flatworms and to eliminate the former from the phylum, which he spelled Plathelminthes. Minot's conception of the phylum therefore corresponds with that adopted here, and hence the phylum is attributed to him. The etymologically correct form of the phylum name is Platyhelminthes, from the Greek *platys*, flat, and *helminthes*, worms; the spellings Platyelminthes, Plathelminthes, Platyelmia, and the recently proposed Platyhelmintha are not acceptable. Some other names sometimes used are Leuckart's Platodes and Haeckel's (1896) Platodaria, which latter has the advantage of being euphonious with Cnidaria; but as these authors had very poor conceptions of the scope and limitations of the phylum, their names should not be honored.

The phylum Platyhelminthes has had the attention of a long succession of distinguished zoologists. Pioneer work on the Turbellaria was done by such men as O. F. Müller, von Baer, Ehrenberg, and Oersted; but modern knowledge of this class (except Polycladida) is due almost entirely to the herculean labors of Ludwig von Graff, of the University of Graz, Austria. He has recorded his work in numerous papers and several large volumes, notably the two volumes on the Turbellaria in Bronn's *Klassen und Ordnungen des Tier-Reichs* (1904–1908, 1912–1917). Von Graff has been followed by a long succession of worthy students of the Turbellaria, many of them disciples of his; among them may be mentioned Arndt, Beauchamp, Beklemichev, Böhmig, Bresslau, Hofsten, Iijima, Kenk, Komarek, Luther, Meixner, Nasonov, Reisinger, Steinböck, Steinmann, Westblad, and J. Wilhelmi. Arnold Lang, in his famous monograph of the polyclads (1884), brought together and greatly enlarged our knowledge of this order: since then notable advances in this group have been made by Bock, Kaburaki, Kato, Palombi, and Stummer-Traunfels. The study of the parasitic flatworms owes its first clarification, as noted above, to Zeder and Rudolphi; through the nineteenth century there were numerous contributors in this field, of whom some of the more prominent were Braun, Cobbold, Diesing, Filippi, Kölliker, Leidy, Leuckart, Linstow, Looss, Lühe, Moniez, Monticelli, Pagenstecher, Pintner, von Siebold, Steenstrup, Stossich, Van Beneden, and Zschokke. Modern students of trematodes and cestodes are legion, and the study of these forms and their life cycles has con-

stituted one of the most active fields of zoological research in the United States under the leadership of such men as Chandler, Cort, Faust, Guberlet, Krull, La Rue, Linton, Stiles, Stunkard, and Ward. The outstanding modern account of the flatworms is that of Bresslau for the Turbellaria, and Fuhrmann for the Trematoda and Cestoda in the second volume of the *Handbuch der Zoologie*, and the present text owes much to this work. *The Trematoda* by Ben Dawes (1946) is very useful for the flukes.

II. CHARACTERS OF THE PHYLUM

1. Definition.—The Platyhelminthes or flatworms are dorsoventrally flattened Bilateria without coelom, definitive anus, circulatory, respiratory, or skeletal systems, with flame-bulb protonephridia, and with a connective tissue filling all spaces between organ-systems. More briefly, the Platyhelminthes are *acoelomate Bilateria without a definitive anus.*

2. General Characters.—This phylum stands at the bottom of the bilateral animals. It is characterized by a strongly marked bilateral symmetry accompanied by a greater or less degree of dorsoventral flattening and the differentiation of the anterior end as a head. The members of the phylum have a general worm-like appearance but vary from the typical moderately elongated flattened shape to the excessively long flat ribbons of the tapeworms as one extreme, and the broad leaf-like forms of some polyclads as the other extreme. The body is generally of simple contour, but bizarre shapes occur among the trematodes, and in the majority of tapeworms, the tape-like body is segmented, being divided up into squarish or rectangular segments, termed *proglottids*, which increase in size in the anteroposterior direction. In size the members of the phylum range from microscopic worms no larger than protozoans to the extreme elongation seen in tapeworms, amounting to as much as 10 to 15 m; but most flatworms are of small to moderate dimensions. The majority of flatworms are white or colorless or owe their color to ingested food; the free-living forms when not white are often brown, gray, or black; but bright colors and patterns are seen among the polyclads and the land planarians (Figs. 14*A*, 61*F*).

The anterior end may be set off as an easily recognizable head by a neck-like constriction but in the frequent absence of such a constriction is nevertheless organized as a definite head as shown by the presence therein of the main nervous center; by the numerous sensory organs which it bears, especially in the free-living members; and by its being directed forward in locomotion. In parasitic flatworms the head also usually bears organs of adhesion in the form of hooks and suckers, although these may also occur elsewhere on the body.

A ventral surface on which locomotion occurs and which also bears the mouth and genital pores is well differentiated among the turbellarians

but is less marked in trematodes and in cestodes is established only by arbitrary definitions.

Characteristic of the phylum is the presence of a great variety of adhesive secretions and of organs of adhesion and attachment. These begin in the free-living members as sticky secretions and adhesive papillae, patches, and cushions and reach their culmination in the muscular suckers and formidable hooks of flukes and tapeworms. Fully developed suckers are not, however, limited to parasitic forms but also occur among the fresh-water planarians.

In the class Turbellaria, the body is clothed with a cellular or syncytial one-layered epidermis, ciliated in whole or in part; but in the two parasitic classes, an epidermis is lacking and the body surface is formed of a secreted cuticle. Beneath the surface layer there is generally present a subepidermal musculature, of circular, longitudinal, and often also diagonal fibers. Muscle fibers also course through the mesenchyme and form an important constituent of the pharynx, the copulatory apparatus, and the adhesive structures. The muscle fibers are of the smooth type, although indications of cross striations occur.

The phylum lacks exo- and endoskeleton and therefore is characterized in general by a soft consistency. Hardened parts include the cuticle mentioned above and its differentiations such as surface spines and attachment hooks, further the hooks, spines, thorns, and teeth often borne by the male copulatory organ and also sometimes by other parts of the copulatory apparatus. These hardened parts were formerly considered to be of chitinous nature but are now known to consist of scleroproteins and will be spoken of as *cuticularized;* chitin is conspicuously absent from the phylum, being recorded in only two instances (see pages 144, 413).

All space between the various organ-systems is filled with a mesenchyme, usually called *parenchyma.* This solid construction, this lack of any internal cavity except the lumen of the digestive tract, is one of the most diagnostic characters of the phylum and constitutes what is here termed the *acoelomate* type of structure. It is true that small clefts or spaces may occur in the mesenchyme, especially in the Rhabdocoela, but these never fuse to form large cavities; they would appear to classify as pseudocoel, i.e., as remnants of the blastocoel, but there is considerable confusion of terminology in regard to them. The histological structure of the mesenchyme is a difficult question considered later.

The nervous system of the more primitive flatworms is directly derivable from that of cnidarians, consisting of an epidermal nerve net and a slight massing of nervous tissue representing a brain. In most flatworms, however, the nervous system has sunk to subepidermal and submuscular positions and the main (submuscular) nerve net shows concentration into several longitudinal ganglionated cords of which the two

ventral ones are often the most conspicuous or the only ones present. Thus a system primarily radial becomes bilateral by the elimination of some of the radiating cords. The main nervous center, or brain, located in the head, consists of a pair of conjoined swellings, the *cerebral ganglia*, or *brain*. Numerous transverse connections occur between the longitudinal cords; and when the latter are reduced to two, these two and their transverse connectives represent the first appearance among the Bilateria of the so-called *ladder* type of nervous system. However, in many cases flatworms which are stated to have but two longitudinal cords often actually possess others, which are so inconspicuous as to escape casual notice.

The Turbellaria are richly supplied with sensory organs, but these are greatly reduced in the parasitic classes. Chemo- and tangoreceptors are of wide distribution in the phylum. Statocysts occur in the orders Acoela and Alloeocoela and a few other forms. Ciliated pits and grooves which appear to be chemoreceptive at least in part are of common occurrence among the Turbellaria. Ocelli are found throughout the latter, also in larval and adult monogenetic trematodes, and in larval digenetic trematodes. They are mostly of the pigment-cup type with inverse retinal cells, and vary in number from two to hundreds.

A digestive system is totally absent in the turbellarian order Acoela and in the tapeworms; in other flatworms it resembles that of anthozoans and ctenophores, consisting of mouth, pharynx, and blind intestine. The mouth is primitively situated at about the center of the ventral surface but in various flatworms may occupy any position along the mid-ventral line. The pharynx, which presumably is of stomodaeal nature, shows great variation in the phylum; typically it is a strongly muscular tube, protrusible or not. The intestine also displays a wide variety of form, from a simple sac to complicated branchings; it rarely has one or more anal openings. It consists of a single-layered epithelium which has strong phagocytic and digestive powers.

Respiratory and circulatory systems are absent in the phylum, although some trematodes have a system of tubes of uncertain function which has been called a lymphatic system. An excretory system is of wide occurrence throughout the phylum, consisting of single or paired protonephridial tubules provided with flame bulbs and often entering a terminal contractile bladder. Protonephridia are absent in the Acoela and tend in general to be reduced in marine Turbellaria. Special cells known as *athrocytes* or *paranephrocytes* often accompany the protonephridia.

The Platyhelminthes are with very few exceptions hermaphroditic, and the reproductive system is usually of great complexity, contrasting strongly with the relative simplicity of the other organ-systems. This complexity has, however, evolved within the phylum, as the system is in

a primitive state in the Acoela, which lack definite gonads and oviducts. The gonads come from mesenchyme cells and are primitively numerous and scattered, eventually reduced to one or two. Not infrequently there are numerous testes but only one or two ovaries. Peculiar to the phylum is the separation of the female gonad into two structures, the ovaries proper and the yolk or vitelline glands. Whereas in other animals the ovary provides yolk for the eggs and this yolk is incorporated into the structure of the egg, in the majority of the Platyhelminthes (except Acoela, Polycladida, and a few other Turbellaria) the eggs are devoid of yolk, which instead is supplied by special yolk cells. These yolk cells are abortive eggs given off by the yolk or vitelline glands. They accompany the eggs, become incorporated with them inside the eggshell or capsule, and furnish food to the embryo during development. There is commonly present one pair of oviducts and one pair of sperm ducts, and these generally fuse distally to form common ducts. Despite their hermaphroditism, the flatworms generally practice cross-fertilization, and for this purpose a complicated copulatory apparatus is usually present. This consists in the male of a protrusible penis or eversible cirrus, either of which may be armed with spines, thorns, etc., and of various accompanying glands, as well as a single or paired vesicle for storing sperm. The female apparatus includes a sac, the seminal bursa or copulatory bursa or seminal receptacle, for storing sperm, and various glands associated with the formation of eggshells or the production of adhesive secretions for fastening the eggs after laying. In parasites, a long tubular or branched uterus in which large numbers of ripe eggs accumulate is often a conspicuous part of the female system. There may be a common gonopore or separate male and female pores, or the gonoducts may join the digestive tract and the sex products then exit through the mouth. Other types of genitointestinal connections are not uncommon (see below). In some flatworms there is present an extra female pore, the bursal or vaginal pore, which seems to serve for copulation only. The gonopores usually open on the ventral surface but are occasionally dorsal, mostly lateral in tapeworms. Multiplication of copulatory apparatus and also of gonopores is not uncommon in the phylum.

Internal fertilization obtains among the flatworms, and the fertilized shelled eggs, often already containing embryos, are shed to the exterior or fastened to objects by adhesive secretions. The embryonic development is generally greatly modified because, as mentioned above, the food supplies for the embryo are contained in separate cells, the yolk cells. Only in those groups which lack yolk glands, namely, the Acoela and the Polycladida, is the development of unmodified character. In these groups cleavage is of the spiral determinate type, resembling that of annelids and mollusks, with an entomesoderm derived from the 4*d* cell,

and the production of definite germ layers whose fate can be followed. In part of the polyclads, a free-swimming larva is produced which is supposed to foreshadow the trochophore and hence has been termed a *protrochula*. The development of other groups of flatworms is highly modified and proceeds without the formation of definite germ layers. The various organ-systems arise simply from masses of cells and consequently cannot be assigned to any particular germ layer, except on theoretical grounds. Peculiar to the classes Trematoda and Cestoda is the loss of the surface epithelium during development and to the Acoela and the Cestoda the failure of the entoderm to differentiate from the ento-mesodermal mass. Very complicated life histories with a succession of larval stages in one to three intermediate hosts characterize the Trematoda and Cestoda.

Asexual multiplication occurs in many fresh-water and land triclads by fragmentation or transverse fission without the formation of fission planes; and in two rhabdocoel families (Catenulidae and Microstomidae) and two fresh-water planarians by transverse fission preceded by the formation of fission planes dividing the animal into a chain of zooids. The larval stages of digenetic trematodes multiply by a process regarded by some as parthenogenesis, by others as polyembryony, and the larval stages of some tapeworms propagate by endogenous or exogenous budding.

The flatworms are either free-living or are ecto- or entocommensals or parasites. The free-living flatworms, comprising the class Turbellaria, live in fresh water, in springs, streams, ponds, and lakes; or in the ocean, chiefly along shores; or in moist terrestrial habitats, mostly in tropical or subtropical regions. Some few are commensal or parasitic. The classes Trematoda and Cestoda are wholly parasitic, chiefly entoparasitic; the adult stage parasitizes vertebrates with rare exceptions; the larval stages often occur in invertebrates. The hosts may be fresh-water, marine, or terrestrial animals.

The phylum as here understood is divided into the three classes Turbellaria, Trematoda, and Cestoda. These differ so much in anatomy and life history that a general presentation is not feasible, and hence the account of the phylum will proceed directly to a consideration of the three classes.

III. CLASSIFICATION OF THE PHYLUM

The usual disagreements exist among students of the Platyhelminthes as to the details of the classification, and in particular the classification of the Trematoda is in a very unsettled state.

Class I. Turbellaria, the free-living flatworms. Platyhelminthes clothed with a cellular or syncytial epidermis, usually ciliated at least in

part, usually provided with rhabdoids; body undivided; intestine present except in the Acoela; life cycles simple; mostly free-living, some ecto- or entocommensal or parasitic.

Order 1. Acoela. Small Turbellaria with mouth, pharynx simplex or none, no intestine; without protonephridia, oviducts, yolk glands or definitely delimited gonads; exclusively marine.

Order 2. Rhabdocoela.[1] Small Turbellaria with complete digestive tract; intestine sac-like, without evident diverticula; mostly with protonephridia and oviducts; gonads few, mostly compact; usually with cuticularized structures in place of soft penis papilla; nervous system mostly with two main longitudinal trunks.

Suborder 1. Notandropora or Catenulida. Rhabdocoela with simple pharynx, single median protonephridium, anterior dorsal male pore, single testis mass, unarmed penis; no yolk glands; asexual fission with formation of chains of zooids; exclusively fresh-water.

Suborder 2. Opisthandropora or Macrostomida. Rhabdocoels with simple pharynx, paired protonephridia, ventral male pore behind female pore, compact testes, penis armed with a stylet; no yolk glands; one of the two families forms chains of zooids; fresh-water or marine.

Suborder 3. Lecithophora or Neorhabdocoela. Rhabdocoels with bulbose pharynx, paired protonephridia, ventral gonopores, germovitellaria, or separate ovaries and yolk glands; reproduction exclusively sexual; fresh-water, marine, or terrestrial, mostly free-living, some commensal or parasitic.

Section 1. Dalyellioida. Lecithophora without a proboscis, pharynx of the doliiform type, mouth at anterior tip or nearly so; gonopore single; without rhammite tracts.

Section 2. Typhloplanoida. Lecithophora without a proboscis, pharynx usually of the rosulate type, mouth ventral back from anterior tip; with one or two gonopores; often with rhammite tracts.

Section 3. Kalyptorhynchia. Lecithophora with a protrusible or eversible proboscis in a sheath at the anterior end; pharynx of the rosulate type; without rhammite tracts.

Suborder 4. Temnocephalida. Ectocommensal fresh-water rhabdocoels, devoid of cilia or but slightly ciliated, anterior end extended into 2 to 12 tentacles, posterior end with one or two adhesive disks, pharynx doliiform, gonopore single.

Order 3. Alloeocoela. Small Turbellaria with simple, bulbose, or plicate pharynx; intestine may have short diverticula; protonephridia paired, often with more than one main branch and nephridiopore; testes generally numerous; penis papilla usually present; nervous system with

[1] Formerly the Rhabdocoela and Alloeocoela were often united under the name Rhabdocoelida, but this is no longer customary.

three or four pairs of longitudinal trunks; mostly marine, a few in fresh water.

Suborder 1. Archoophora. Alloeocoels with plicate pharynx and very primitive female system, as in Acoela; one species, marine.

Suborder 2. Lecithoepitheliata. Alloeocoels without typical yolk glands; may have nutritive cells embracing the ova; simple or bulbose pharynx; male apparatus generally with a cuticular stylet; marine, fresh-water, or terrestrial.

Suborder 3. Cumulata or Holocoela. Alloeocoels with germovitellaria or with separate ovaries and yolk glands; bulbose or plicate pharynx; intestine mostly without diverticula; male apparatus mostly unarmed; marine or fresh-water.

Suborder 4. Seriata. Alloeocoels with plicate pharynx and separate ovaries and yolk glands; intestine usually has lateral diverticula; mostly with statocysts; mostly marine, some in fresh water.

Order 4. Tricladida. Larger Turbellaria of elongated form, often very elongated; with plicate pharynx, usually directed backward; intestine with three highly diverticulated branches, one forward, two backward; with one pair of ovaries, two to numerous testes; with yolk glands; female apparatus usually with a bursa (sometimes two), male apparatus with a penis papilla; single gonopore; marine, fresh-water, or terrestrial.

Suborder 1. Maricola or Retrobursalia. With two eyes; bursa when present behind the penis or else with separate pore, may be paired; sexual reproduction only; exclusively marine or brackish.

Suborder 2. Paludicola or Probursalia. With two to many eyes, or eyeless; bursa nearly always present, anterior to the penis, connected with common antrum by a long bursal canal; often with asexual reproduction; fresh-water, sometimes brackish.

Suborder 3. Terricola. With two to many eyes, body mostly elongated; bursa mostly absent, when present behind the penis and may have bursal pore to exterior; usually marked separation of male and female antra; may have asexual reproduction; terrestrial in humid habitats, mostly tropical or subtropical.

Order 5. Polycladida. Larger Turbellaria, mostly of broad flattened form, but some elongated; plicate pharynx opens into a main intestine from which numerous branches radiate to the periphery; nervous system with numerous radiating nerve cords; eyes numerous, more than two (a few eyeless species); ovaries and testes numerous and scattered; without yolk glands; with one or two gonopores; male pore, when separate, anterior to the female pore; almost exclusively marine.

Suborder 1. Acotylea. Polyclads without a sucker behind the female pore; tentacles when present of the nuchal type; eyes not in paired clusters on the anterior margin.

end with an adhesive disk usually provided with hooks; excretory pores paired, anterior, dorsal; uterus short to moderate containing few eggs; ecto- or entoparasites with a simple life cycle and no alternation of hosts.

Suborder 1. Monopisthocotylea. Ectoparasitic monogenetic trematodes in which the posterior adhesive organ is single, although it may be subdivided by septa.

Suborder 2. Polyopisthocotylea. Ecto- or entoparasitic monogenetic trematodes with a large posterior adhesive organ bearing several to many suckers and usually also hooks.

Order 2. Aspidobothria or Aspidocotylea. Oral sucker absent; anterior end without paired adhesive structures; with an enormous ventral sucker subdivided into compartments or with a ventral row of suckers; no hooks; single nephridiopore, posterior; entoparasites with simple life cycle and no alternation of hosts.

Order 3. Malacocotylea or Digenea. Mostly with two suckers, an anterior sucker that generally encircles the mouth and a ventral sucker, but either or both may be reduced or wanting; no hooks; single excretory pore; uterus usually a relatively long tube containing many capsules; entoparasites with a complicated life cycle and several larval stages occupying one or more intermediate hosts.

The classification of the Digenea is at the present time in a state of great confusion. An arrangement based on the suckers has been strongly supported by Faust (1932) and has been widely promulgated in textbooks but, as repeatedly pointed out in the following text, the number and location of the suckers are not reliable taxonomic characters. The arrangement of the flame bulbs has also been repeatedly urged by Faust and others as a basis for classification but appears less reliable than formerly supposed. It has therefore been thought best in the present state of knowledge to omit any grouping of the Digenea into suborders or sections and to consider them only by family names. Probably the classification proposed by Poche (1926) is the best at present available. There appears to be a general agreement that those families in which the miracidia have two pairs of flame bulbs are related and the group so formed is usually called Strigeata. Other attempted family groupings have failed to meet with general approval from students of the Digenea.

Class III. Cestoda, the tapeworms. Entoparasitic Platyhelminthes without an epidermis, rhabdoids, or external cilia; body clothed with a cuticle and usually divided into a few to many segments, although sometimes undivided; adhesive structures limited to the anterior end except in Cestodaria; mouth and digestive tract wholly wanting; each segment with one or two complete hermaphroditic reproductive systems; embryo hooked; life cycle complicated, usually involving two or more hosts; majority inhabiting the intestine of vertebrates.

Subclass 1. Cestodaria. Tapeworms with undivided body, no scolex, one set of reproductive organs, and 10-hooked larva.

Order 1. Amphilinidea. With a protrusible proboscis and frontal glands at the anterior end; uterus traverses body length three times, opening near anterior end; male and vaginal pores posterior.

Order 2. Gyrocotylidea. Anterior end with eversible proboscis; posterior end with adhesive ruffle; uterus runs directly to pore; uterine, male, and vaginal pores together in anterior half.

Subclass 2. Eucestoda. Body usually very elongated and ribbon-like, divided into a few to many segments, but sometimes undivided; anterior end generally expanded into a scolex bearing adhesive organs; generally with more than one set of reproductive organs; larva six-hooked.

Order 1. Tetraphyllidea or Phyllobothrioidea. Segmented tapeworms with a scolex bearing four bothridia, often armed with hooks or subdivided by septa; intestine of elasmobranch fishes.

Order 2. Lecanicephaloidea. Segmented tapeworms with scolex bearing four acetabula; yolk glands numerous; reproductive system as in Tetraphyllidea; in intestine of elasmobranchs.

Order 3. Proteocephaloidea. Segmented tapeworms with scolex provided with four acetabula and an apical sucker or glandular organ; otherwise as in Tetraphyllidea; in the intestine of fish, amphibians, and reptiles.

Order 4. Diphyllidea. Segmented tapeworms of not more than 20 segments with scolex provided with two bothria and a spiny head stalk; in intestine of elasmobranchs; contains only the genus *Echinobothrium*.

Order 5. Trypanorhyncha or Tetrarhynchoidea. Segmented tapeworms with a scolex provided with four bothria and four protrusible spiny proboscides; parasitic in fishes.

Order 6. Pseudophyllidea or Bothriocephaloidea. Segmented or unsegmented tapeworms with a scolex provided with two to six shallow bothria, or sometimes without adhesive organs; yolk glands numerous; in intestine of all classes of vertebrates.

Order 7. Nippotaeniidea. Segmented tapeworms with a scolex having an apical sucker but no other adhesive structures; yolk gland single; excretory system of numerous longitudinal vessels; in intestine of fishes.

Order 8. Taenioidea or Cyclophyllidea. Segmented tapeworms with a scolex bearing four acetabula, also often provided with an apical rostellum armed with hooks; yolk gland single, compact; excretory system of four longitudinal canals; mostly in the intestine of birds and mammals.

Order 9. Aporidea. Unsegmented tapeworms with a scolex provided with four acetabula and an armed rostellum; excretory system

as in Taenioidea; devoid of sex ducts, sex pores, and distinct yolk glands; follicles of germovitellaria become uterine capsules; contains only the genera *Nematoparataenia* and *Gastrotaenia*, in swans.

IV. CLASS TURBELLARIA

1. Definition.—The Turbellaria are mostly free-living, sometimes commensal or parasitic, unsegmented flatworms with simple life cycles, clothed with a cellular or syncytial epidermis, which is usually ciliated, at least in part, and is usually provided with rhabdoids.

2. External Features.—The Turbellaria are on the whole rather small animals, and the majority are less than 5 mm. in length, many being of microscopic dimensions. Larger forms are limited to the orders Tricladida and Polycladida; the land planarians may reach 50 cm. or more in length, and the polyclads are usually of considerable size. The body shape is typically vermiform, i.e., several times longer than wide, and this shape obtains among the smaller forms. The larger types vary on the one hand to the long slender shape common among land planarians (Fig. 14*D*) and on the other to the leaf-like oval to almost circular forms seen among polyclads. The body is mostly dorsoventrally flattened, usually strongly so in triclads and polyclads, but many forms are cylindroid. The ventral surface is generally flat, the dorsal convex, often greatly so. The body contour is generally simple, mostly wider in the middle and tapering to one or both ends, or broadest at one end and tapering toward the other. In some species of the acoel genus *Convoluta*, the sides of the body are held curved ventrally (Fig. 13*B*). There are usually no projections, but the acoel genera *Amphiscolops* (Fig. 13*D*) and *Polychoerus* (Fig. 13*E*) have two caudal lobes, the latter and some sand-dwelling rhabdocoels have a little tail filament, and tentacles are not uncommon. Thus a pair of tentacles occurs at the anterior end of the alloeocoel *Vorticeros* (Fig. 14*C*), and many polyclads bear a pair of tentacles, either as *nuchal* tentacles on the dorsal surface near the brain (Fig. 63*B*) or as *marginal* tentacles formed by a pair of folds of the anterior margin (Fig. 14*B*). The presence of 2 to 12 pointed tentacles at the anterior end or in one genus also along the body sides is characteristic of the suborder Temnocephalida (Figs. 57, 58). In some polyclads the dorsal surface is covered with tubercles or papillae (Fig. 15*A*), and in the genus *Thysanozoon* there is an intestinal branch inside each papilla. *Adhesive organs* (see below) are of common occurrence among the Turbellaria and may constitute conspicuous external features. In some fresh-water planarians the head bears delicate lateral projections, known as *auricles*, which carry numerous sensory cells (Fig. 15*B*).

The anterior end may be set off as an obvious head by a neck-like constriction, notably in fresh-water planarians of the genus *Dugesia*

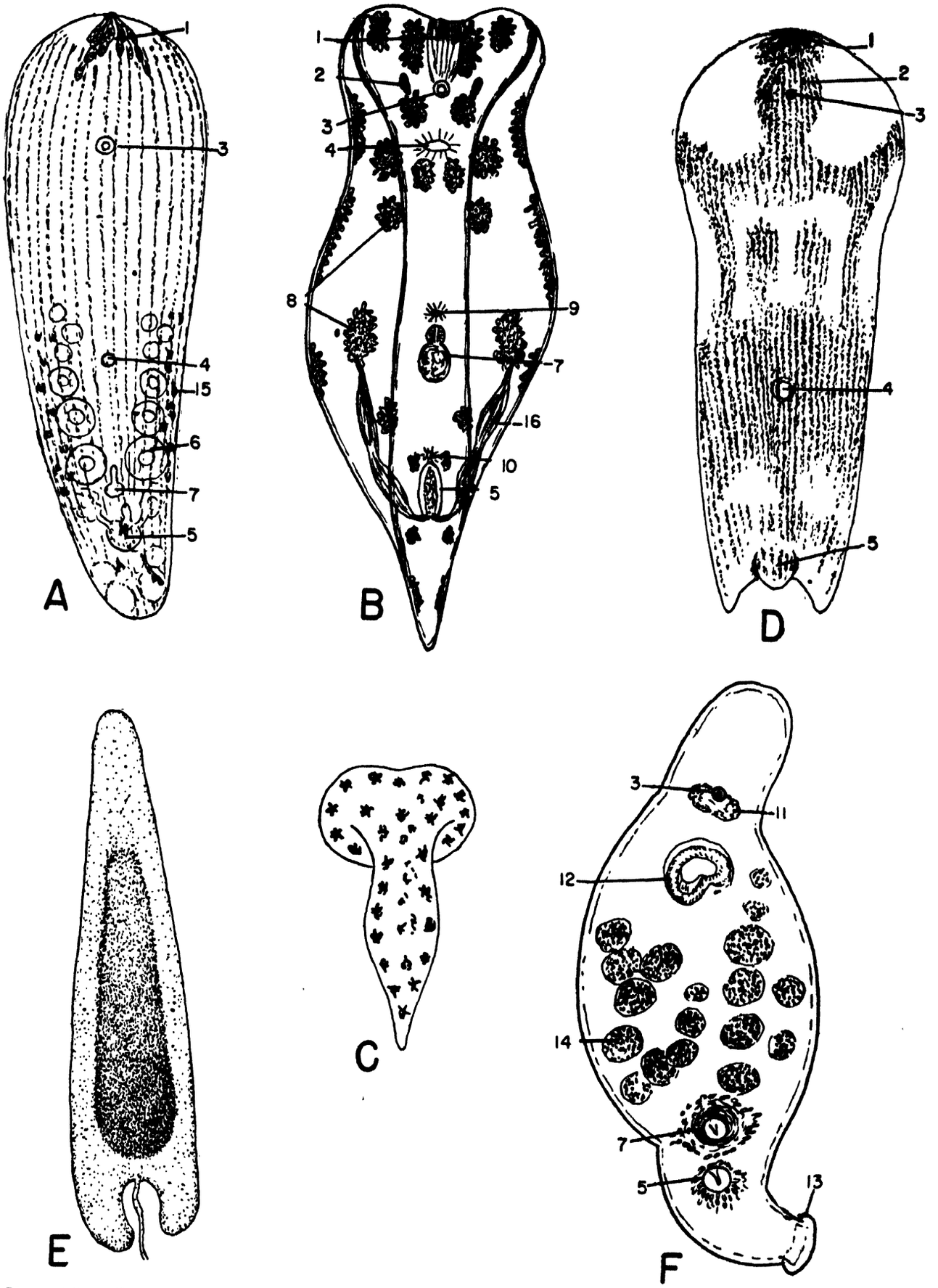

FIG. 13.—Some representatives of the Acoela. *A*. Typical acoel, from life, California. *B–F*, less usual shapes. *B*. *Convoluta*, with curved sides and pigment cells (*after Graff*, 1904). *C*. Same, crawling (*after Graff*, 1904). *D*. *Amphiscolops bermudensis*, from life, Bermuda, showing caudal lobes and pattern of concrement granules. *E*. *Polychoerus carmelensis*, from life, California, with caudal lobes and tail filament. *F*. *Ectocotyla paguri*, ectocommensal on hermit crabs, Maine, with plicate pharynx and caudal adhesive disk (*from sketches and specimens courtesy of Dr. E. G. Reinhard*). 1, frontal glands; 2, eyes; 3, statocyst; 4, mouth; 5, penis; 6, strands of eggs; 7, seminal bursa; 8, pigment cells; 9, female pore; 10, male pore; 11, brain; 12, pharynx; 13, caudal adhesive disk; 14, embryos; 15, strands of sperm; 16, sperm ducts.

(= *Euplanaria*) and in land planarians of the genus *Bipalium* (Figs. 14*D*, 15*B*). Usually, however, there is no such constriction, and often in fact the head end may be the narrowest part of the body. The head is always recognizable by being directed forward, by the presence of eyes and other sense organs, and by the accumulation of nervous tissue within. Among the sensory organs borne by the head are tentacles, auricles, eyes, ciliated pits and grooves, and sensory hairs, spines, and bristles.

The Turbellaria, especially the smaller forms, when not translucent or white, are generally of sober coloration, mostly brown, gray, or black. However, brilliant colors and striped, barred, and flecked patterns occur among the larger members, especially the land planarians and the polyclads (Fig. 14*A*). In the former, white, yellow, or orange stripes on a dark ground or vice versa are common (Fig. 61*F*). Frequently forms really white or transparent appear to be colored from the ingestion of colored food. The intrinsic coloration is generally caused by pigment granules or rods located in or beneath the epidermis, or by dissolved pigment in these locations.

3. Epidermis.—The Turbellaria are clothed with a one-layered epidermis (Figs. 16, 17*C*) which varies from a flat to a columnar form, being generally cuboidal, and also varies in thickness in different body regions; usually the dorsal epidermis is taller than the ventral; and often also the body margins, including the two ends, have an especially tall epidermis. The epidermis is generally ciliated, completely so in most members, especially the smaller forms, but not infrequently the dorsal surface lacks cilia, as in the case in the marine and fresh-water planarians; the ciliation also tends to degenerate in commensal and sand-dwelling forms. The Temnocephalida, a group that leads an ectocommensal existence, are mostly devoid of cilia. Cilia are also absent from glandular and adhesive areas but may be especially developed on sensory areas, acting to bring water currents to the sensory endings. The cilia may vary in length in different body regions, and the ventral cilia are often longer than the dorsal ones, being of greater importance in locomotion. In many land planarians, especially those of cylindroid shape, the ventral surface bears a special median strip, ridge, or group of ridges, termed the *creeping sole*, on which the animal glides and which is provided with especially powerful and closely placed cilia (Figs. 14*D*, 16*E*). The cilia are provided with basal bodies, have roots extending into the epidermis, and appear to be interconnected by a fibrillar system similar to that of ciliate Protozoa (P–C, page 167).

The epidermis is devoid of any secreted protective layer or structures, such as a cuticle, as this would be incompatible with ciliation. However, the nonciliated Temnocephalida have a clear structureless border resem-

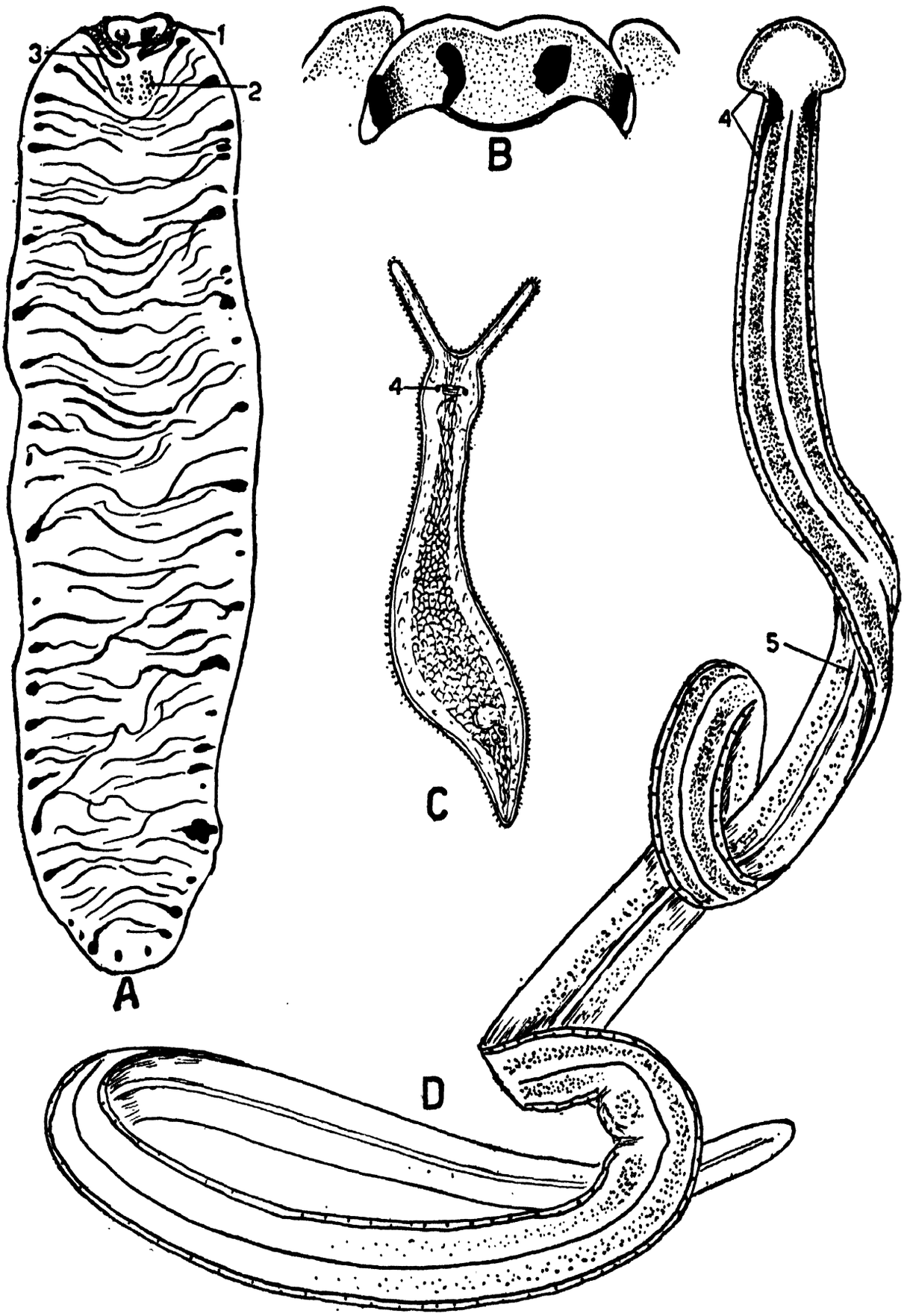

FIG. 14.—Various Turbellaria. *A*. Cotylean polyclad, *Pseudoceros crozieri*, from life, Bermuda, with marginal tentacles and pattern of black bars on a greenish ground. *B*. Anterior end of same, to show marginal type of tentacle. *C*. Plagiostomid alloeocoel, *Vorticeros*, only alloeocoel with tentacles, European Coast (*after Schmidt*, 1852); has red central net-like pigment. *D*. *Bipalium kewense*, cosmopolitan land planarian, found in greenhouses and outdoors in Florida, Louisiana, and California, 20 to 35 cm, long, has expanded head, three narrow and two broad purple to black stripes on a yellow, olive, or gray ground; dark pigment areas at the "neck" are distinctive; note creeping sole and numerous eyes on head margin and in row along body margin. 1, tentacular eyes; 2, cerebral eyes; 3, marginal tentacles; 4, eyes; 5, creeping sole.

bling a cuticle, and the polyclad genus *Enantia* has spines along the body margin (Fig. 17*A*). Each spine begins as a secretion over an epidermal papilla and is later broadened by columns secreted by adjacent cells (Fig. 17*B*). The chemical nature of these spines is unknown, but they are presumably scleroprotein.

The epidermis may be cellular and usually is so in the larger forms, the triclads and polyclads; it then consists of polygonal or prismatic cells, cuboidal to columnar (Figs. 16, 17*C*), often narrowed basally. Not infrequently, however, the epidermis is syncytial or partly so, especially among the Acoela, Rhabdocoela, and Alloeocoela (Fig. 16*C*). Further it may exhibit a peculiar condition termed *insunk* ("eingesenkt" by German writers), in which the nuclei accompanied by some cytoplasm have descended into the mesenchyme internal to the subepidermal musculature (Fig. 16*E*). In such cases the epidermis appears as a flat almost structureless layer devoid of nuclei. An insunk epidermis is seen in many Acoela and Alloeocoela, in the Bdellouridae, a family of marine triclads, and in the creeping sole of land planarians of the family Bipaliidae (Fig. 16*E*). The epidermis may contain fluid-filled spaces that divide the syncytial cytoplasm into vertical strands or columns; this condition is often seen in the Acoela (Fig. 16*C*). Often, too, the epidermis contains large oval gland cells secreting a mucous substance and opening at the surface between the bases of the cilia (Fig. 16*D*). Other types of gland cells may also occur sparingly in the epidermis, but in general the gland cells of Turbellaria are situated in the mesenchyme and only their necks traverse the epidermis. Various types of sensory cells (discussed later) also occur in the epidermis; the participation of the epidermis in adhesive structures is also considered later.

Very characteristic of the epidermis of the Turbellaria are bodies known as *rhabdoids*. The most common of these are the *rhabdites*, straight or slightly curved rods shorter than the height of the epidermis (Fig. 17*D*). They occur singly or grouped into bundles, oriented with their long axis at right angles to the surface, and are often so numerous as to obscure the structure of the epidermis (Fig. 16*A*). Rhabdites are secreted by gland cells (Fig. 16*A*) located either in the epidermis or in the mesenchyme; if the former, they are termed *epidermal* rhabdites, if the latter, *adenal* rhabdites. Rhabdites are frequently more numerous dorsally and along the body margins or body ends than ventrally (Figs. 16*A*, *B*) and are also usually longer in such locations. A second, less common type of rhabdoid is the *rhammite* (Fig. 17*F*), long, slender, and often sinuous, longer than the height of the epidermis. Rhammites are always adenal, and in some rhabdocoels there are two anterior groups of rhammite-forming glands, so that the rhammites traveling to the anterior margin along the necks of these gland cells form two conspicuous "rod

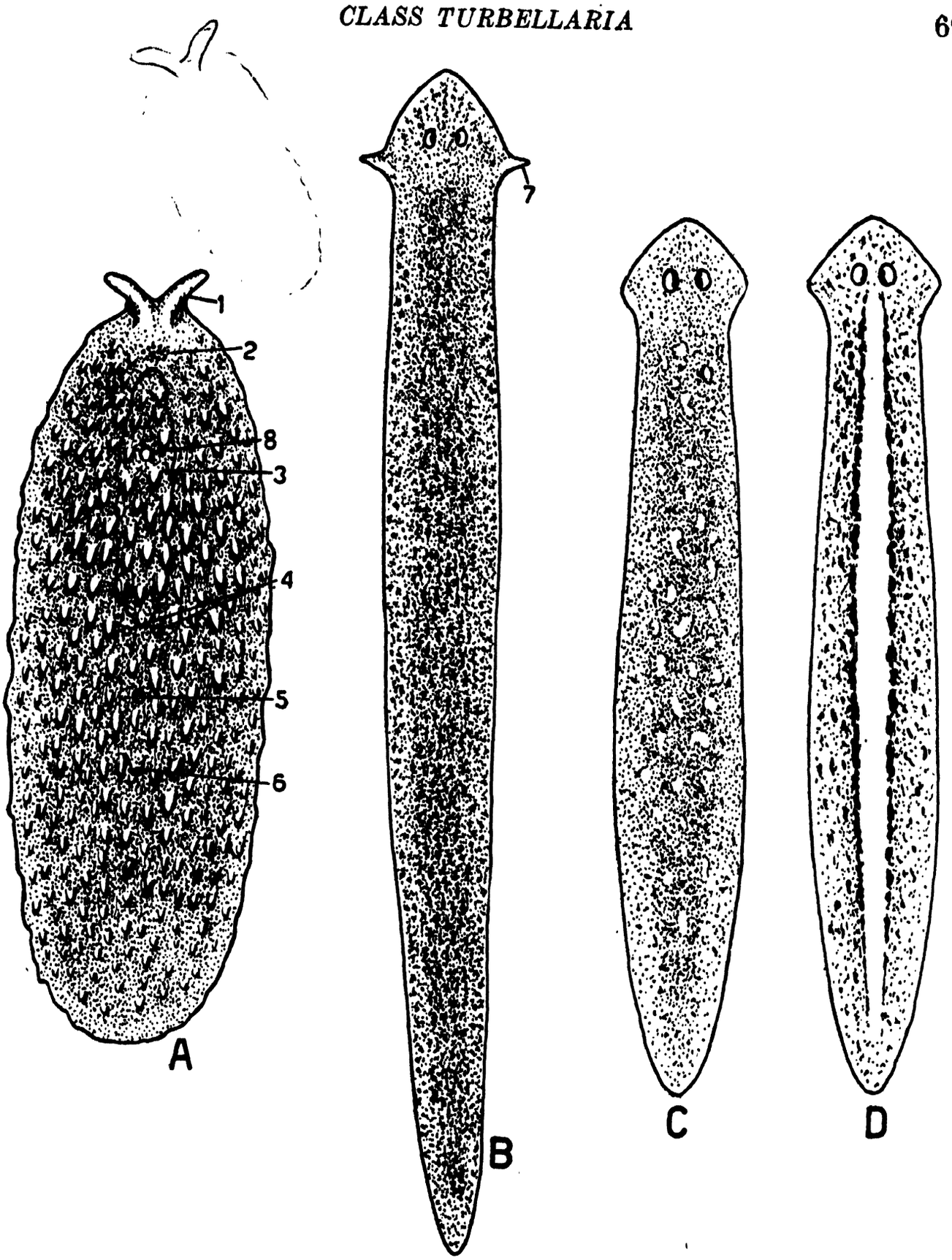

FIG. 15.—Types of Turbellaria. *A*. Cotylean polyclad, *Thysanozoon nigrum*, from life, Bermuda, black, with marginal tentacles, dorsal papillae, and double male apparatus. *B–D*, fresh-water planarians of the genus *Dugesia* with triangular head and definite auricles, from life. *B. Dugesia dorotocephala*, common United States planarian, dark brown to black, to 30 mm. long, may have light middorsal stripe, found in springs. *C, D*. Color variants of *Dugesia tigrina* (= *Planaria maculata*), most common United States planarian, brown, 10 to 20 mm. long, found in ponds, lakes, and streams. 1, marginal tentacles; 2, cerebral eyes; 3, outline of ruffled pharynx; 4, double male pores; 5, female pore; 6, adhesive disk ("sucker"); 7, auricles; 8, mouth.

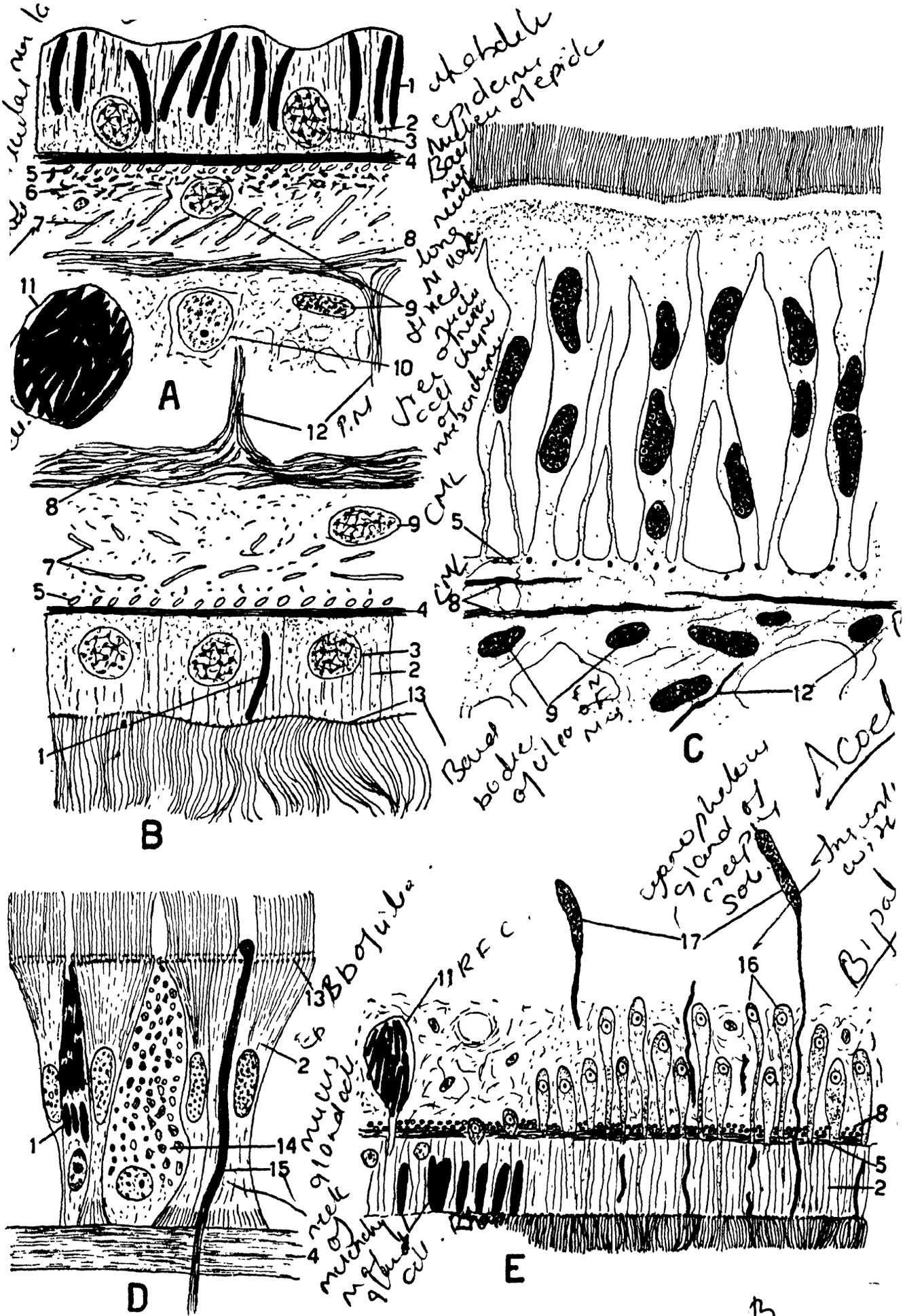

FIG. 16.—Structure of the epidermis. *A*. Longitudinal section through the dorsal epidermis of a fresh-water planarian, showing also the subepidermal musculature. *B*. Same through the ventral epidermis; note ciliation, paucity of rhabdites. *C*. Longitudinal section through the epidermis of an acoel (*after An der Laan*, 1935–1936). *D*. Section through the epidermis of a polyclad (*after Bock*, 1913). *E*. Cross section through the creeping sole of the land planarian *Bipalium*, showing insunk type of epidermis; at left

tracks." A third kind of rhabdoid, limited to land planarians, is the chondrocyst (Fig. 17*G*), merely an especially large rhabdite of somewhat granular texture. Rhabdoids in general consist of a hull enclosing material of more fluid consistency. Rhabdoid-secreting cells belong to the general category of eosinophilous glands (see below). Rhabdoids are absent in many Acoela, some of the more primitive Rhabdocoela and Alloeocoela, sand-dwelling Rhabdocoela, and in parasitic and commensal Turbellaria generally; also on glandular and sensory areas and on the creeping sole of land planarians. Polyclads mostly lack adenal rhabdoids. Two other kinds of epidermal inclusions that appear related to rhabdoids are *pseudorhabdites,* indefinite masses of slimy secretion inside epidermal cells, found commonly in polyclads and alloeocoels, occasionally in rhabdocoels; and *sagittocysts,* pointed vesicles containing a central protrusible rod or needle (Fig. 17*E*), limited to certain Acoela.

Little is definitely known of the nature or function of rhabdoids. According to Prenant (1919) rhabdoids are formed by nuclear breakdown, consist of a calcium nucleoproteinate, and are useless excreta en route to elimination through the surface. This last view appears incompatible with the general occurrence throughout the Turbellaria of special rhabdoid-forming gland cells. The usual belief is that rhabdoids on discharge to the exterior disintegrate to form a slimy or adhesive hull about the animal that protects it from enemies or adverse conditions, participates in cyst formation, and may have some toxic action on prey. However, definite proof of these statements is lacking. It is a fact that extensive discharge of rhabdites occurs when turbellarians are put into harmful solutions; but such discharge might be the incidental result of the convulsive contractions induced under those circumstances.

Nematocysts are found in the epidermis of a few Turbellaria, especially the rhabdocoel *Microstomum* (Fig. 50*B*); also in a few other rhabdocoels, and two or three polyclads and alloeocoels. It is now known that these originate from ingested hydroids (Martin 1908, 1914). The nematocysts freed by the digestion of the soft parts of the hydroids are ingested by the gastrodermis, passed into the mesenchyme, and engulfed by mesenchyme cells which carry them to the epidermis. According to Kepner and his students, who have made a study of the ingestion of hydra by *Microstomum,* the nematocysts are actually employed against prey, being discharged when sufficiently bumped by the prey. These workers also state that *Microstomum* eats hydra only when in need of a

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junction with normal epidermis. 1, rhabdites; 2, epidermis; 3, nucleus of epidermis; 4, basement membrane; 5, circular muscle layer; 6; pigment; 7, diagonal muscle layer; 8, longitudinal muscle layer; 9, fixed nuclei of mesenchyme; 10, free cell of mesenchyme; 11, rhabdite-forming gland cell; 12, parenchymal muscles; 13, basal bodies of cilia; 14, mucous gland cell; 15, neck of mesenchymal gland cell; 16, insunk nuclei with cytoplasm; 17, cyanophilous gland cells of the creeping sole.

new supply of nematocysts, that it normally prefers other food, that it will reject hydra if already loaded with nematocysts, and regurgitate other food to make room for hydra if in need of nematocysts (Kepner *et al.*, 1924, 1929, 1938). These workers therefore conclude that *Microstomum* seeks out hydras "for the purpose of" obtaining their nematocysts "in order" to use these nematocysts against prey. The question whether *Microstomum* is able to capture prey without the use of nematocysts is not considered by these authors; the lack of this control weakens the whole argument. The discharge of the nematocysts would seem to depend upon the prey's accidentally striking the nematocysts in just the right fashion, not upon any behavior of the *Microstomum.*

The epidermis is generally separated from the underlying mesenchyme by a definite basement membrane (Fig. 16*D*), sometimes very thick, usually homogeneous, but sometimes showing a lamellate structure. A basement membrane is lacking in many Acoela (Fig. 16*C*) and other primitive Turbellaria, and in such case there is a close relation of the epidermis with the mesenchyme and subepidermal musculature.

4. The Subepidermal Glands.—The Turbellaria are richly provided with glands, which nearly always are unicellular glands. Although, as seen above, gland cells may occur in the epidermis, the vast majority are located in the mesenchyme and send their long "necks" or canals through or between the epidermal cells, to open at the surface. They apparently are insunk epidermal cells. The gland cells have a rounded, pyriform, or elongated body and a long neck which also serves as a canal for the discharge of the secretion. The cell is commonly packed with fine to coarse granules representing the secretion. Little is known directly of the chemistry or function of these secretions. From histological studies of the staining properties of the gland cells it has been found that the latter fall into two categories: the *cyanophilous* glands which take haematoxylin and stain blue with connective tissue stains; and the *eosinophilous* or *erythrophilous* glands which stain pink with eosin, erythrosin, fuchsin, and similar dyes. From these staining reactions and scattered observations on the secretions in life, it is inferred with reasonable probability that the cyanophilous secretion is of slimy or mucus-like nature and acts to lubricate the ventral surface and to form a slime trail on which the cilia get a purchase; and the eosinophilous secretion is of a sticky or adhesive nature, used for adhesion, capture of prey, cementing eggs to a substratum, etc. There are a number of different kinds of glands in each category, and each of these presumably plays a specific role in the activities of the animal.

a. The Cyanophilous Glands.—The common type of cyanophilous gland cell occurs anywhere in the body but is particularly abundant in the ventral mesenchyme, especially in the anterior body half (Fig. 19*A*, *H*). These ventral cyanophilous glands undoubtedly secrete the slime

trail, important in locomotion, also acting to entangle prey. The mucous secretion also probably serves to protect the animal from harmful substances or conditions, to make a cyst under some circumstances, and, according to Wilhelmi, to prevent the eosinophilous secretion from reaching the ventral surface (Wilhelmi, 1909). In land planarians having a creeping sole, the cyanophilous glands open on the sole (Fig. 16*E*).

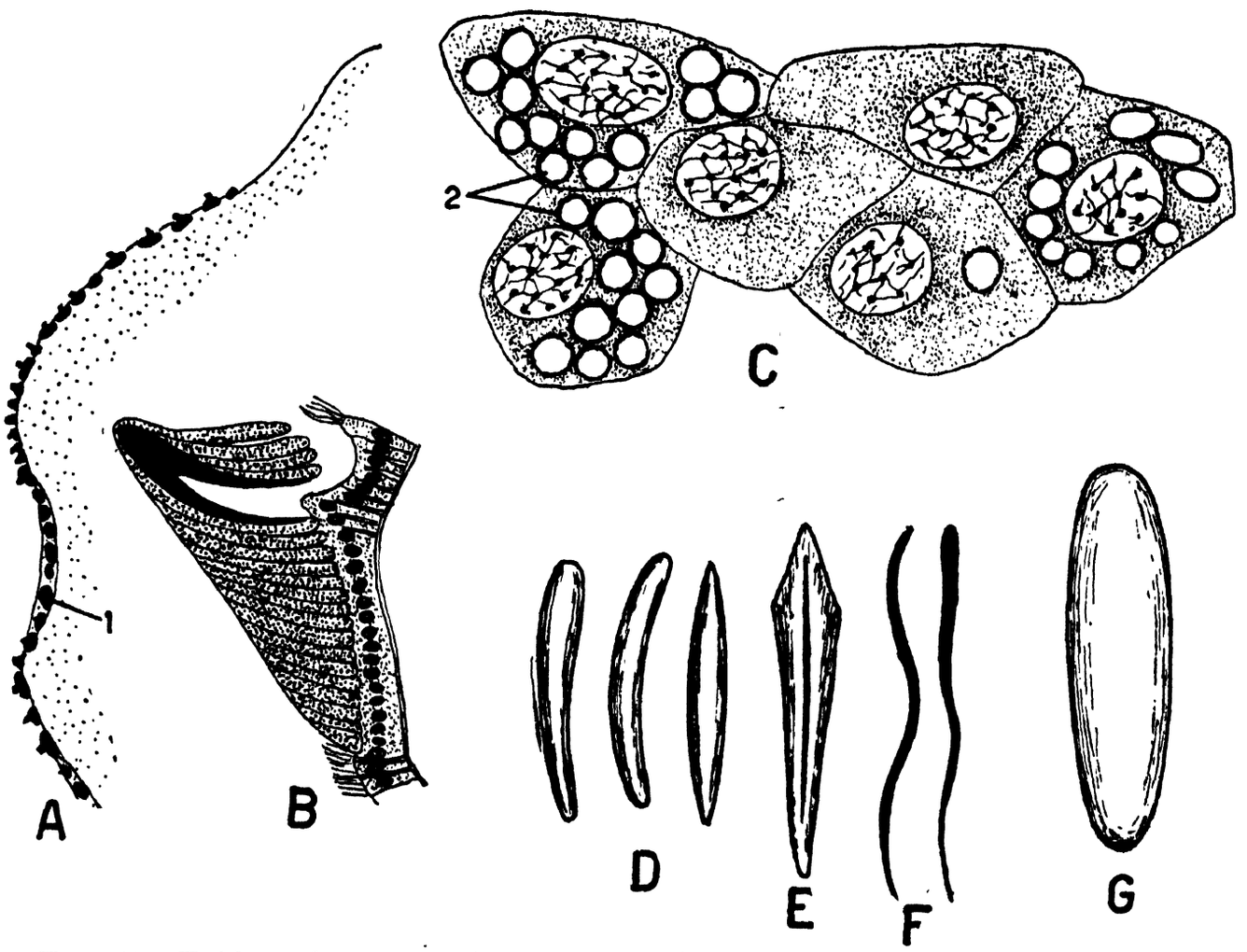

FIG. 17.—Epidermal structure (continued). *A*. Margin of the polyclad *Enantia spinifera*, showing spines. *B*. Section through one of the spines. (*A*, *B after Graff*, 1889.) *C*. Section through the epidermis of a fresh-water planarian, showing polygonal shape of epidermal cells and cross sections of rhabdites. *D*. Various shapes of rhabdites. *E*. Sagittocyst of *Convoluta* (*after Graff*, 1891). *F*. Rhammites. *G*. Chondrocyst of *Bipalium*. 1, spine; 2, section through rhabdites.

A characteristic structure of the Turbellaria is the frontal gland. This consists of a cluster of cyanophilous gland cells located near the brain with long necks that form a bundle and open by a pore or group of pores on the anterior tip, into an area devoid of rhabdoids and cilia, but often abundantly supplied with sensory cells (Fig. 18). The frontal gland is common among the Acoela and Alloeocoela, infrequent in the Rhabdocoela, and lacking in the other orders, although the adhesive organ found in the center of the anterior margin in many fresh-water triclads and the kalyptorhynchid rhabdocoels (Figs. 22, 56) is probably phylogenetically related to the frontal gland. The frontal gland seems to play a role in the capture of food.

b. The Eosinophilous Glands.—The ordinary type of eosinophilous gland occurs singly and sparingly anywhere in the body (Fig. 19*A*, *B*) and is characterized by its coarse granules staining red with eosin. Its exact function is not known. The rhabdoid-forming cells mentioned above, often very numerous, especially in the dorsal mesenchyme, are eosinophilous cells whose secretion takes the form of rods rather than the usual granules (Figs. 16*A*, 19*A*).

The most striking of the eosinophilous glands are the *marginal adhesive glands* of the fresh-water and marine triclads, whose pores form a zone or ring encircling the ventral surface near the margin (Fig. 19). This *marginal adhesive zone* is devoid of rhabdoids and cilia and consists of epidermal cells perforated by the fine necks of the eosinophilous gland cells (Fig. 19*C*). These necks terminate in little knobs that can be protruded beyond the epidermis as *adhesive papillae* acting like little suckers (Wilhelmi, 1909, Fig. 19*C*). The animal can therefore cling very strongly to objects by means of this adhesive zone supplied by the sticky secretion of the eosinophilous cells. Among ectocommensal triclads, the adhesive zone may be broadened in some regions to form an adhesive disk (e.g., *Bdelloura*, Fig. 19*D*, *E*). In land planarians that lack a specialized creeping sole and hence creep on the entire ventral surface, as the Geoplanidae, there is often present at or just ventral to the margin a white strip, the *Drüsenkante* or *glandular margin*. This bounds the creeping surface and appears to correspond to the marginal adhesive zone of other triclads, being fed by eosinophilous glands, although apparently not identical with that zone in histological details.

A group of eosinophilous glands termed *caudal glands* opening at the posterior tip or along the posterior margin occurs commonly among the Acoela, Rhabdocoela, and Alloeocoela. These glands appear to have an adhesive function; and in some forms, notably members of the rhabdocoel genus *Macrostomum* and the alloeocoel family Monocelididae, their terminations are protrusible or permanently protruded as clear finger-like *adhesive papillae* (Figs. 29*C*, 51*C*).

c. Multicellular Glands.—These are uncommon among the Turbellaria, but what seem to be multicellular glands have been reported for the acoel genus *Convoluta*. Flask-shaped multinucleate bodies are probably genuine glands, but the so-called poison glands are more probably of the nature of prostatoids (see page 117).

5. The Muscular System.—This consists in general of the subepidermal and the parenchymal musculature; the muscular layers of the pharynx and of the copulatory apparatus are treated with those organs. The *subepidermal musculature* forms a stratum just beneath the epidermis or the basement membrane when the latter is present. It consists in its simplest form of an outer layer of circular fibers and an inner layer

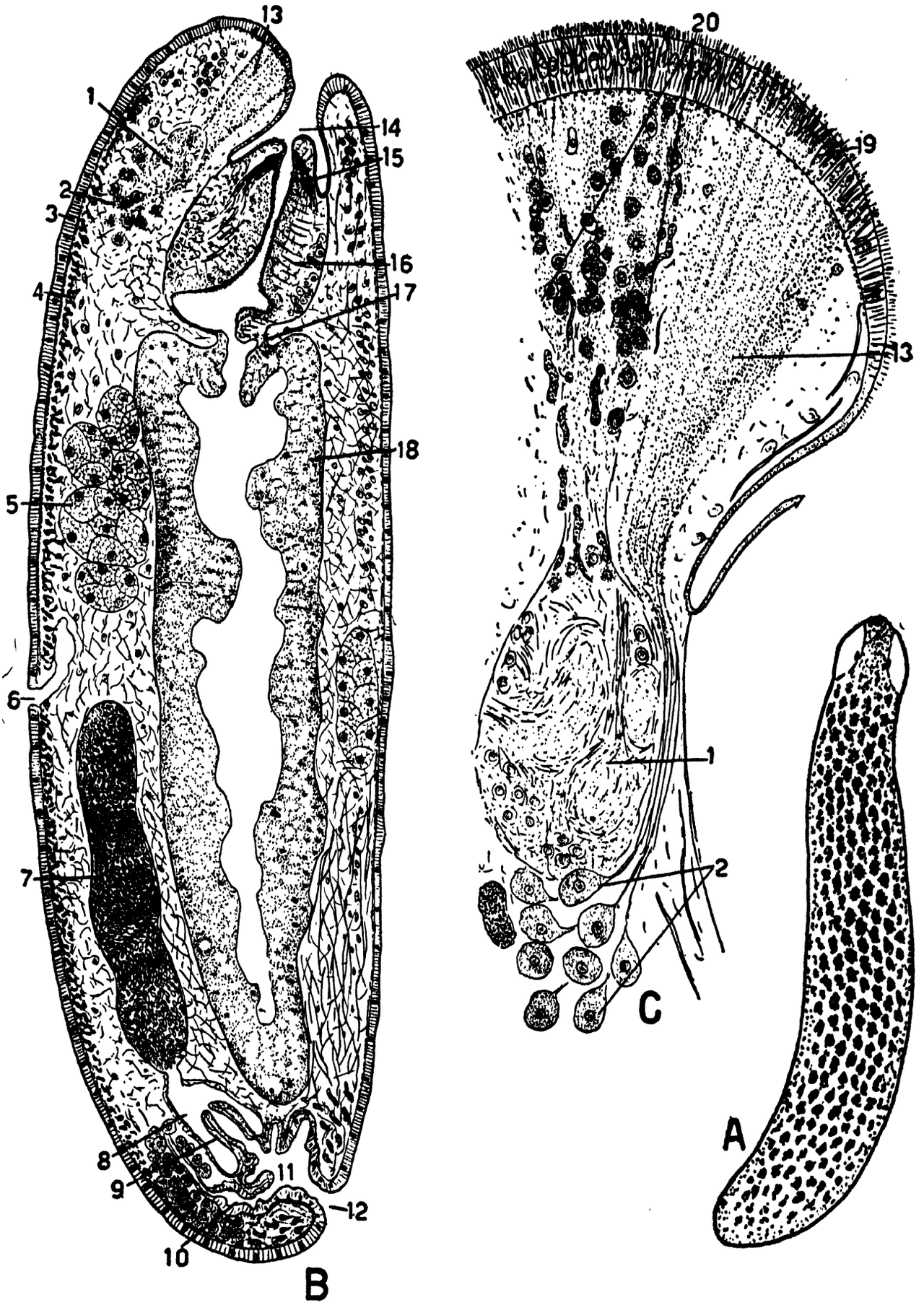

FIG. 18.—The frontal gland. *A. Hydrolimax grisea*, from life, fresh-water plagiostomid alloeocoel of the eastern United States. *B.* Median sagittal section of same showing general structure and relations of frontal gland. *C.* Enlarged view of frontal gland and accompanying sensory tracts. (*B, C after Hyman*, 1938). 1, brain; 2, frontal gland; 3, epidermis; 4, pigment; 5, yolk gland; 6, excretory pore; 7, prostatic vesicle; 8, penis bulb; 9, introverted penis papilla; 10, common ovovitelline duct; 11, genital antrum; 12, common gonopore; 13, bundle of ducts of frontal glands; 14, buccal cavity; 15, bundle of gland ducts of pharynx; 16, pharynx; 17, esophagus; 18, intestine; 19, outlets of frontal glands; 20, sensory tract just above frontal gland ducts.

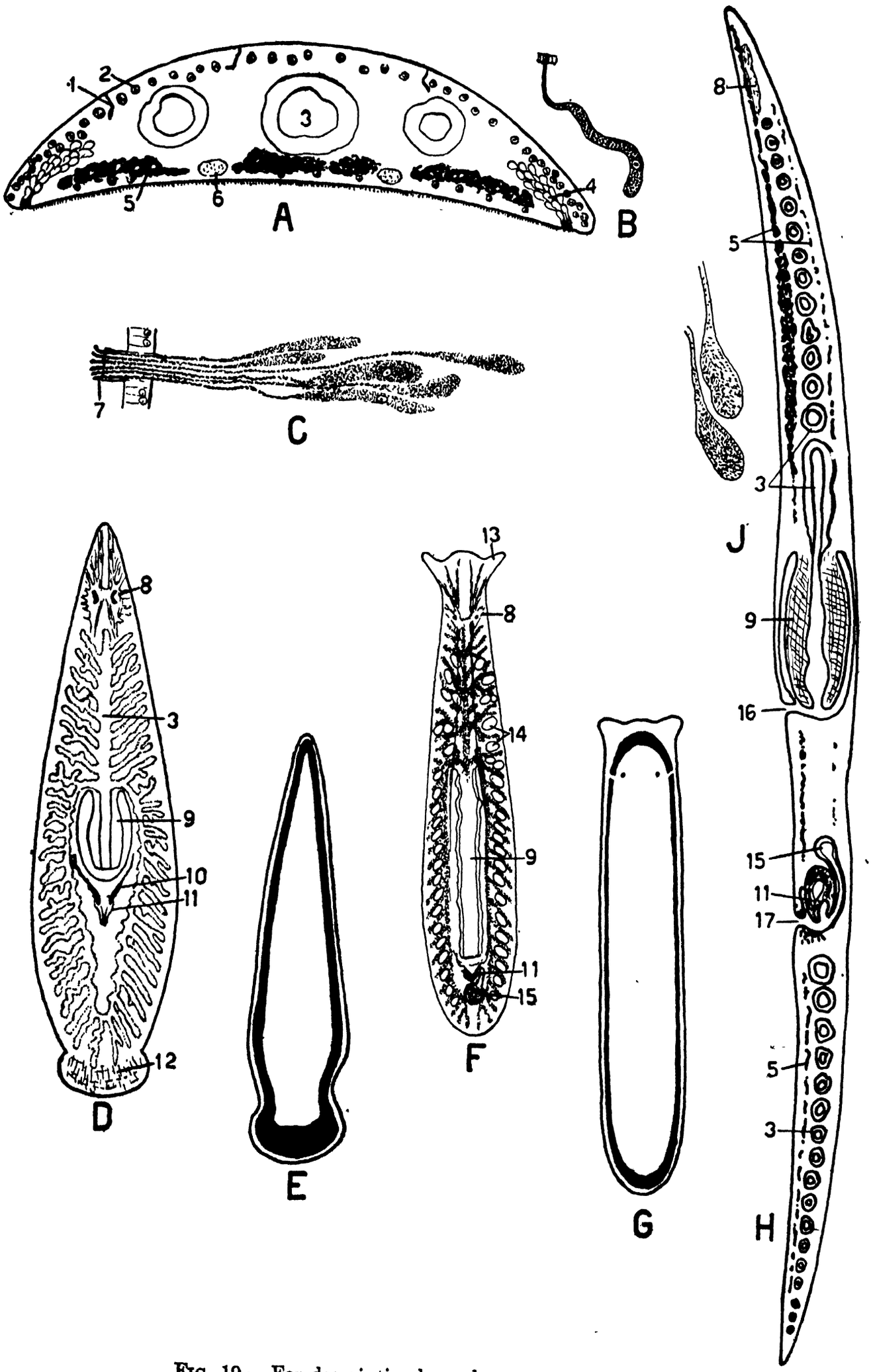

FIG. 19.—For descriptive legend see opposite page.

of longitudinal fibers; usually there is interpolated between these one or more layers of diagonal fibers (Fig. 20*C*). The subepidermal musculature is often extremely delicate in the small forms such as the Acoela but may be very thick and strong in larger members as planarians (Fig. 20*B*) and polyclads. It is frequently more powerfully developed ventrally than dorsally and often thins toward the margins and anteriorly. In polyclads the subepidermal musculature of the ventral side usually consists of five or six layers: outer circular, outer longitudinal, outer diagonal, inner circular, inner diagonal, inner longitudinal. The longitudinal fibers are often highly developed in the larger Turbellaria and may occur in bundles rather than as a simple stratum (Fig. 20*B*).

Very interesting is the fact that in several primitive turbellarians muscle fibers course through the epidermis parallel to the surface and appear to be part of the epidermis as in coelenterates (Fig. 20*D*). This condition has been found in the acoels *Childia* and *Palmenia* (Luther, 1912), the rhabdocoel *Rhynchoscolex* (Reisinger, 1924a), and the alloeocoels *Prorhynchus* (Steinböck and Reisinger, 1924) and *Hofstenia* (Bock, 1923). This epidermal musculature usually consists of outer longitudinal and inner circular fibers, and the latter may substitute for the usual circular layer of the subepidermal musculature.

The subepidermal musculature is undoubtedly homologous with the muscle cylinder of the coelenterates and is one of the indications of a coelenterate ancestry of the Turbellaria; the existence just mentioned of epithelio-muscular cells in Turbellaria greatly strengthens this supposition.

The parenchymal musculature consists of fibers coursing through the mesenchyme and comprises dorsoventral, transverse, and longitudinal fibers. This musculature may be of bewildering complexity in the larger turbellarians (Fig. 20*B*). Usually the dorsoventral fibers are the best developed, but often also there are strong longitudinal bundles in the ventral mesenchyme.

In ordinary preparations, the muscle fibers appear as long slender strands, either homogeneous or fibrillar; in some highly muscular organs they may show a primitive cross striation. The beautiful silver prepara-

FIG. 19.—Subepidermal glands. *A*. Transverse section through a fresh-water planarian, to show location and arrangement of the main gland cells. *B*. Eosinophilous gland cell enlarged. *C*. Cluster of marginal adhesive glands enlarged showing also adhesive papillae. *D*. *Bdelloura candida*, from life, marine triclad ectocommensal on Limulus, has caudal adhesive plate. *E*. Adhesive zone (in black) of *Bdelloura candida*. *F*. *Procerodes littoralis*, from life, marine triclad of New England Coast. *G*. Same, showing adhesive zone. (*C*, *E*, *G after Wilhelmi*, 1909.) *H*. Longitudinal section of fresh-water planarian, showing distribution of the cyanophilous glands. *J*. Cyanophilous gland cells enlarged. 1, eosinophilous glands; 2, rhabdite-forming gland cells; 3, intestine; 4, marginal adhesive glands; 5, cyanophilous glands; 6, nerve cords; 7, adhesive papillae; 8, brain; 9, pharynx; 10, sperm ducts; 11, penis; 12, caudal adhesive disk: 13. auricles: 14, testes; 15, copulatory bursa; 16, mouth; 17, common gonopore.

tions of Gelei (1912, 1927) show, however, that the fibers ordinarily seen are only the contractile part of the muscle cell and that in many cases such fibers are enveloped by a protoplasmic sheath containing a nucleus and often sending off processes believed to be of nutritive nature (Fig. 20*A*). The muscle fibers commonly terminate on the basement membrane of the epidermis by one or more fine filaments that may even extend into the epidermis.

6. The Mesenchyme.—The interior of the flatworm body between organs is filled with a connective tissue or mesenchyme (parenchyma). This appears to be an entomesoderm except in the Acoela where it seems to be compounded of ectomesoderm, entoderm, and entomesoderm. The histological construction of the mesenchyme is exceedingly difficult to ascertain and is not yet thoroughly understood. In some Turbellaria, the mesenchyme consists simply of contiguous rounded cells. In most cases, however, it is composed of a fixed net-like *syncytium* and of *free cells* that wander about through the syncytium (Prenant, 1922, Fig. 20*E*). The syncytium is nucleated, often has a fibrillar appearance, and contains numerous fluid-filled interstices. In a few rhabdocoels and alloeocoels these interstices may fuse to form spaces of some size. Such spaces are usually considered to be remnants of the blastocoel and hence to classify as pseudocoel. The free cells of the mesenchyme are somewhat rounded cells capable of amoeboid wandering; they are often termed *formative* cells since they play an important role in regenerative and reproductive processes, but to avoid unwarranted implications they will here be called simply amoebocytes or free mesenchymal cells. The mesenchyme is not to be regarded as a mere filling tissue, for it functions importantly in the assimilation and transport of food and in the disposal of excretory substances.

7. Pigment.—The coloration of the Turbellaria is caused by dissolved or particulate pigment situated in either the epidermis or the mesenchyme or both. Epidermal pigment is common in all the orders except Tricladida; in the Acoela it usually consists of rods in epidermal cells; in the Rhabdocoela and Alloeocoela it may be dissolved or in the form of granules or rods; in the Polycladida the yellow to red pigments are mostly epidermal, vested in cells that contain a large vacuole filled with a colored fluid or a colorless fluid containing pigment granules. Epidermal pigment cells are probably modified gland cells.

Mesenchymal pigment occurs throughout the Turbellaria, consisting of pigment granules strewn in the syncytium, or of granules or dissolved pigment in the lymph of the syncytial interstices, or of vesicular cells containing dissolved pigment, or of branched pigment cells. Pigment cells (Fig. 13*B*) occur chiefly among the smaller orders, being rare in the triclads and polyclads. The mesenchymal pigment is commonly limited

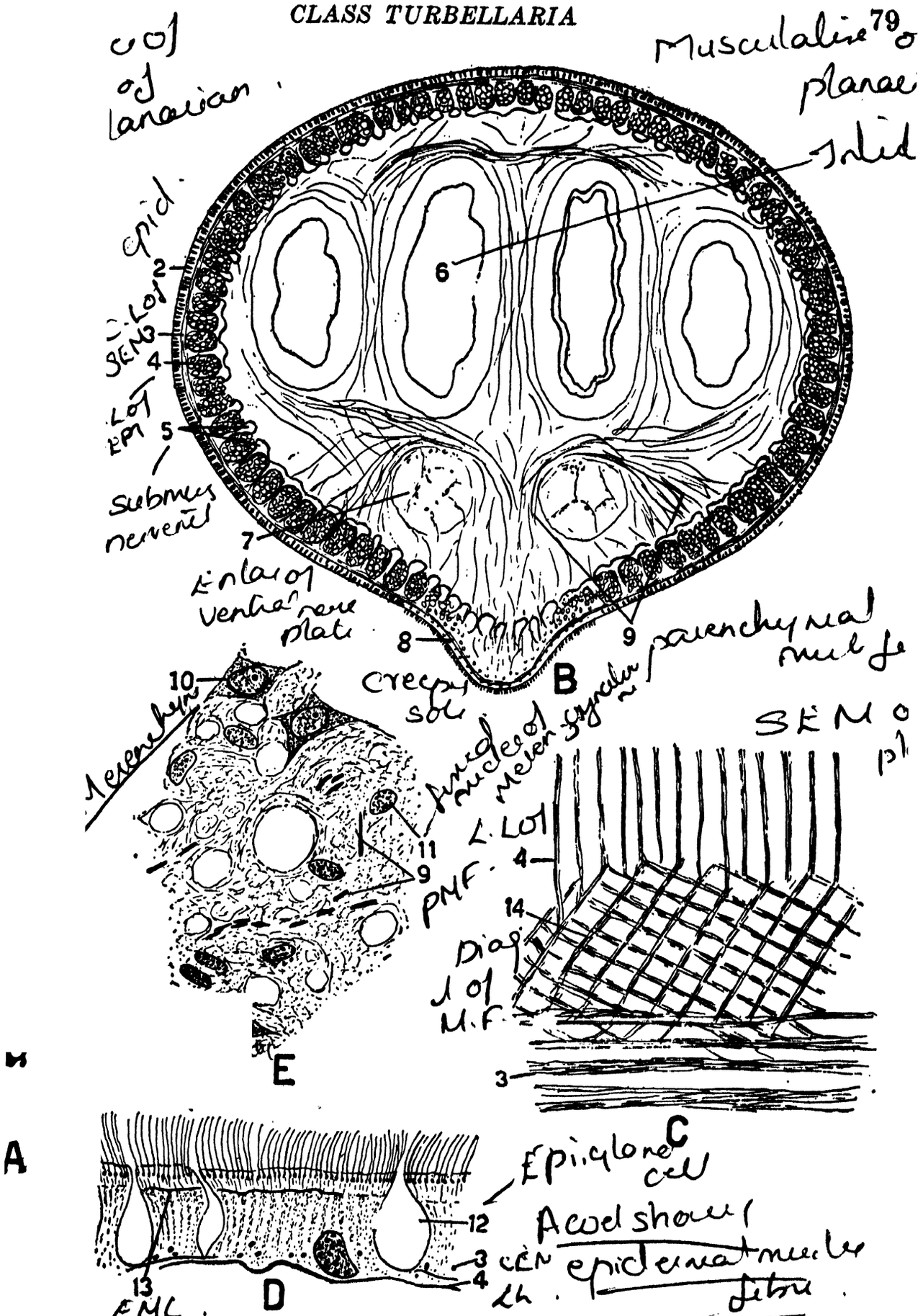

FIG. 20.—Musculature. *A*. Muscle cells of the longitudinal layer of the subepidermal musculature of a planarian (*after Gelei*, 1917). *B*. Cross section of a land planarian of the family Rhynchodemidae, showing musculature and nervous system. *C*. Tangential section through the subepidermal musculature of a planarian, showing the three layers. *D*. Section through the epidermis of the acoel *Palmenia*, showing epidermal muscle fiber (*after Luther*, 1912). *E*. Mesenchyme (parenchyma) of a planarian. 1, bulge containing nucleus; 2, epidermis; 3, circular layer of subepidermal musculature; 4, longitudinal layer of same, arranged in bundles; 5, submuscular nerve net; 6, intestine; 7, so-called ventral nerve cords, enlargements in ventral nerve plate; 8, creeping sole; 9, parenchymal muscle fibers; 10, free cells of the mesenchyme; 11, fixed nucleus of the mesenchymal syncytium; 12, epidermal gland cell; 13, epidermal muscle fiber; 14, diagonal layer of muscle fibers.

to or more abundant in the dorsal side. The pigmentation of triclads is almost exclusively mesenchymal, consisting of a fine granulation in the syncytium; pigment cells have been reported in a few land planarians. Polyclads also have mesenchymal pigment granules which are usually responsible for the gray, brown, and black colors of these animals, although in some black species the pigment is in the vesicular epidermal cells mentioned above. Color patterns of polyclads often result from combinations of epidermal and mesenchymal pigment.

The chemical nature of turbellarian pigment appears not to have been investigated, although it is often surmised that the granules in some cases are excretory bodies. Certain Acoela have large accumulations of crystal-like bodies, called *concrement* by von Graff, chiefly in the epidermis, but also in the mesenchyme. These are regarded without good evidence as urates by some. They are brown in transmitted, white in reflected light, and confer a pattern on the animal which varies with individuals (Fig. 13*D*).

Green and brown colors among the Acoela and Rhabdocoela are often caused by symbiotic organisms, zoochlorellae or zooxanthellae living in the mesenchyme.

8. The Adhesive Organs.—The Turbellaria are richly supplied with adhesive organs, and in this regard no distinction can be drawn between them and the parasitic classes of flatworms. These adhesive organs are generally compounded of epidermis, gland cells, muscle layers, and mesenchyme. Many types of adhesive organs have been described and named by von Graff, but such complication appears unnecessary; there are in fact three general types.

a. Glandulo-epidermal Adhesive Organs.—These, already noted, consist of altered areas of epidermis, usually devoid of cilia and rhabdites, through which open the necks of subepidermal eosinophilous glands. This type lacks especial musculature. It is exemplified by the marginal adhesive zone (Fig. 19) already described (Haftzellenring of the Germans) which may expand to an adhesive plate (Haftplatte) or disk. The adhesive properties of such epidermis appears to result in part from the sticky secretion of the glands (Haftdrüsen) and in part from the ability of the gland exits to protrude as adhesive papillae (Haftpapillen) (Fig. 19*C*).

b. Glandulo-muscular Adhesive Organs.—These are of common occurrence among the fresh-water and land triclads and have been classified as cushions (Drüsenpolster), swellings (Haftwülste), pockets (Drüsentaschen), and pits (Haftgruben, Sauggruben). As any one of these is highly variable in shape and often can be protruded and withdrawn, there appears no good basis for the variety of names. In general, these organs consist of crescentic to circular, often irregularly folded protrusions

bordering one or more depressions (Fig. 21*C*, *D*). The epidermis of the organ is highly modified into slender attenuated cells without cilia or rhabdites, crowded almost out of recognition by the necks of subepidermal eosinophilous glands that reach the surface between them (Fig.

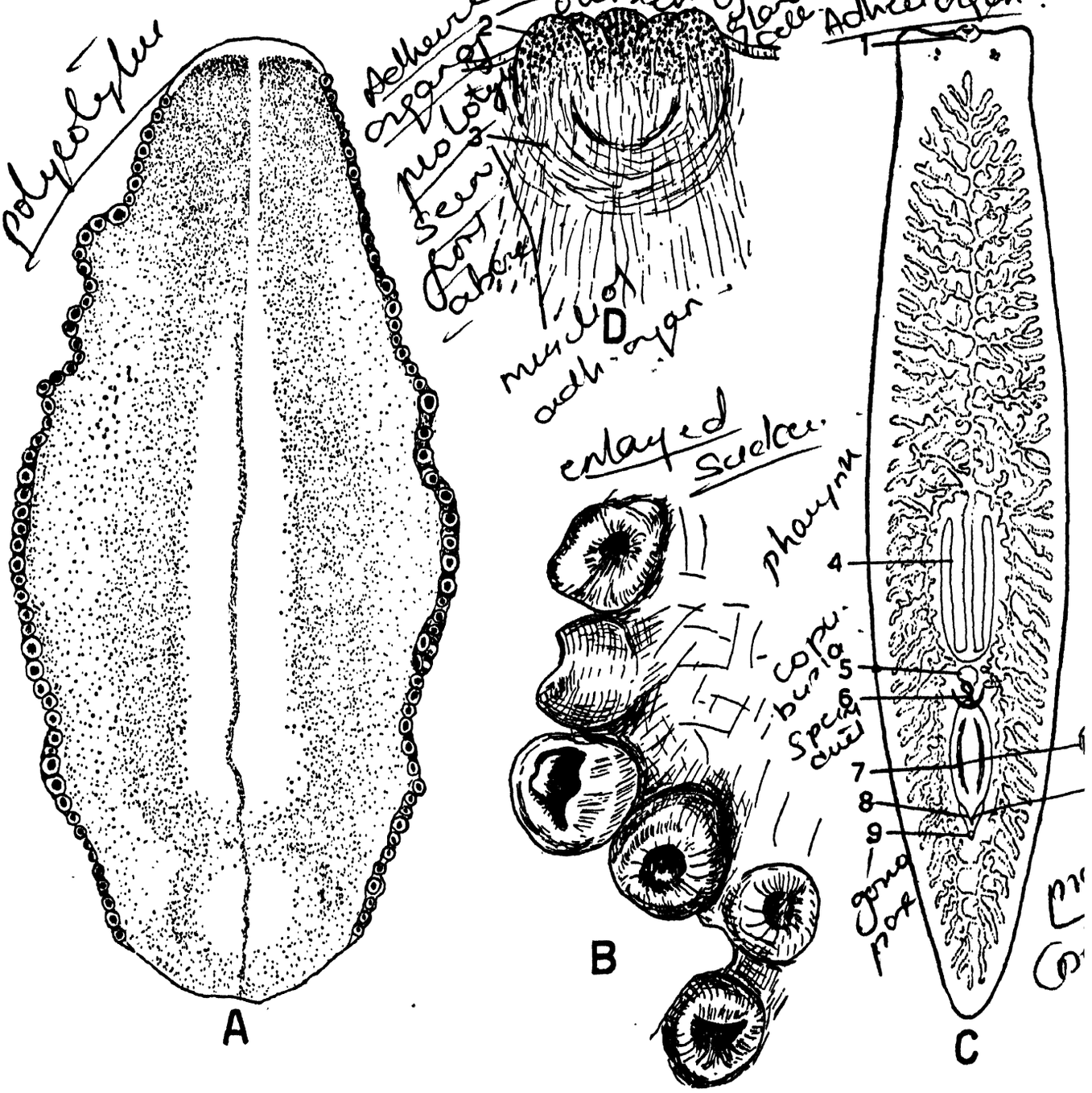

FIG. 21.—Adhesive organs. *A*. *Polycotylus validus*, triclad from Lake Baikal, Siberia, with marginal rows of suckers (acetabula). *B*. Some of the suckers enlarged. (*A*, *B* after *Korotnoff*, 1912.) *C*. *Procotyla fluviatilis* (family Dendrocoelidae), common white planarian of the northeastern United States, with an adhesive organ in the center of the anterior margin. *D*. Adhesive organ of *Procotyla* seen from below. 1, adhesive organ; 2, outlets of gland cells; 3, muscles of adhesive organ; 4, pharynx; 5, copulatory bursa of sex apparatus; 6, sperm duct; 7, penis bulb; 8, penis papilla; 9, gonopore.

22*A*). The organ is also supplied with an extensive musculature derived from the subepidermal muscle stratum and often attaining great complexity with fibers running in various directions (Fig. 22*A*, *C*). Conspicuous among the muscles is often a longitudinal bundle acting as a retractor. Many of these adhesive organs can be rapidly protruded and retracted.

The glandulo-muscular adhesive organ reaches its best development in fresh-water planarians, especially the families Dendrocoelidae and Kenkiidae, and the remarkable triclads found in Lake Baikal, Siberia (Korotneff, 1912). There is usually present a single such organ, in the center of the anterior margin or on the ventral side of the head; but there may be two or even four such organs on the ventral side of the head and in *Polycotylus* from Lake Baikal there are about 200 in a row along the lateral body margins (Fig. 21*A*, *B*). Probably the most remarkable of all these organs is that of the triclad *Kenkia rhynchida* from an Oregon cave (Hyman, 1937). The organ here consists of a muscular cylindrical snout (Fig. 22*B*) having a central lumen provided distally with cyanophilous glands, proximally with eosinophilous glands; a strong retractor muscle attached to the eosinophilous portion indicates that this can be everted to the outside (Fig. 22*C*). The function of the glandulo-muscular adhesive organ in the triclads appears to be twofold; the organ is used for adhesion in locomotion in a leech-like manner, and it is used in the capture of prey. Planarians provided with such an organ have been seen to lunge at small crustaceans and grasp them by folding the margins of the organ over them. In general planarians provided with these adhesive organs also have a zone of especially large rhabdites along the body margin; and it would appear that these are used to grip the substratum while the animal is struggling with prey.

Probably the proboscis in the anterior end of rhabdocoels of the section Kalyptorhynchia is to be regarded as a special form of glandulo-muscular adhesive organ. This shows varying degrees of complexity (Figs. 55, 56) but typically is a highly muscular conical or bipartite body provided with eosinophilous glands and sharply marked off from the parenchyma by a septum. The proboscis is protrusible or eversible through a pore at the anterior tip of the animal and is employed in the capture of prey.

Polyclads of the suborder Cotylea are provided on the ventral surface with an adhesive organ usually called sucker but really a glandulo-muscular organ. A similar organ, the genital sucker, is found between the male and female gonopores in the acotylean genus *Leptoplana;* it apparently assists in copulation.

c. True Sucker or Acetabulum.—This is distinguished from the glandulo-muscular type through being separated from the body parenchyma by a distinct muscular septum. The true sucker is generally of circular form with a raised rim and marked central depression and may or may not be stalked. Its adhesive action is attained by the vacuum principle rather than by sticky secretions. Among the Turbellaria a true sucker is found only in some of the Lake Baikal triclads mentioned above (Fig. 21*A*, *B*).

9. Nervous System.—The nervous system of the most primitive Turbellaria is in a condition resembling that of coelenterates, and this condition appears to be the original type of nervous system of the phylum. In such forms as the acoels *Tetraposthia* and *Nemertoderma* (Steinböck, 1931, An der Lan, 1936, Westblad 1937) and the alloeocoel *Hofstenia* (Bock, 1923), the nervous system consists of a layer in the base of the epidermis, outside the subepidermal musculature, the same situation that it possesses in the Cnidaria (Fig. 23). This epidermal nervous layer is best developed anteriorly and there forms a more or less continuous stratum; posteriorly it thins out, becoming a net-like plexus with some indications of longitudinal strands, mostly three pairs. In *Hofstenia* there is in the anterior tip an additional delicate plexus outside the main nervous layer. What is to be considered brain in these forms is a matter of dispute; some regard a pair of lateral thickenings of the main stratum to constitute the brain whereas others designate as brain a nervous layer over the statocyst. The latter view is probably correct if one judges from conditions in other Acoela. Whether the brain of these forms has retrogressed or is in process of evolution cannot be stated.

In all other Turbellaria the main nervous system has sunk into the mesenchyme immediately to the inner side of the subepidermal musculature where it forms what will be here termed the *submuscular plexus.* In this plexus there are usually emphasized a number of longitudinal cords which primitively have a radiating arrangement and of which the ventral pair is usually the most prominent. Transverse connections between the longitudinal strands are also often differentiated in the plexus and may form regularly repeated rings (Fig. 24*A*). In the anterior part of the body the plexus communicates, chiefly by way of the ventral cords, with the *brain* situated more internally than the plexus. The brain, also called *cerebral ganglia,* commonly is a slightly or deeply bilobed mass but may consist simply of the thickened anterior beginnings of the ventral cords. The shape of the brain is frequently correlated with the shape of the head. From the brain numerous nerves of sensory nature radiate to the margins and sense organs of the head, and there are connections, direct or indirect, with the other longitudinal cords of the submuscular net. In many Turbellaria there is, in addition to the submuscular plexus, a delicate plexus just beneath the basement membrane of the epidermis; this will here be called the *subepidermal plexus.*

In the Acoela (except those named above), the nervous system is composed of a brain and a submuscular plexus in which there are evident three to six, mostly five, pairs of longitudinal strands (Fig. 23*B*, *E*), dorsal, dorsolateral, marginal, ventrolateral, and ventral, spaced around the periphery. Lack of the marginal pair reduces the number of nerve

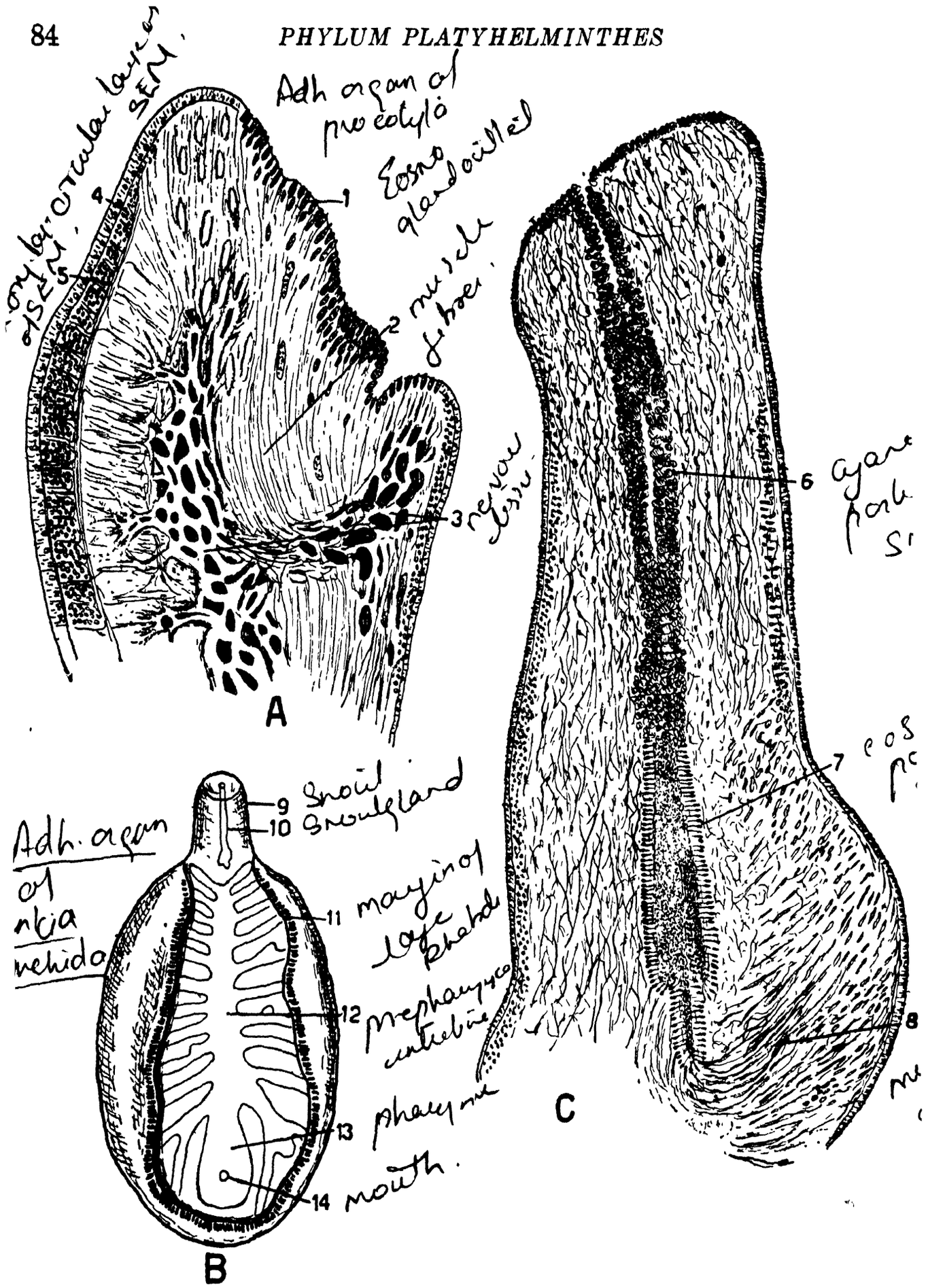

FIG. 22.—Adhesive organs (continued). *A.* Longitudinal section of the adhesive organ of *Procotyla*, showing its glandulo-muscular construction. *B. Kenkia rhynchida*, remarkable planarian from an Oregon cave with snout-like adhesive organ containing a complicated gland; animal lacks postpharyngeal intestine. *C.* Longitudinal section of the snout of *Kenkia rhynchida*. (*B*, *C after Hyman*, 1937.) 1, eosinophilous gland outlets; 2, muscle fibers; 3, nervous tissue; 4, circular layer of subepidermal musculature; 5, longitudinal layer of subepidermal musculature; 6, cyanophilous portion of snout gland; 7, eosinophilous portion of snout gland; 8, retractor muscle of snout; 9, snout; 10, snout gland; 11, margin of large rhabdites; 12, prepharyngeal intestine; 13, pharynx; 14, mouth.

strands to eight, but this cannot be regarded as a ctenophore reminiscence since ten is the more common number. The plexus consists of large meshes connected by a finer net. The brain is a mass around the statocyst and is usually formed into four lobes by the passage through it of the bundle of necks of the frontal glands. *Polychaerus* has in addition to the main brain mass a ganglion on each side from which the dorsal strands proceed (Löhner, 1910, Fig. 24*D*).

The polyclad nervous system is similar to that of the Acoela, consisting of a large-meshed submuscular plexus much more strongly developed ventrally than dorsally (Fig. 24*B*). In the ventral part of the plexus there are evident many larger strands radiating from the brain. Of these, the pair that runs alongside the pharynx is often the most conspicuous, especially in slender polyclads, and probably corresponds to the ventral cords of other Turbellaria. A fine subepidermal net is general among the polyclads. The brain is a rounded, bilobed body enclosed in a capsule; there is frequently present a group of small deeply staining sensory ganglion cells at the front end of each brain lobe outside the capsule (Fig. 28). These were formerly taken to be some kind of granule, hence were called Körnerhaufen (granule masses).

In the remaining groups of Turbellaria, the nervous system takes on a more bilateral character. There are primitively differentiated in the submuscular plexus four pairs of longitudinal cords, *dorsal*, *lateral* or *marginal*, *ventrolateral*, and *ventral*, as seen in such forms as *Prorhynchus*, *Bothrioplana*, and *Rhynchoscolex* (Fig. 24*A*). These are connected by ring commissures often regularly repeated and also of course by the meshes of the plexus. In the marine triclads, most alloeocoels, and some rhabdocoels, there are three pairs of cords, through loss of the ventrolateral pair. Direct vertical commissures between the dorsal and ventral cords may occur (Fig. 25*C*). Some fresh-water triclads also have the three pairs of cords, but in this group the dorsal cords are often lacking and the lateral cord, also called marginal or ring nerve, is usually merely the marginal bend of the submuscular plexus (Fig. 25*D*). Consequently in most fresh-water planarians, only the ventral cords are present; these are strongly developed with transverse connectives and lateral branches, and often continue anterior to the brain. A subepidermal plexus is general in triclads and alloeocoels. In most rhabdocoels, probably because of their small size, the nervous system is somewhat reduced, and here too usually only the ventral longitudinal cords are present, although short dorsal ones may occur, as in *Mesostoma* (Fig. 24*C*). There is a dearth of lateral branches and transverse connectives; commonly the ventral cords have one or more cross connections behind the pharynx (Fig. 24*C*) or else a nerve ring encircles the pharynx (Fig. 51*A*). A submuscular plexus has been seen in *Mesostoma* (Bresslau and Voss, 1914)

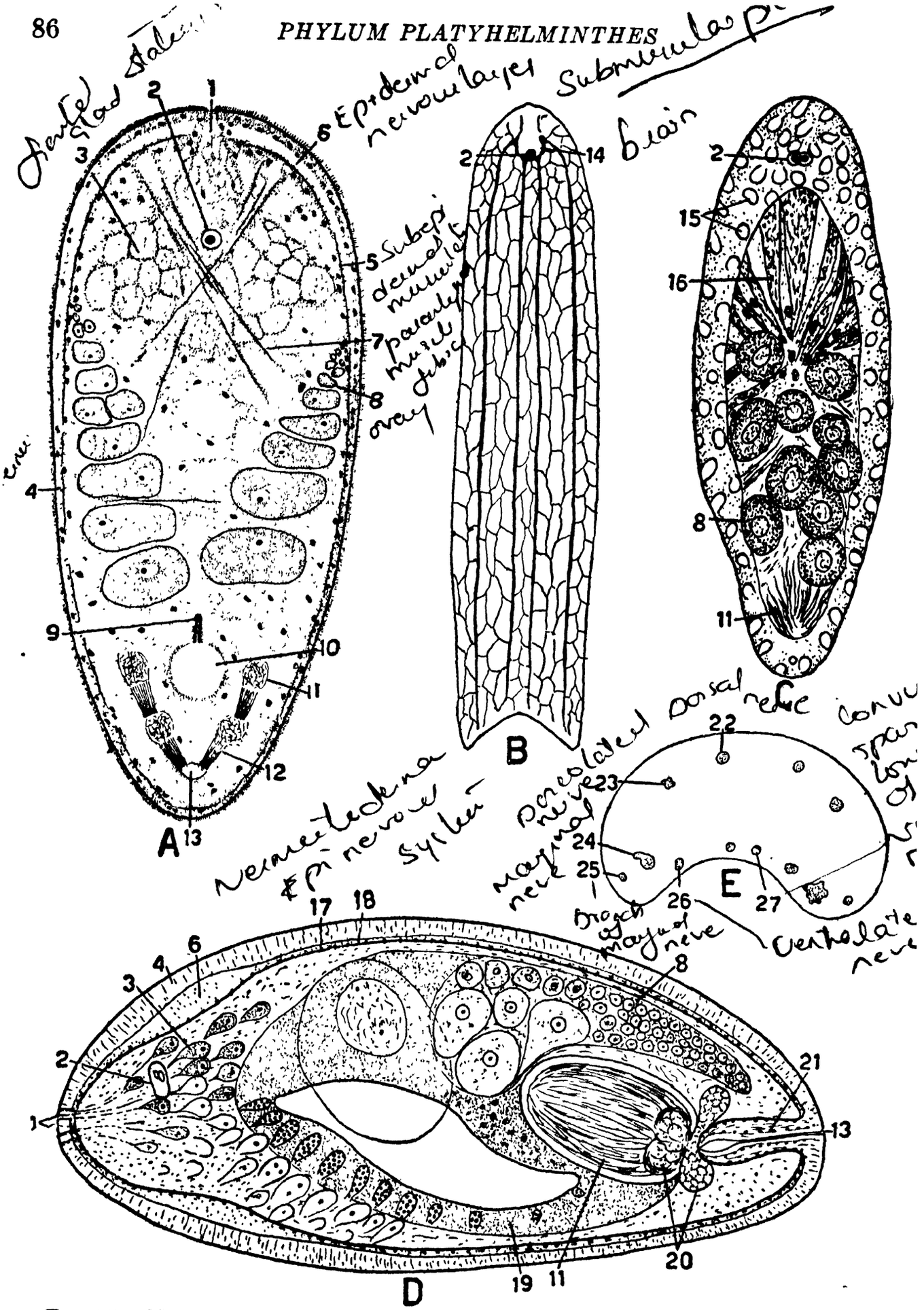

FIG. 23.—Nervous system of Acoela. *A*. Frontal section of *Tetraposthia colymbetes* showing general structure and epidermal nervous system (*after An der Lan*, 1936). *B*. Dorsal half of the submuscular plexus of *Amphiscolops*, from life, Bermuda; there are eight longitudinal strands in the plexus. *C*. *Nemertoderma bathycola*, general appearance with central epidermis removed to show internal structure (*after Westblad*, 1937). *D*. Sagittal section of *Nemertoderma*, showing general structure and epidermal nervous system (*after Westblad*, 1937). *E*. Section through *Convoluta*, showing the five pairs of longitudinal cords

and is probably general among rhabdocoels. The brain in rhabdocoels, alloeocoels, and fresh-water and marine triclads is either an anterior thickening of each ventral cord or a bilobed mass springing from the dorsal surface of these cords. Forms with triangular heads tend to have the thickened cords as brain (Fig. 26*A*), whereas those with truncate heads are more apt to have two rounded brain ganglia with radiating nerves (Fig. 26*B*). The exact arrangement of the nerves of the head has been worked out in several alloeocoels (Fig. 25*A*) and fresh-water and marine planarians, but the details vary with each species (*Bothrioplana*, Reisinger, 1925; *Prorhynchus*, *Geocentrophora*, Steinböck, 1927; *Procerodes*, *Bdelloura*, Wilhelmi, 1909; fresh-water planarians, Micoletzky, 1906, 1907; Weiss, 1910). In general, the dorsal part of the brain receives a number of sensory nerves from the head margins and the main sense organs of the head and also connects by commissures with the dorsal longitudinal cords or gives rise to these directly (Fig. 26). The ventral part of the brain is continuous with the ventral cords and may give off connectives to the marginal nerve or plexus. Frequently the ventral cords continue beyond the brain to the anterior tip and in this precerebral region are provided with transverse and lateral connectives (Fig. 26).

The most complicated nervous system in the phylum occurs among the land planarians. In this group there is a subepidermal and a strongly developed submuscular plexus. The latter, however, has no differentiated longitudinal cords. Instead there is a thick nervous layer, termed the *ventral nerve plate*, in the mesenchyme below the digestive tract; this is continuous laterally with the submuscular plexus (Fig. 25*E*). In this nerve plate, which is either solid or a plexus, there may be evident a number of longitudinal thickenings or, especially in land planarians of cylindroid shape, a single pair of thickenings, that simulate the ventral cords of other Turbellaria and are often so called. A definite brain is wanting; the nerve plate simply continues to the anterior end where in the Bipaliidae it expands into a lunate head plate.

The nerve cells resemble those of other animals, being uni-, bi-, or multipolar, with neurites all morphologically alike (no differentiated axone). Although the turbellarian nervous system is plexiform, with nerve cell bodies strewn everywhere along the strands of the plexus, it is a strictly synaptic system with no continuity of neurites. The finer details of the nervous system have been worked out by means of the Golgi

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of the submuscular plexus (*slightly altered after Graff*, 1891). 1, frontal pore; 2, statocyst; 3, frontal glands; 4, epidermis; 5, subepidermal musculature; 6, epidermal nervous layer; 7, parenchymal muscle fibers; 8, ovary; 9, nozzle; 10, seminal bursa; 11, seminal vesicle; 12, armed penis; 13, male gonopore; 14, brain; 15, large epidermal glands; 16, digestive gland cells; 17, circular fibers of subepidermal musculature; 18, longitudinal fibers of same; 19, intestine; 20, prostatic glands; 21, male canal (penis); 22, dorsal nerve; 23, dorsolateral nerve; 24, marginal nerve; 25, branch of marginal nerve; 26, ventrolateral nerve; 27, ventral nerve.

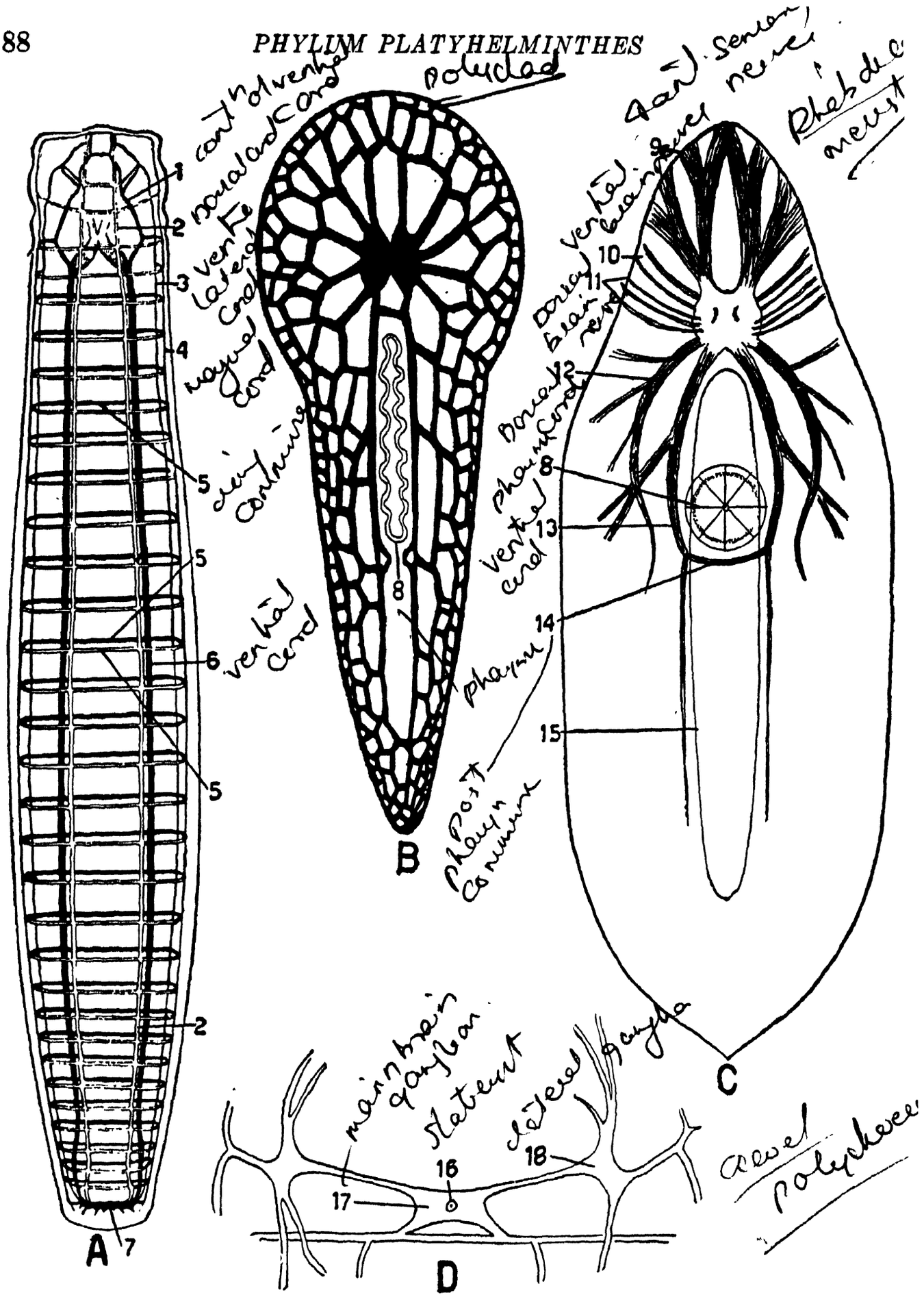


FIG. 24.—Nervous system of various Turbellaria. *A*. Nervous system of the alloeocoel *Bothrioplana* (*after Reisinger*, 1925); dorsal part in white, ventral part in black. *B*. Ventral part of the submuscular net of the pelagic polyclad *Gnesioceros*, from life, Bermuda. *C*. Nervous system (submuscular) of the rhabdocoel *Mesostoma* (*after Bresslau and Voss*, 1913). *D*. Brain of the acoel *Polychoerus* (*after Löhner*, 1910). 1, anterior continuation of ventral cords; 2, dorsal cords; 3, ventrolateral cords; 4, marginal cords; 5, ring commissure; 6, ventral cords; 7, terminal fusion; 8, pharynx; 9, four anterior sensory nerves; 10, ventral brain nerves; 11, dorsal brain nerves; 12, dorsal cords; 13, ventral cords; 14, postpharyngeal commissure; 15, intestine; 16, statocyst; 17, main brain ganglion; 18, lateral ganglia.

silver technique by Hanström (1926) for the marine triclad *Bdelloura candida*. His preparations show that the so-called marginal nerve here consists of sensory nerve cells and their much-branched neurites penetrating the epidermis (Fig. 27). Certain cells whose neurites lie entirely within the ventral cords or transverse commissures are regarded by Hanström as probably associative cells. Richly branched unipolar cells in the ventral cords are motor, since they send one long neurite into parenchymal muscles. The brain of the Turbellaria consists centrally of bundles of fibers, peripherally of the bodies of nerve cells, of several different types and sizes, generally arranged in groups (Fig. 28*B*). The brain appears to reach its highest complication in the polyclads where a detailed study has been made by Hadenfeldt (1929). The fiber bundles of the brain are continuous with the main nerves but subdivide and reconnect to make complicated pathways. What is known of the functions of the brain is discussed later under behavior.

The nervous system of the pharynx is considered with that organ. There is also a rich nerve supply to the copulatory apparatus and to the adhesive organs.

10. Sense Organs.—The Turbellaria are richly supplied with sensory cells, of which the most common is the *tactile* cell or *tangoreceptor*. These are sensory nerve cells that send one or more processes to the surface, each terminating in one or more hairs or bristles (Fig. 29*F*). These bristles are often longer than the cilia and easily seen along the margins in the living animal (Fig. 51*A*, *B*). In the rhabdocoel *Mesostoma*, Gelei (1930) found that every epidermal cell is pierced by three to five such sensory bristles (Fig. 30*B*), and the same probably holds for other Turbellaria. The tangoreceptors are even more thickly strewn on special tactile regions such as tentacles, auricles, and along the body margins where there is, in land planarians, a definite sensory strip (Sinneskante).

Chemoreception is well developed among the Turbellaria, all of which perceive and orient toward food juices at a distance. The chemoreceptors are mostly limited to the head region and comprise ciliated pits and grooves and their variants; these are depressed epidermal areas devoid of rhabdoids and usually also of gland-cell exits, although sometimes well supplied with gland cells. Ciliated pits are rounded or flask-like depressions lined by an altered, usually depressed epidermis; generally the pit sides are heavily ciliated whereas the bottom bears short stiff cilia that are probably really the bristles of sensory cells (Fig. 30*A*). Pits are supplied with a sensory nerve or else are so close to the brain as to be directly connected with it (Fig. 30*A*). A single pit on the ventral side of the head is seen in a number of land planarians. A pair of pits on the sides of the head occurs in a number of rhabdocoels (*Stenostomum*, Fig. 29*A*; *Rhynchoscolex*, *Microstomum*, Fig. 50*B*; some species of *Macro-*

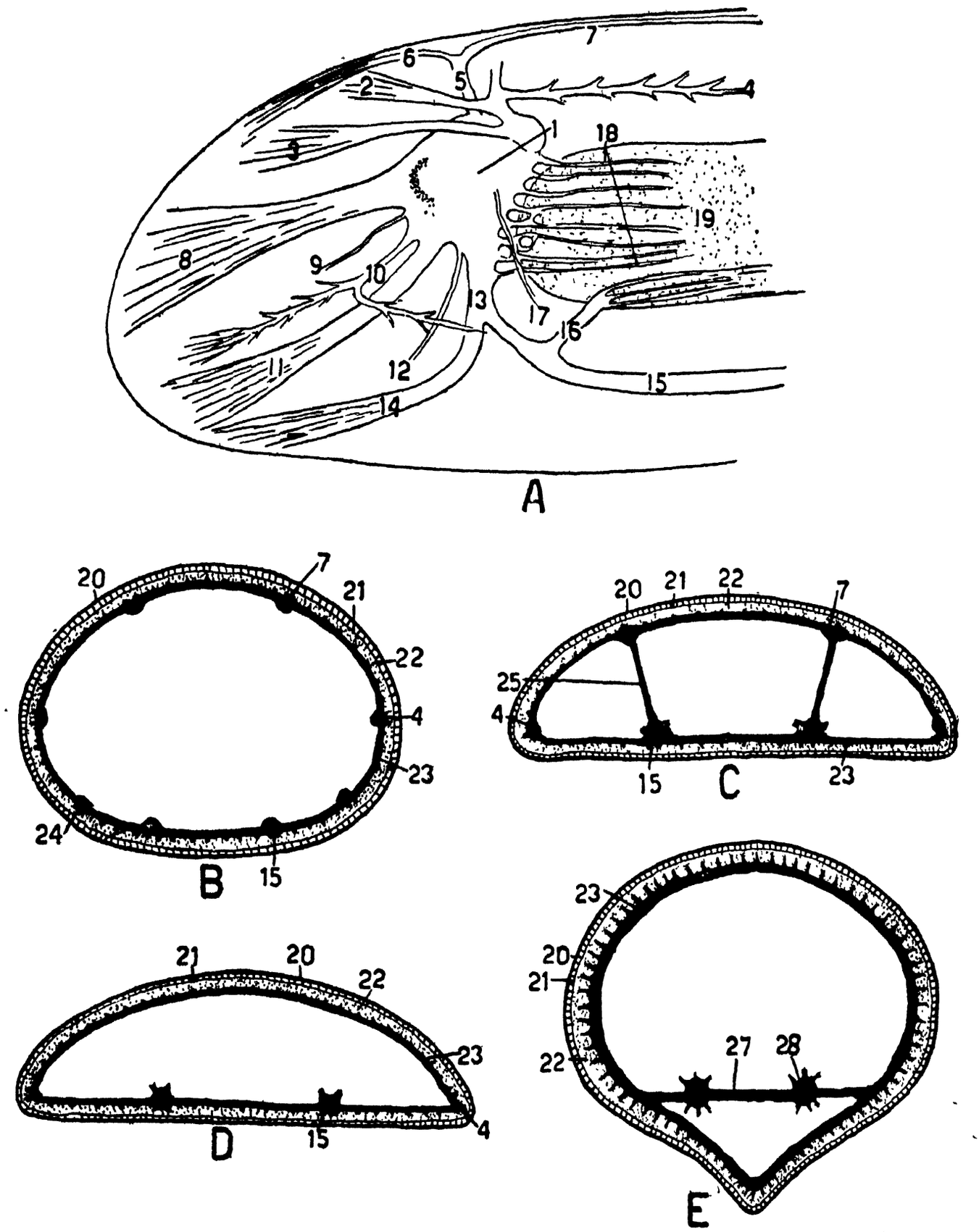
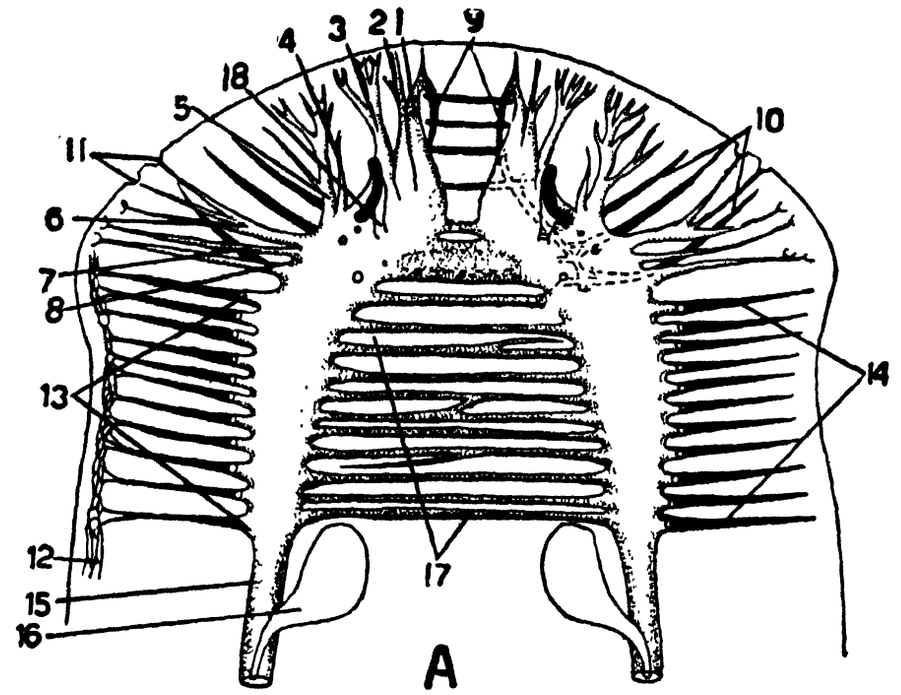


FIG. 25.—Nervous system of Turbellaria (continued). *A*. Side view of the anterior end of the alloeocoel *Hydrolimax* (*after Hyman*, 1938), showing main brain nerves and manner of origin of the three main nerve cords. *B–E*. Diagrams of cross sections comparing the nervous systems of *B*, alloeocoel; *C*, marine triclad; *D*, fresh-water triclad; *E*, land planarian. 1, brain; 2, 3, dorsal sensory branches; 4, lateral nerve cord; 5, main mediodorsal trunk; 6, anterior sensory branch of 5; 7, dorsal nerve cord; 8–14, anterior and ventral sensory nerves; 13, main ventral trunk; 15, ventral nerve cord; 16, pharyngeal branch of 15; 17, small nerve; 18, branches from brain into pharynx; 19, pharynx; 20, epidermis; 21, subepidermal nerve net; 22, subepidermal musculature; 23, submuscular nerve net; 24, ventrolateral nerve cord; 25, commissure between dorsal and ventral cords; 27, ventral nerve plate; 28, simulated ventral cords in the ventral nerve plate.

stomum and *Mesostoma*, Fig. 45*B*) and alloeocoels (*Otoplana*, Fig. 60*D*; *Prorhynchus*, Fig. 59*A*; *Geocentrophora*, Fig. 59*B*); two pairs of head pits are found in the alloeocoel genera *Bothrioplana* (Fig. 35*D*) and *Otomesostoma*. Ciliated grooves are also of common occurrence. A pair of such grooves borders the anterior end of the creeping sole in a number of land planarians, or sometimes the creeping sole terminates anteriorly in a groove or cleft of glandulo-sensory nature. A transverse ciliated furrow partly or wholly encircling the rear of the head occurs in several alloeocoels (*Plagiostomum*, *Allostoma*, *Pseudostomum*, Fig. 60*E*). Among the marine and fresh-water triclads there is constantly present on each side of the head a groove, the *auricular groove* or *auricular sense organ* (Fig. 31*H*). This is readily noticed in dark-colored planarians as a white line along the head margin or across the base of the auricles when present; it may be straight or curved or broken up into a line of short grooves (Fig. 31*B–E*). The passage of a water current along the auricular groove from in front backward can be demonstrated by adding carbon or carmine particles to the water (Steinmann, 1929). The various kinds of sensory groove consist of a depressed altered epidermis, devoid of rhabdoids and gland-cell exits, generously provided with nerves and bearing short cilia that are probably sensory bristles (Fig. 30*A*). In the rhabdocoels *Mesostoma* (Gelei, 1930) and the related *Bothromesostoma* (Müller, 1936), the presence of sensory endings in the chemoreceptive grooves of the head has been demonstrated by special nerve stains (toluidin blue). The cells concerned are bipolar nerve cells whose neurite to the surface subdivides into a number of short stiff hairs (Fig. 30*B*). Wherever definite chemoreceptors are absent, probably the general head margin or lateral sensory margin serves the same function. The sensory margin (Sinneskante) of land planarians consists of a marginal groove bearing various pits and swellings, some probably chemoreceptive. The frontal gland (page 73) also probably participates in chemoreception, since the gland outlets are usually accompanied by numerous sensory fibers (Fig. 18*C*) so that the whole forms a *frontal organ* with tactile and chemical sensitivity. The necessity of associating chemoreceptive elements with a food-catching organ will be obvious. No definite chemoreceptive organs have been reported for polyclads, but a sensory groove along the anterior margin is general throughout this order, and the epidermis may have depressed cells, probably of chemoreceptive nature.

The chemoreceptive nature of ciliated pits and grooves has been demonstrated by Müller (1936), who showed that *Stenostomum* after extirpation of its ciliated pits cannot detect the presence of food juices or orient toward food, and the same is true of *Bothromesostoma* after removal of the pair of sensory grooves on the sides of its head corresponding to the auricular sense organ of planarians (Fig. 29*E*). The chemoreceptive



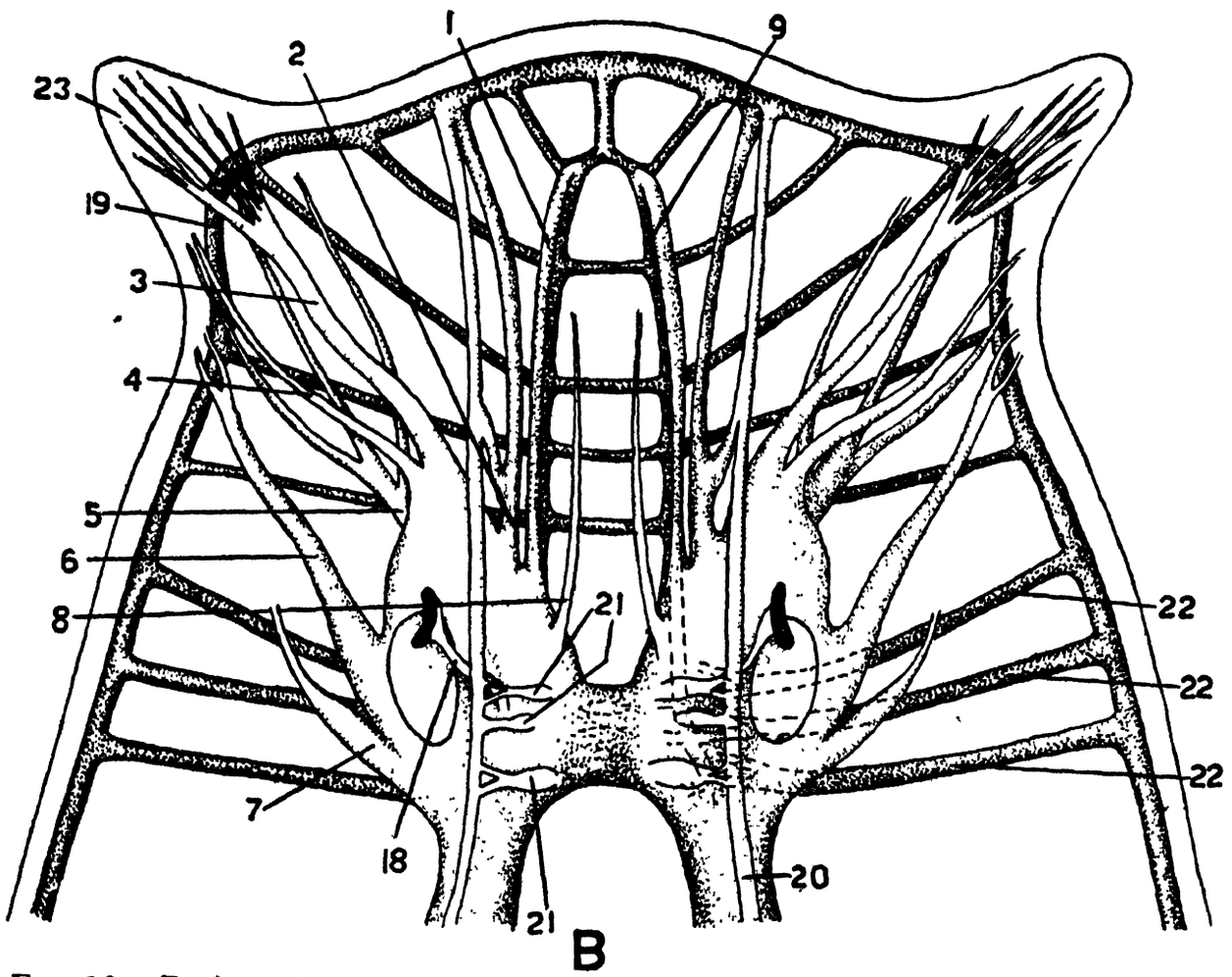


FIG. 26.—Brain and anterior nervous system of fresh-water triclads. *A*. Type with triangular head (*Dugesia polychroa*). *B*. Type with truncate head (*Crenobia alpina*). (*Both after Micoletzky*, 1907.) Dorsally located nerves white, ventral ones black. In *A* the transition of brain to ventral cord is believed to occur after nerve 8. The grouping of the sensory nerves in *A*, and the origin of the dorsal cords from three roots in *B* indicate that the brain ganglia are composed of three fused ganglia. 1–8, main sensory brain nerves; 9, anterior continuation of ventral cords; 10, three lateral nerves from 9; 11, auricular sensory groove; 12, marginal plexus; 13, series of dorsal sensory nerves from ventral cords; 14, ventral commissures between ventral cords and marginal plexus; 15, ventral cords; 16, ovaries; 17, dorsal commissures between ventral cords; 18, optic nerve to eye; 19, marginal nerve; 20, dorsal cords; 21, roots of dorsal cords; 22, commissures between ventral and marginal cords; 23, auricle.

organs are thus also directive or chemotopotactic, enabling their possessors to find food by means of the water currents that pass along the organs. For this reason cilia are a necessary part of chemoreceptive organs.

Rheoreceptive cells have been identified in *Mesostoma* and *Bothromesostoma* (Gelei, 1930; Müller, 1936) and are probably of general occurrence. In these animals there are four pairs of such cells distributed along the body sides (Fig. 29*E*). Each is a large cell that branches into a number of sensory bristles that project through the epidermis (Fig.

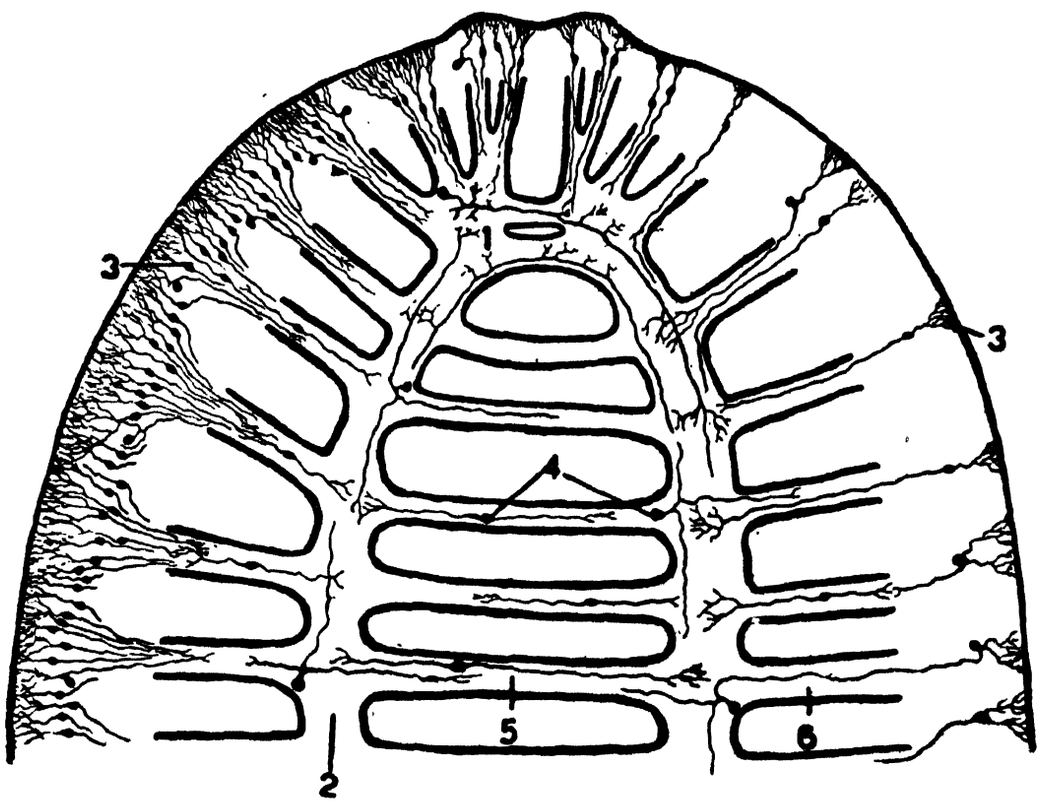


FIG. 27.—Anterior end of *Bdelloura candida* showing details of nerve-cell arrangement (*after Hanström*, 1926). 1, brain; 2, ventral cords; 3, sensory nerve cells forming marginal nerve; 4, associative neurons; 5, transverse commissures; 6, lateral nerves.

30*B*, 31*A*). The extirpation experiments of Müller (1936) indicate that these groups of bristles act as current detectors.

A statocyst is general throughout the Acoela, is also common among the Alloeocoela (*Hofstenia*, Fig. 31*F*, *Otomesostoma*, all members of the family Monocelididae, Fig. 29*C*), and occurs in the rhabdocoel genus *Catenula* (Fig. 29*D*); in short, a statocyst is characteristic of the more primitive Turbellaria and is probably inherited from coelenterate ancestors. Structurally the turbellarian statocyst is similar to the hydrozoan statocyst. It consists of a nucleated vesicle within which there is a lithocyte (sometimes two) enclosing a statolith (Fig. 31*G*). The statocyst is embedded in the brain or is very close to it and therefore has a strong nervous supply, although sensory endings have not been traced into the statocyst. The close association of the brain with the statocyst suggests that the brain may have arisen phylogenetically as a

nervous accumulation around the statocyst. Conditions in *Hofstenia*, if they could be shown to be primitive, would strongly support this suggestion (page 83).

Light perception is of general occurrence among the Turbellaria and is mediated by definite photoreceptors, the eyes or ocelli. General body sensitivity to light apart from the ocelli is also present, but the sensory structures involved have not been identified. The eyes are rarely epidermal pigment spots (acoel *Otocelis*, rhabdocoels *Microstomum*, *Alaurina*, Fig. 32*C*); nearly always they are pigment-cup ocelli sunk into the mesenchyme. There is usually one pair of eyes, sometimes two or three pairs, near the brain; but many eyes occur in some groups. Thus in the fresh-water triclads *Sorocelis* (Fig. 32*E*) and *Polycladodes* there are two clusters of eyes in place of the usual two eyes, and the genus *Polycelis* has a band of eyes around the anterior margin (Fig. 32*D*). The land planarian family Rhynchodemidae has but one pair of eyes; but in the Geoplanidae there are numerous eyes in a band or row along the whole body margin (Fig. 32*A*), and the Bipaliidae also possess numerous eyes on the lunate head and along the body margin (Fig. 14*D*). Polyclads nearly always have numerous eyes, in paired clusters in the brain region, on tentacles, in a band along whole or part of the body margin, or strewn over the head (Figs. 35*F–J*, 63*A*, 63*B*). Eye arrangement is employed as an important taxonomic character in land planarians and polyclads. Eyes are altogether lacking in the cave-dwelling planarians of the family Kenkiidae (Figs. 22*B*, 61*B*), in some endoparasitic rhabdocoels (Fig. 53), in many acoels, rhabdocoels, and alloeocoels, especially sand- and muck-dwelling forms, and in other cases without apparent relation to habits of life.

Each eye has the structure of a pigment-cup ocellus (page 37). It consists of one or more pigment cells forming a bowl or cup and of one to many photosensitive neurosensory cells projecting into the cup through its opening. The eye is therefore of the inverse type. The photosensitive cells, or *retinal* cells, are bipolar nerve cells whose rounded, expanded, or club-shaped distal end projects into the cup and whose proximal fiber joins the central nervous system (Fig. 32*F*, *G*). The distal tip is marked with longitudinal striations forming the *rod border*, of uncertain function. In the more advanced types, termed *retinal clubs*, the rod border extends along the whole surface of the club-like end of the sensory cell; hypothetical stages in the evolution of the retinal club are shown in Fig. 32*G*. In a very few turbellarians pigment cells are lacking and the retinal cells lie free in the mesenchyme near the brain. The most advanced eyes occur among the land planarians, but their structure is not thoroughly understood. Here the retinal clubs pass into the cup between the pigment cells (Fig. 32*F*) so that at least some of the clubs face the mouth of

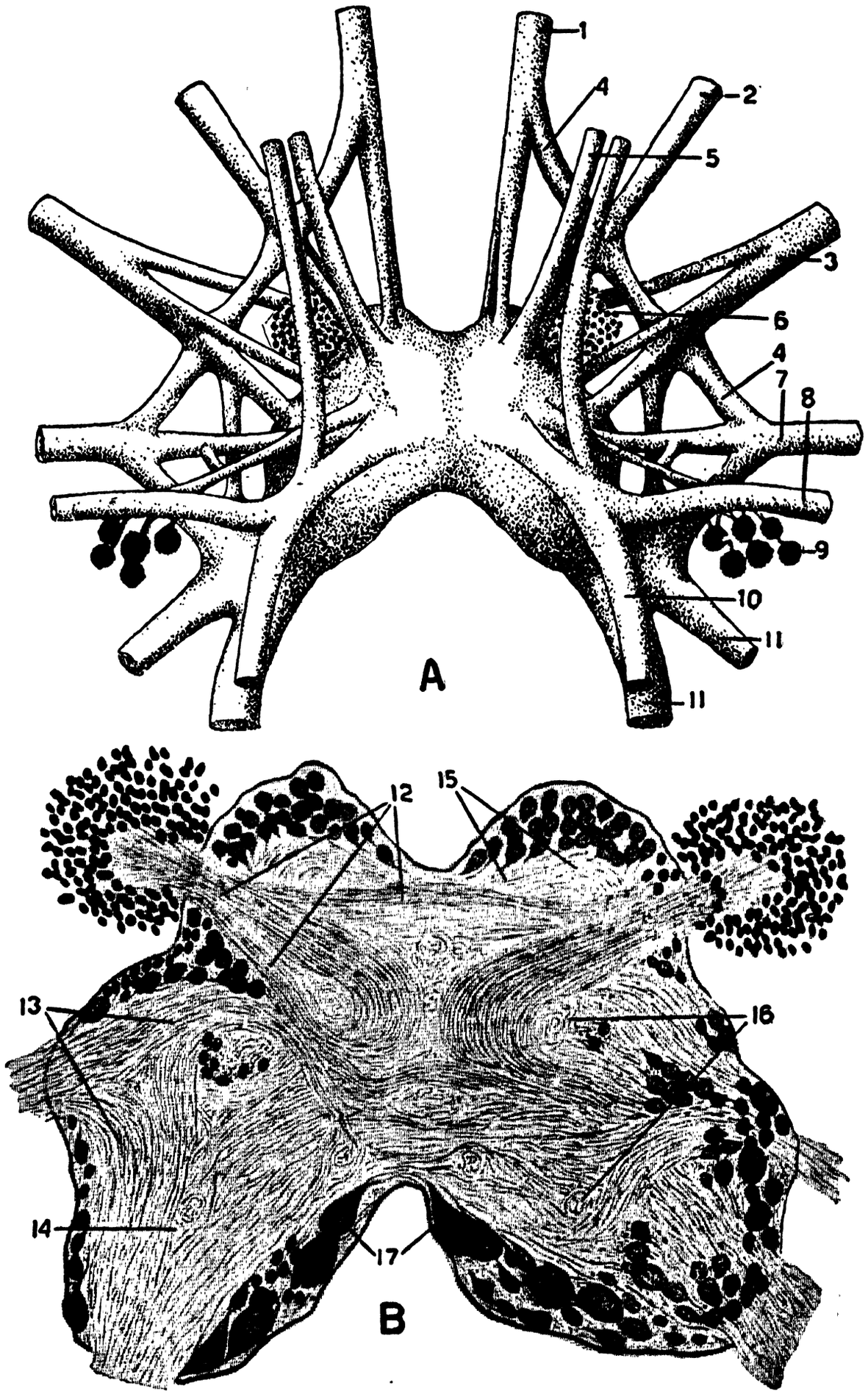


FIG. 28.—Brain of the leptoplanid polyclad *Notoplana atomata* (*after Hadenfeldt*, 1929). *A*. Dorsal view of the brain showing nerves. *B*. Horizontal section through the brain showing different types of nerve cells. 1, 2, 3, anterior nerves; 4, commissure connecting them; 5, anterior dorsal nerve; 6, granule mass (group of sensory cells outside the brain capsule); 7, lateral nerve; 8, lateral dorsal nerve; 9, cluster of tentacular eyes; 10, posterior dorsal nerve; 11, posterior nerves; 12, tracts of the granule mass; 13, tracts of the lateral nerve; 14, tract of the posterior nerve; 15, anterior nerve tract; 16, vertical tracts; 17, two types of large nerve cells.

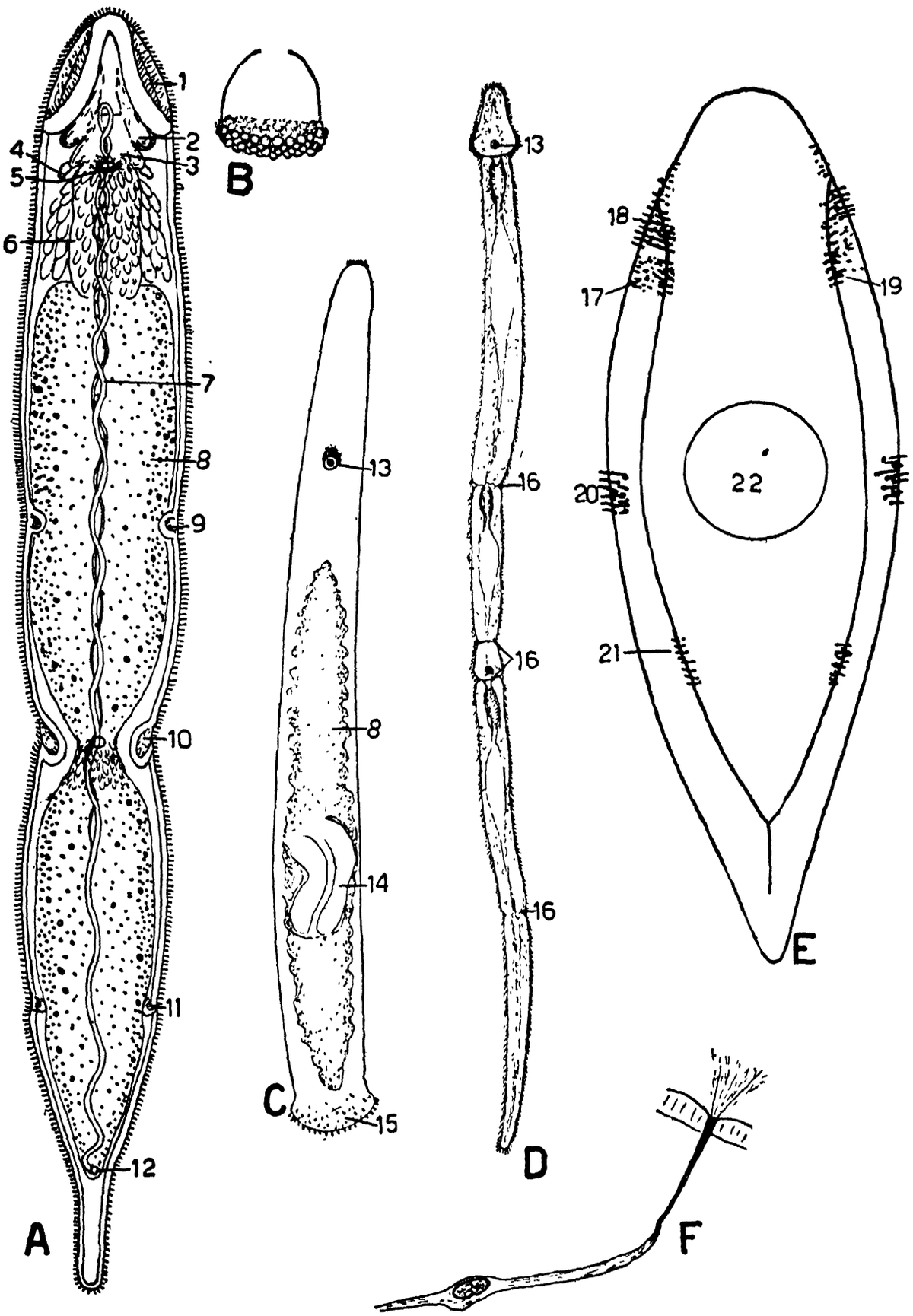


FIG. 29.—Some Turbellaria with conspicuous sense organs. *A*. Catenulid rhabdocoel *Stenostomum tenuicauda*, from life, with a pair of ciliated pits and bowl-shaped bodies; note single protonephridium. *B*. Bowl-shaped body of *A* enlarged. *C*. Alloeocoel *Monocelis*, from life, with conspicuous statocyst. *D*. Catenulid rhabdocoel *Catenula lemnae*, from life, with statocyst but no ciliated pits. *E*. Typhloplanid rhabdocoel *Bothromesostoma* (*after Müller*, 1936) with four pairs of rheoreceptors and one pair of chemoreceptive areas. *F*. A tangoreceptor, from the alloeocoel *Otoplana* (*after Hofsten*, 1918). Note that *A* and *D* consist of a chain of zooids. 1, ciliated pit; 2, pit ganglion; 3, brain; 4, bowl-shaped body; 5, mouth; 6, simple pharynx with gland cells; 7, protonephridium; 8, intestine; 9–11, ciliated pits of zooids; 12, nephridiopore; 13, statocyst; 14, plicate pharynx; 15, caudal adhesive area with adhesive papillae; 16, fission planes of zooids· 17, chemoreceptive areas; 18–21, the four rheoreceptive areas; 22, rosulate pharynx.

the cup, hence are of the converse type. There is further an epithelium over the mouth of the cup, forming a cornea, probably with some refractive power, so that possibly such eyes can form dim images. But in general the turbellarian eye can only distinguish light from dark and cannot form images, since it has no refractive apparatus. When two or few in number the eyes are close to or in contact with the brain so that the retinal nerve fibers enter the brain directly or form a short optic nerve passing to the brain. Otherwise, the retinal fibers enter the general submuscular plexus.

In a few rhabdocoels, especially *Stenostomum*, there are found in place of eyes one to four pairs of bodies attached to the brain and believed to be of light-refractive nature. These bodies consist of one to many refringent granules, plates, or rods or a single biconvex or bowl-shaped mass; they are generally attached to a clear vesicle that in turn connects with the brain (Fig. 29*A*, *B*). Since the mass or collection of bodies usually (but not always) forms a bowl over the vesicle (Fig. 29*B*), the structure is often termed the *bowl-shaped* (schüsselformig) body. There is no good evidence for the assumption of a photosensitive function of the bowl-shaped body.

11. Digestive System.—The digestive system consists of mouth, pharynx, and intestine. A mouth is present in all Turbellaria except the endoparasitic rhabdocoel family Fecampiidae in which it is lost in the adult state with other accompanying degeneration. The mouth is primitively situated at about the middle of the ventral surface but may occur anywhere along the mid-ventral line from anterior to posterior end. It is generally circular but may be a longitudinal or transverse slit and is provided with radial and circular fibers from the subepidermal musculature, by which it can be opened and closed. It is usually very expansible and capable of admitting large objects. The mouth may be regarded as phylogenetically identical with the blastopore of the Radiata.

A pharynx is primitively absent in some Acoela, secondarily lost in the *Fecampiidae;* otherwise the Turbellaria are provided with a pharynx, which is a muscular tube, presumably of stomodaeal nature, serving to grasp food and convey it to the intestine. The pharynx exists in three grades of structure: *simple*, *bulbous*, and *plicate*. The simple pharynx or *pharynx simplex* occurs in Acoela, *Hofstenia*, and the rhabdocoel suborders Notandropora and Opisthandropora. It is merely a short tube formed of inturned ciliated epidermis accompanied by the usual subepidermal musculature not noticeably thickened or altered (Fig. 33*A*) except in *Hofstenia* which has an extremely long and muscular pharynx simplex (Fig. 31*F*). The simple pharynx is not delimited from the mesenchyme; mesenchymal unicellular glands may open through its epithelium.

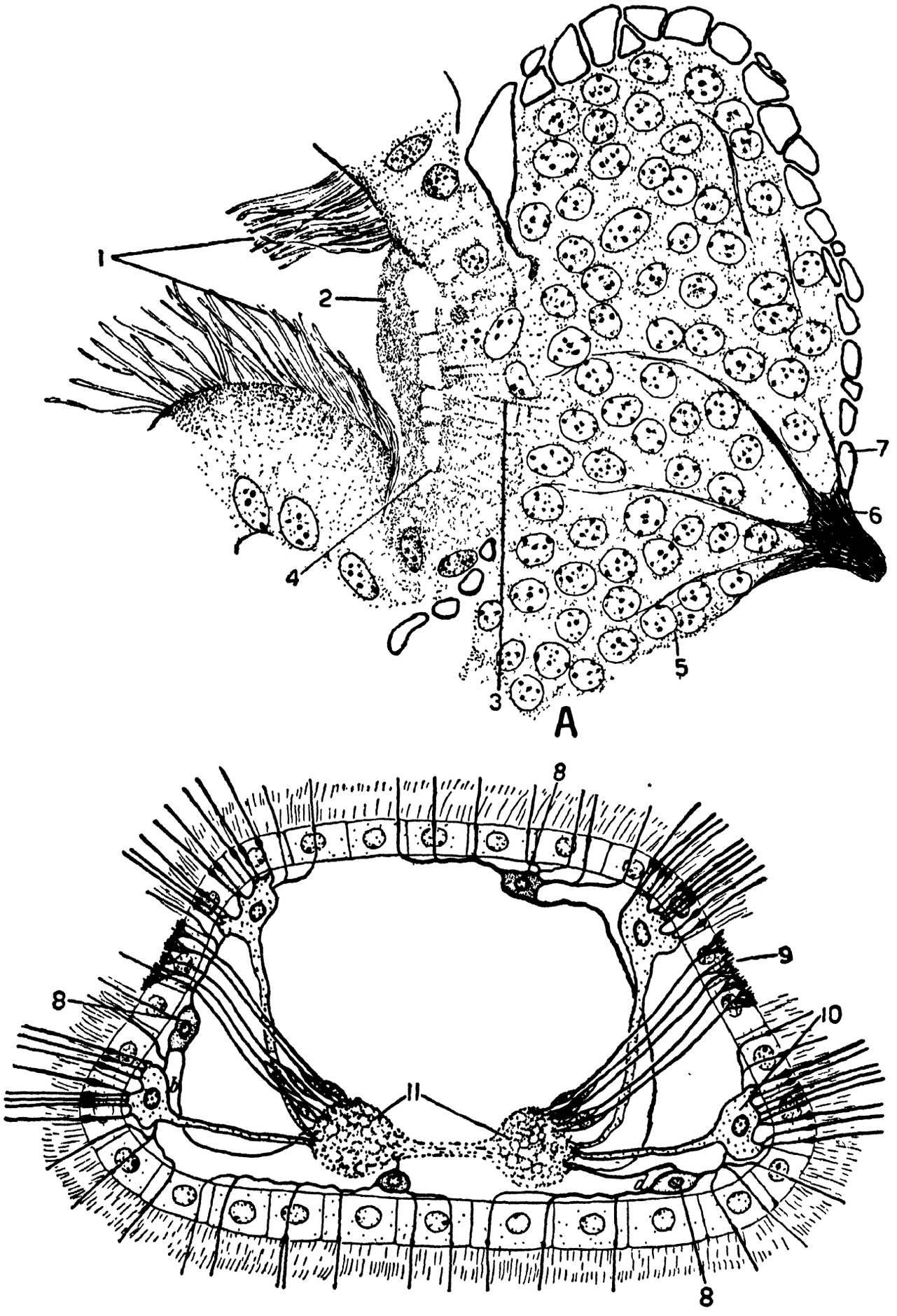


FIG. 30.—Rhabdocoel sense organs. *A*. Section through the ciliated pit of *Stenostomum* (*after Kepner and Cash*, 1915). *B*. Diagrammatic section through the head of *Mesostoma* to show four of the eight rheoreceptors, the two groups of chemoreceptors, and four tangoreceptors (*after Gelei*, 1930). 1, cilia of the sides of the pit; 2, secretion mass in bottom of pit; 3, sensory epithelium of bottom of pit; 4, sensory processes of same; 5, pit ganglion; 6, fibers to brain; 7, muscles; 8, tangoreceptor; 9, group of chemoreceptors; 10, rheoreceptor; 11, brain.

In the bulbous type of pharynx, the proximal part of the pharyngeal tube is much thickened, has greatly increased muscularity, and is sharply delimited from the mesenchyme (Fig. 33*B*). The distal portion remains nonmuscular, forming the *pharyngeal cavity* into which the tip of the bulbous part may project. The pharyngeal cavity is generally short and broad but may be much lengthened, forming a *buccal tube* (Fig. 59). These cavities are lined by an altered epidermis, flattened, unciliated, often syncytial, underlain by the usual subepidermal musculature. The pharynx bulb consists of muscles, mesenchyme, gland cells, and nervous tissue. There are outer and inner muscle strata of circular and longitudinal fibers, of which the inner stratum, next the lumen, is the stronger, particularly as to its circular layer; this may form a sphincter at one or both ends of the pharynx. Numerous radial fibers also course between the two surfaces of the bulb (Fig. 33*B*). The pharynx is provided with gland cells, eosinophilous or cyanophilous, or both, strewn between the muscle fibers and also often entering the pharynx from without. Their necks usually open at the pharynx tip, often after aggregating into bundles (Fig. 18*B*). The bulbous pharynx has an abundant nerve supply (Fig. 25*A*) by way of one or more pairs of nerves entering it from the brain or from the ventral cords; these break up into a plexus in the bulb often concentrated into a nerve ring near the tip. Besides its intrinsic musculature, the bulbous pharynx is also usually attached to the body wall by extrinsic muscle bands that permit its eversion and retraction. Usually the pharynx bulb can be protruded by the turning inside out of the pharyngeal cavity.

The bulbous pharynx occurs in two main types, the *rosulate* and the *doliiform*. The rosulate pharynx, characteristic of the rhabdocoel section Typhloplanoida, is spherical, oriented at right angles to the body axis, and provided with conspicuous radial muscle fibers and numerous gland cells, both intrinsic and extrinsic (Fig. 36*A*). The doliiform pharynx, characteristic of the section Dalyellioida, is cask-shaped, oriented parallel to the body axis, has a sparse gland supply, and its muscle layers, viewed from above, often have a lattice-like appearance (Fig. 34*D*). A variant of the doliiform pharynx called the *variable* pharynx is found among the lower Alloeocoela, differing in a less rigid shape and various alterations of the arrangement of the muscle layers.

The plicate pharynx is a free cylindrical fold projecting into the large pharyngeal cavity (Fig. 11*A*, *B*). It may project from the anterior end of the cavity, hence point backward, or from the rear end, hence point forward, or may depend from the roof of the cavity, hence hang downward. It is usually a simple hollow cylinder but is much ruffled in those polyclads in which it hangs from the roof and also in some land planarians. The plicate pharynx is characteristic of triclads, polyclads, and the higher

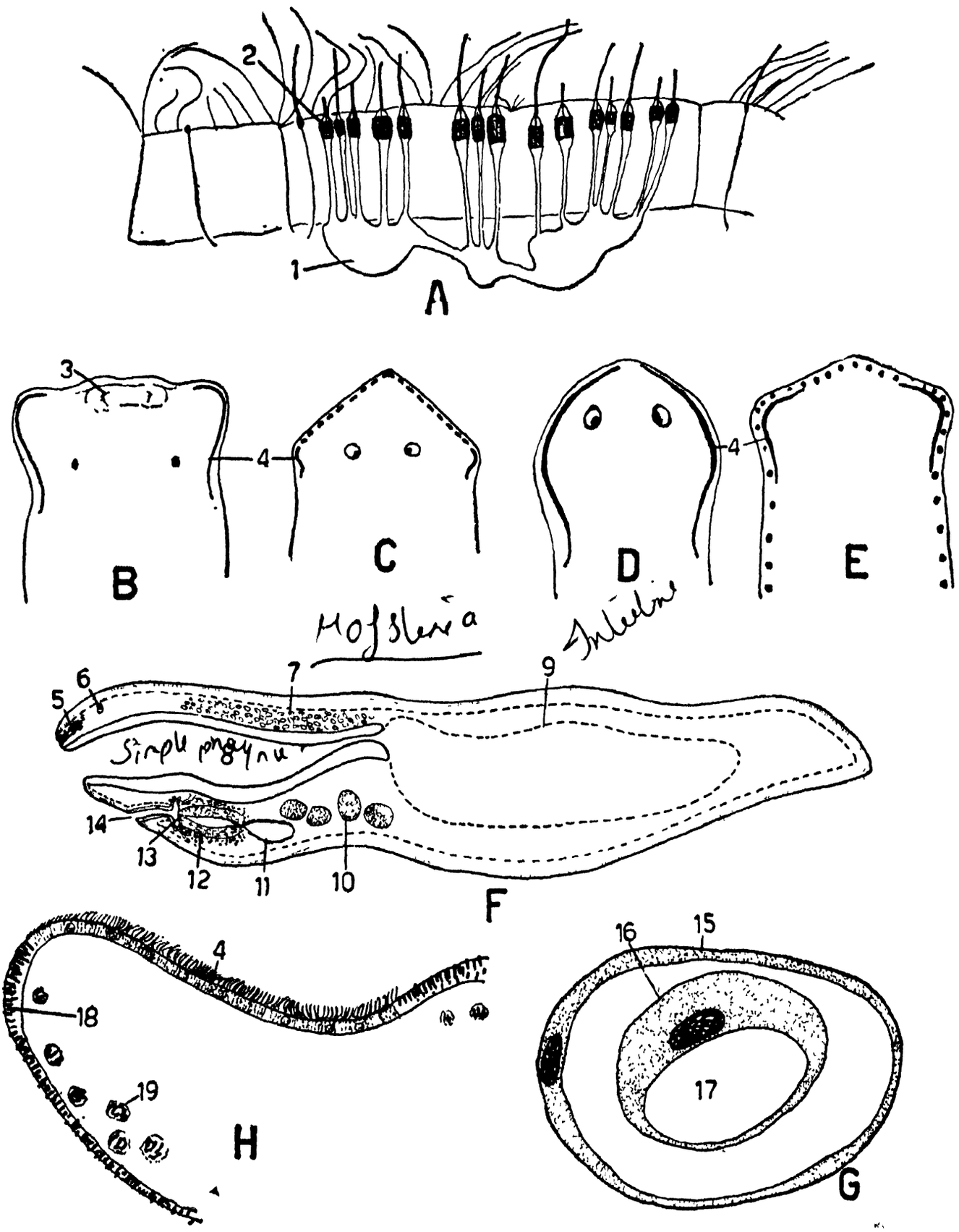


FIG. 31.—Sense organs of Turbellaria (continued). *A*. One of the rheoreceptors of *Mesostoma* (*after Gelei*, 1930). *B–E*, Heads of four species of European fresh-water planarians to show the auricular sense organ (*after Steinmann*, 1930). *B. Dendrocoelum lacteum*. *C. Dugesia gonocephala*. *D. Dugesia polychroa*. *E. Polycelis tenuis*. *F*. Sagittal section of *Hofstenia atroviridis*, Japan, to show general structure (*after Bock*, 1923). *G*. The statocyst of *Hofstenia* (*after Bock*, 1923). *H*. Transverse section through the auricle of a fresh-water planarian, to show the auricular sense organ. 1, rheoreceptive neurosensory cell; 2, sensory processes of same; 3, adhesive organ; 4, auricular sense organ; 5, frontal gland; 6, statocyst; 7, testes; 8, simple pharynx; 9, intestine; 10, ovary; 11, seminal vesicle; 12, prostatic vesicle; 13, penis; 14, male gonopore; 15, vesicle; 16, lithocyte; 17, statolith (dissolved out); 18, rhabdites; 19, rhabdite-forming glands.

alloeocoels. It belongs to the protrusible type (Fig. 11*A*, *B*), i.e., when used becomes much elongated through muscular action and is protruded through the mouth. Hence in those turbellarians which have a plicate pharynx, food is ingested through the orifice of the pharynx and not through the mouth. Numerous pharynges occur in some fresh-water and land planarians (Fig. 34*C*), and this *polypharyngy* may be accompanied by a similar multiplication of mouth openings.

The plicate pharynx is of complicated histological construction, having muscular, glandular, and nervous layers. The layers usually present are: outer epithelium, outer longitudinal muscle layer, outer circular muscle layer, outer zone of gland cells, nerve plexus, inner zone of gland cells, inner longitudinal muscle layer, inner circular muscle layer, lining epithelium; and all these layers are crossed by numerous radial muscle fibers extending from the inner to the outer epithelium (Fig. 33*D*). The pharyngeal epithelia are mostly of the insunk type, with nuclei sunk beneath the muscle layers, and are provided with peculiar short stiff cilia. The gland cells are of both cyanophilous and eosinophilous types and open mostly at the pharynx tip. They appear to be similar to body gland cells and seem to have no special digestive function; rather their slimy and sticky secretions serve to entangle, possibly also to paralyze, prey and to lubricate the ingestion process. The pharynx is often also supplied with extrinsic gland cells situated in the mesenchyme near its attached end. The nerve plexus of the plicate pharynx springs from the ventral cords and is usually a thick conspicuous layer but may be limited to a nerve ring near the free end. Not uncommonly subsidiary plexi occur among the muscle layers (Fig. 33*D*). In the pharyngeal plexus of the marine triclad *Bdelloura candida* (Fig. 34*A*), there occur sensory nerve cells whose fibers break up into numerous endings at both epithelia, motor cells with endings on the pharynx musculature, and associative cells (Hanström, 1926). Hence the nerve plexus of the triclad pharynx forms a self-sufficient system, and the isolated pharynx can carry out all activities, including the ingestion of food (Wulzen, 1917; Kepner and Rich, 1918).

The plicate pharynx is not delimited from the mesenchyme, as is the bulbous pharynx, and its histological layers are continuous with those of the general body.

The pharynx may lead directly into the intestine, but often a very short narrow *esophagus* intervenes. The intestine, absent in the Acoela, varies from a simple rounded or elongated sac to a highly branched tubular system (Fig. 35). It is composed of a single-layered epithelium, the gastrodermis, sometimes syncytial, especially during digestion, but usually consisting of large clavate cells with narrowed bases and bulging free ends. The gastrodermal cells may be all of one kind but often are of

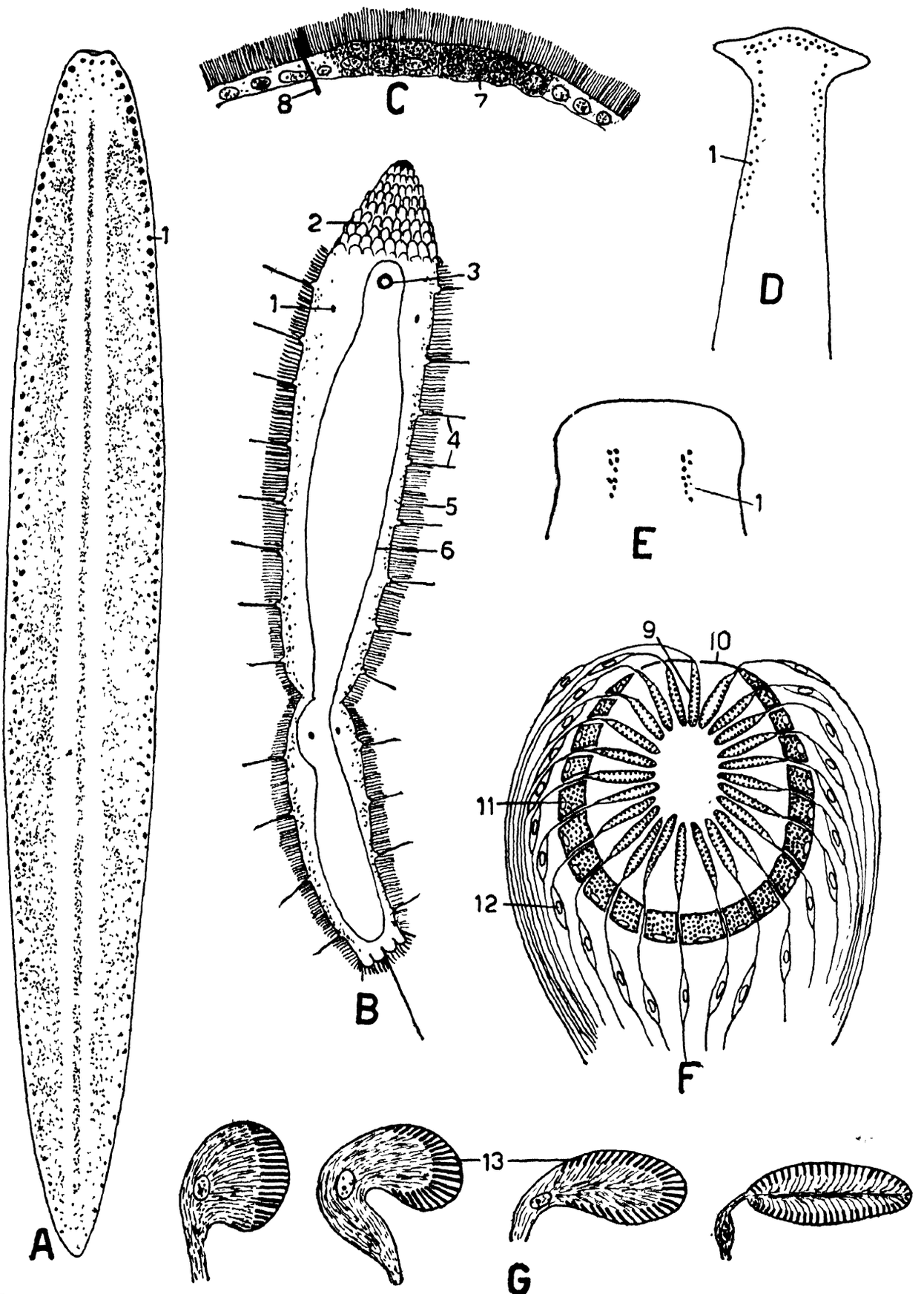


FIG. 32.—Eyes of Turbellaria. *A.* Land planarian *Geoplana mexicana* (*after Hyman*, 1939a), introduced into California; has row of eyes along entire margin. *B.* Pelagic microstomid rhabdocoel *Alaurina prolifera* (*after Busch*, 1851) with papillate snout, buoyant bristles, and epidermal eyes. *C.* Section through the eye of Alaurina (*after Brinkmann*, 1906). *D.* Head of fresh-water planarian, *Polycelis coronata*, northwestern United States, to show eye arrangement, from life. *E.* Head of fresh-water planarian *Sorocelis americana*, from Oklahoma cave, to show eyes. *F.* Diagram of advanced type of eye of a land planarian with retinal clubs (*after Hesse*, 1902). *G.* Stages in the evolution of the retinal club (*after Hofsten*, 1918). 1, eyes; 2, papillate snout; 3, mouth; 4, bristles; 5, cilia; 6, intestine; 7, epidermal eye; 8, neck of gland cell; 9, retinal clubs; 10, cornea; 11, pigment cells; 12, nerve cell bodies of retinal clubs; 13, rod border.

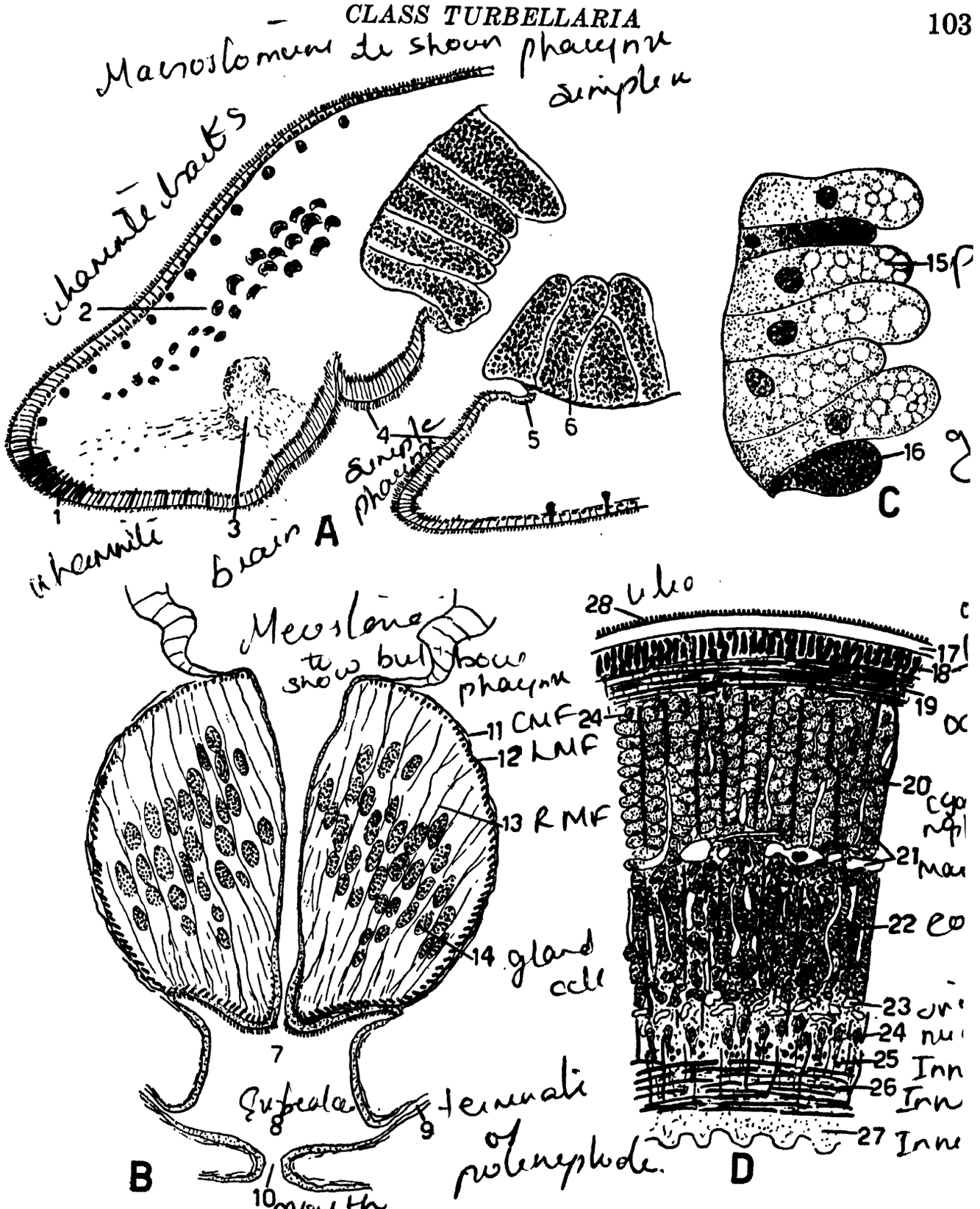


FIG. 33.—Digestive system. *A*. Longitudinal section through the anterior end of *Macrostomum* to show the pharynx simplex. *B*. Cross section through *Mesostoma* to show the bulbous pharynx of the rosulate type; also shows excretory beaker. *C*. Gastrodermis of a planarian, showing the two types of cells. *D*. Cross section through the triclad pharynx showing its histological construction. 1, rhammites, 2, rhammite tracks; 3, brain; 4, simple pharynx; 5, esophagus; 6, intestine; 7, pharyngeal cavity; 8, excretory beaker; 9, termination of protonephridium; 10, mouth; 11, circular muscle fibers; 12, longitudinal muscle fibers; 13, radial muscle fibers; 14, gland cells; 15, phagocytic cells; 16, granular clubs; 17, outer insunk epithelium; 18, outer longitudinal muscle layer; 19, outer circular muscle layer; 20, zone of cyanophilous gland cells; 21, main nerve plexus; 22, zone of eosinophilous gland cells; 23, inner nerve plexus; 24, nuclei of insunk epithelium; 25, inner longitudinal muscle layer; 26, inner circular muscle layer; 27, inner insunk epithelium; 28, cilia.

two sorts: the regular intestinal cells just described, usually called *phagocytic* cells; and the smaller *granular clubs*, cells filled with spherules, usually of eosinophilous nature (Fig. 33*C*). The granular clubs are generally regarded as gland cells and their spherules as forerunners of digestive enzymes, but they have not been consistently observed to show any changes during digestion and it is probable that they are protein reserve cells (page 204). The phagocytic cells generally contain much stored fat and after feeding are packed with food vacuoles. The gastrodermis is ciliated in the lower rhabdocoels (Catenulida, Macrostomida), a few alloeocoels such as *Bothrioplana*, and throughout the polyclads. The gastrodermis is underlain by a muscular stratum in some rhabdocoels and alloeocoels and especially in the polyclads.

In the Acoela the mouth may open directly into the mesenchyme or a short, rarely long, pharynx simplex, lined by ciliated epidermis, may intervene. The remarkable acoel, *Ectocotyla paguri* (Fig. 13*F*, page 129), differs from all other Acoela in having a protrusible plicate pharynx of simple histological construction. The Acoela lack an intestine (Fig. 37*D*), and the phagocytic cells occur in the mesenchyme, either scattered throughout this in the simpler cases, or limited to a central region where they may fuse to form a digesting syncytium, more or less definitely distinguishable from the peripheral mesenchyme. The food consists of diatoms, algae, and small animals such as protozoans and copepods, swallowed whole and digested entirely by the intracellular method in the phagocytic cells or the central syncytium.

A pharynx simplex (Fig. 33*A*) is characteristic of the rhabdocoel orders Catenulida and Macrostomida; other rhabdocoels have a rosulate or doliiform bulbous pharynx preceded by a pharyngeal cavity. A brief esophagus is usually present leading into the blind intestine of sac-like or tubular form, generally of simple contour but sometimes with slight lateral outpouchings. Prey is generally swallowed whole or sucked in by forms with a rosulate pharynx as this is not distensible.

The Alloeocoela may have any type of pharynx; the intestine is often similar to that of rhabdocoels but in the higher alloeocoels tends to have lateral diverticula and in *Bothrioplana* approaches the triclad condition, parting around the pharynx although single again behind this (Fig. 35*D*).

The digestive system is of very uniform construction throughout the triclads. The mouth situated near the body middle leads into a large cylindrical pharyngeal cavity from whose anterior wall the tubular plicate pharynx projects posteriorly. A very short esophagus leads into the intestine which immediately forks into three branches or rami (whence the name Tricladida), one running anteriorly to the anterior end and two passing backward, one to either side of the pharyngeal cavity (Fig. 35*E*). Each ramus gives off numerous lateral diverticula, often secondarily

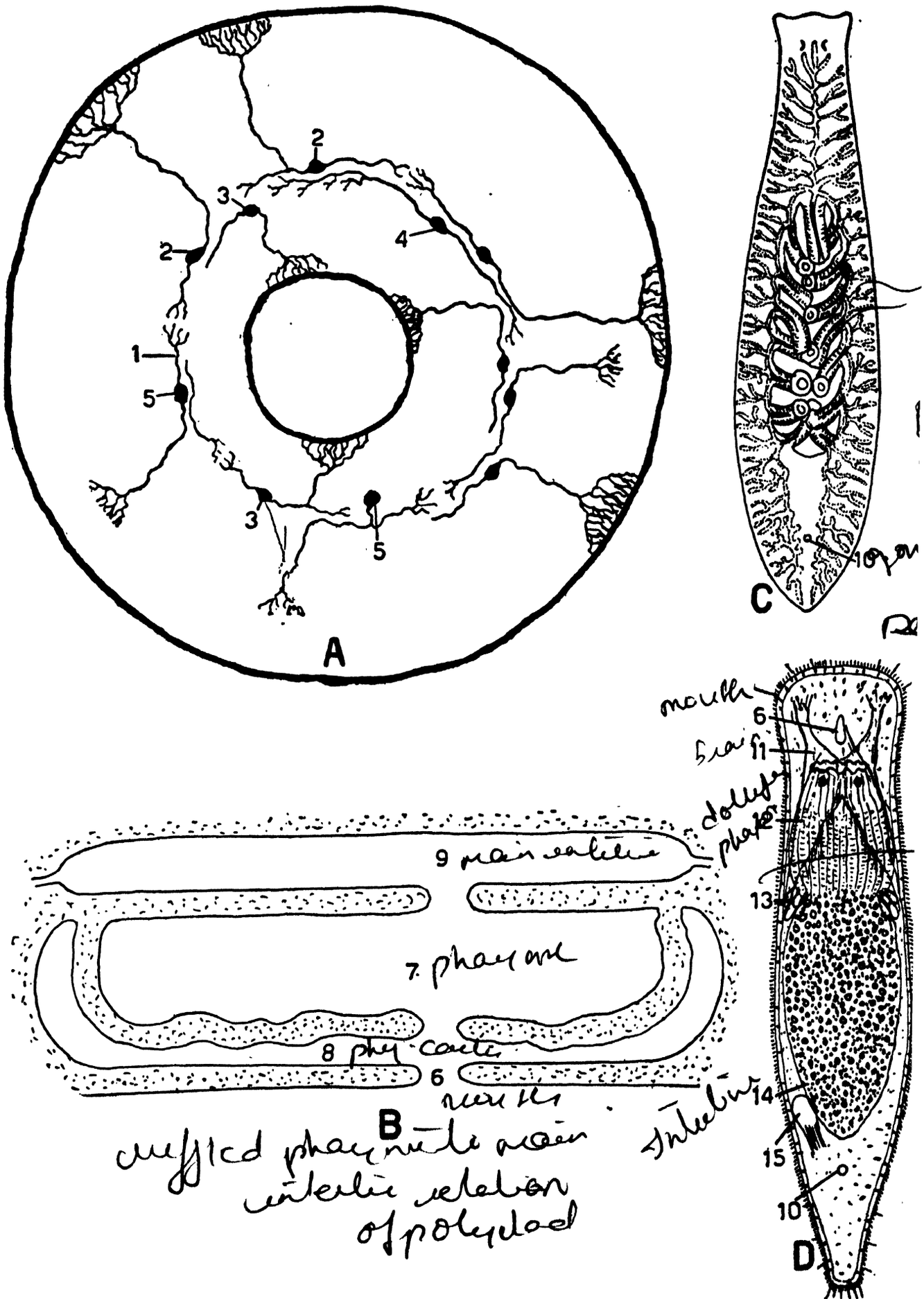


FIG. 34.—Digestive system (continued). *A*. Golgi preparation of a cross section through the triclad pharynx showing neuron arrangement (*after Hanström*, 1926). *B*. Longitudinal median section of a polyclad showing relation of ruffled pharynx to the main intestine. *C. Phagocata gracilis* with multiple pharynges, from life, Pennsylvania. *D. Dalyellia*, with doliiform pharynx, from life, Maine. 1, main nerve plexus; 2, sensory nerve cells with nerve endings at outer surface; 3, sensory nerve cells with nerve endings at inner surface; 4, associative neuron; 5, motor neurons; 6, mouth; 7, pharynx; 8, pharyngeal cavity; 9, main intestine; 10, gonopore; 11, brain; 12, doliiform pharynx; 13, pharyngeal gland cells; 14, intestine; 15, penis stylet.

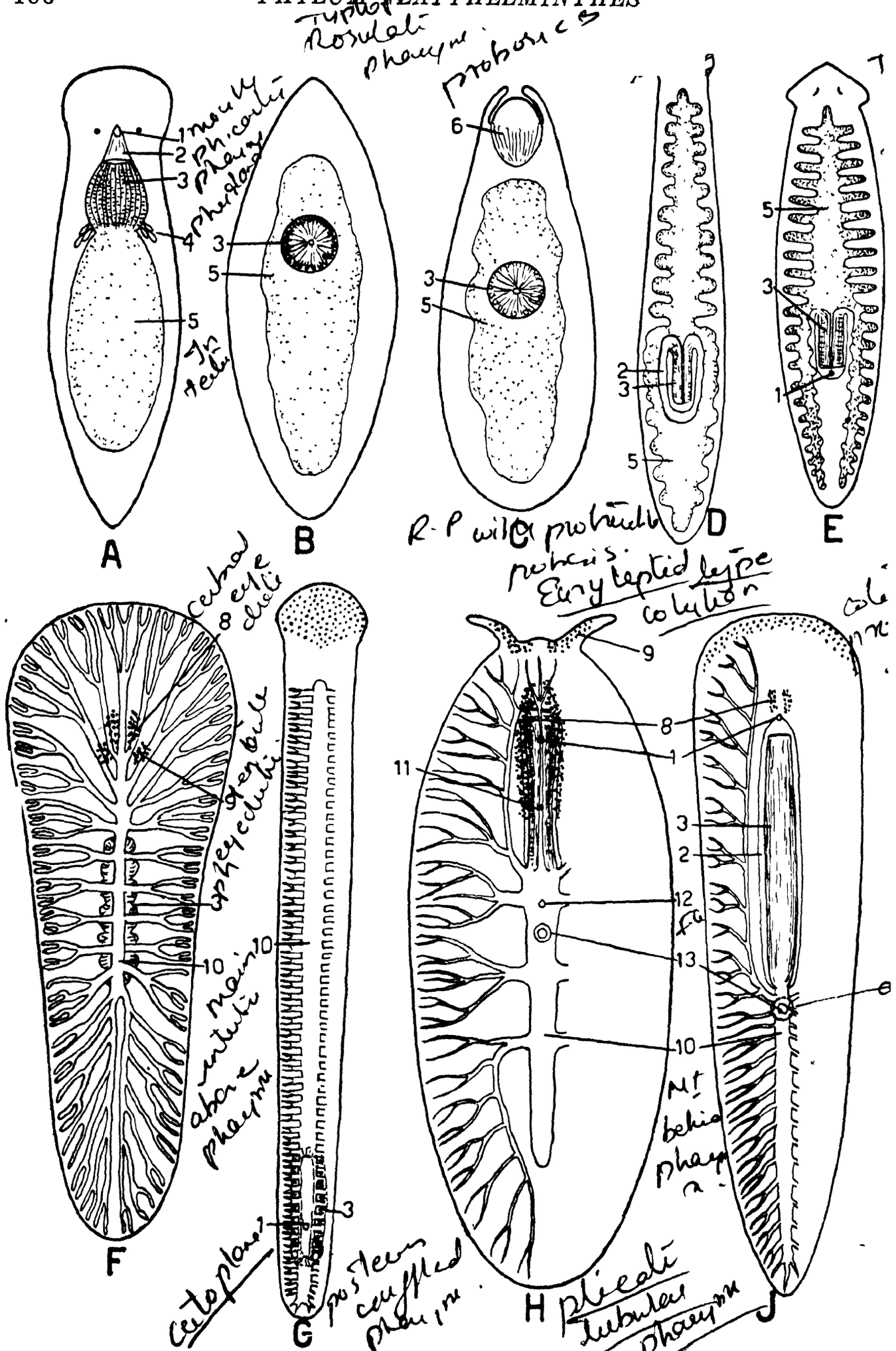


FIG. 35. Digestive system (continued). Diagrams of various turbellarian digestive tracts. *A*. Dalyellioid rhabdocoel, with doliiform pharynx. *B*. Typhloplanoid rhabdocoel, with rosulate pharynx. *C*. Kalyptorhynchid rhabdocoel, with rosulate pharynx and anterior protrusible proboscis. *D*. Alloeocoel *Bothrioplana* with two pairs of ciliated

branched and united by anastomoses. The two posterior rami may be united by cross branches and confluent at the posterior ends. The gastrodermis has many granular clubs and usually lacks a muscular layer. The only exceptions to the above description occur in some land planarians that may have a flaring or ruffled pharynx. The triclads do not swallow their food whole but suck it in by peristaltic action of the protruded pharynx.

The polyclad digestive system (Fig. 35*F–J*) is less uniform. The mouth may open into the anterior, middle, or rear part of the pharyngeal cavity which also may be situated anywhere in the body, although usually central or anterior. The pharynx is always plicate but varies from ruffled to tubular. The ruffled type found in most Acotylea and several cotylean families hangs down from the dorsal wall of the pharyngeal cavity as a much frilled or ruffled oval or circular curtain (Fig. 34*B*) whose attachment is also sinuous and whose folds are accompanied by corresponding pouches of the pharyngeal cavity. Through transitional bell-like or flaring shapes of pharynx whose attachment tends to shift horizontally, the cylindrical horizontal type of pharynx like that of triclads is attained in the higher acotylean and cotylean families; this is, however, attached at its rear end and directed anteriorly (Fig. 35*H*, *J*). The polyclad intestine consists of the *main* or *central* intestine, a median tube that lies either above the ruffled type of pharynx (Fig. 34*B*) or behind the anteriorly located tubular type; and of the numerous branches (whence the name Polycladida) given off from the main intestine and ramifying throughout the body, often uniting to form a network. The form of the branching depends upon the shape of the animal; several types of intestinal branching in polyclads are shown in Fig. 35*F–J*. Anal pores occur in a few cotylean polyclads, usually as a series of dorsal or lateral pores (*Cycloporus*, Fig. 65*C*, *Yungia*), but in one species (*Leptoteredra maculata*) as a single posterior dorsal pore.

12. Excretory System.—This consists of protonephridia provided with terminal flame bulbs. It is entirely wanting in the Acoela and in general is less developed in marine than in fresh-water Turbellaria. The tubule consists of a one-layered, usually unciliated cuboidal or syncytial epi-

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pits, plicate pharynx, and intestine forked around the pharynx. *E*. Triclad, with plicate pharynx and three-forked intestine. *F–J*. Various types of polyclad digestive tracts; note also eye arrangement. *F*. Acotylean leptoplanid type, seen from above, with four eye clusters, central ruffled pharynx, main intestine above it, and radiating branches. *G*. Acotylean genus *Cestoplana*, with eyes strewn over the anterior end, posterior ruffled pharynx, long main intestine with lateral branches. *H*. Cotylean euryleptid type with marginal tentacles bearing eyes, also cerebral eye clusters, plicate tubular pharynx directed forward, adhesive disk, and main intestine behind the pharynx, giving off a few main branches. *J*. Cotylean prosthiostomid type with band of eyes across the anterior margin, otherwise similar to *H*. 1, mouth; 2, pharyngeal cavity; 3, pharynx; 4, pharyngeal glands; 5, intestine; 6, proboscis; 7, ciliated pits; 8, cerebral eye cluster; 9, tentacular eye cluster; 10, main intestine; 11, male gonopore; 12, female gonopore; 13, adhesive disk.

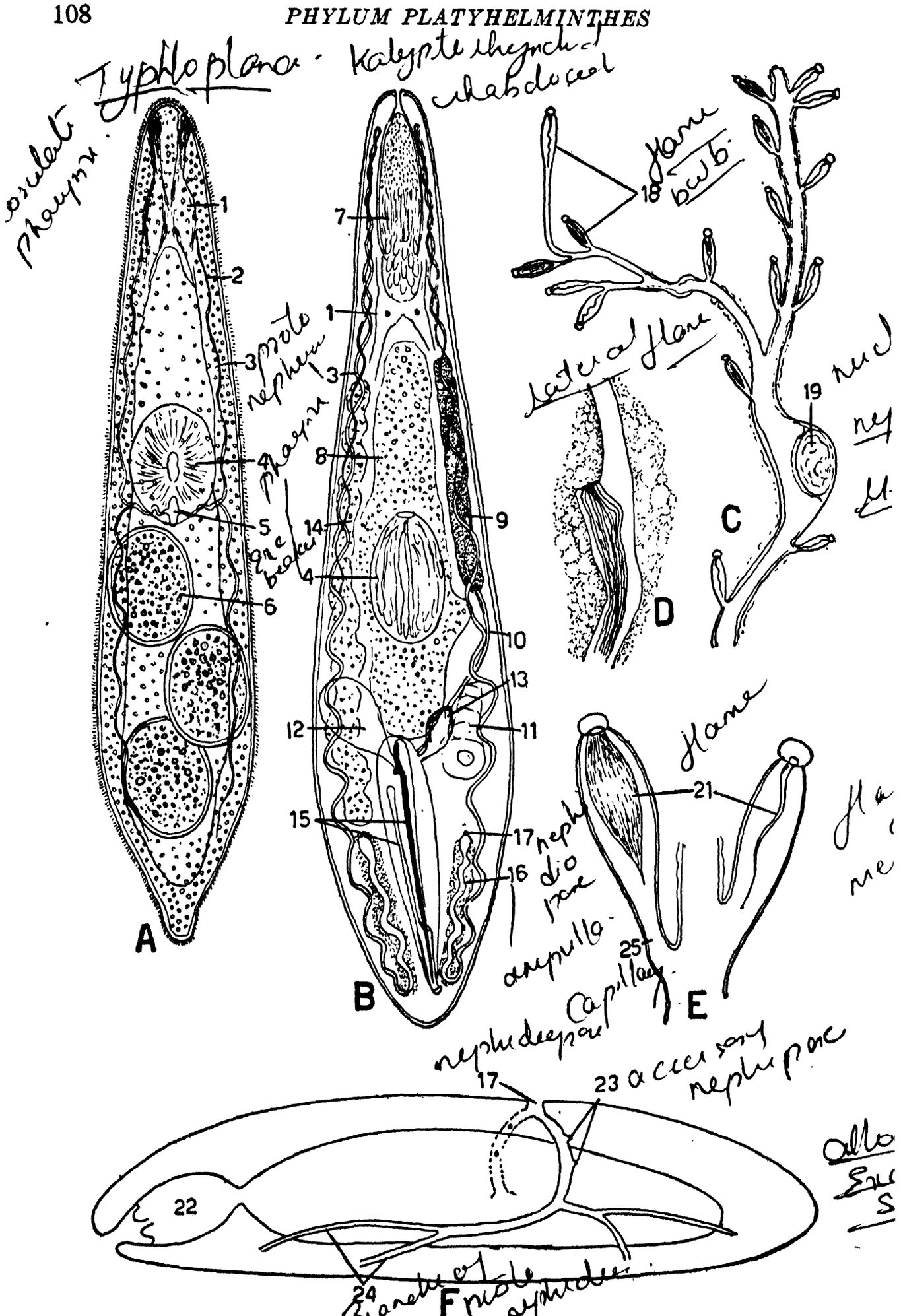

FIG. 36. Excretory system. *A. Typhloplana viridata*, from life, rhabdocoel with rosulate pharynx, symbiotic zoochlorellae, three subitaneous eggs, and protonephridia opening into the pharyngeal cavity by way of an excretory beaker. *B. Gyratrix hermaphroditus*, from life, kalyptorhynchid rhabdocoel with posterior nephridiopores preceded by ampullae. *C.* Part of the nephridium of *Mesostoma*, showing numerous flame bulbs derived from one cell (*after Reisinger*, 1923). *D.* Lateral flame of *Mesostoma* (*after Luther*, 1904). *E.*

thelium. The tubule gives off numerous fine branches termed capillaries, each of which terminates in a flame bulb. The capillary is considered to be part of the cell that forms the bulb or bulbs. Generally the flame bulb and its capillary constitute a single tubular cell, the flame cell, whose bulbous free end bears a tuft of cilia, the "flame," that vibrates within the capillary. However, in some rhabdocoels, especially mesostomine genera, one cell may differentiate into a number of capillaries and flame bulbs (Reisinger, 1923, Fig. 36*C*), so that the name flame cell should not be used as synonymous with flame bulb. The ciliary flame may be flat and ribbon-like (Fig. 36*E*) or may have the shape of a hollow cone or cylinder (Fig. 12*B*). The free end of the flame bulb may send delicate cytoplasmic processes into the mesenchyme. Not uncommonly in rhabdocoels, tufts of cilia, here termed *lateral flames*, may occur along the main tubule (Fig. 36*D*), and their occurrence may be correlated with a paucity of terminal flame bulbs.

The external opening of the protonephridium is termed the nephridiopore, and the terminal part of the tubule just prior to the pore may be expanded into a contractile region, the ampulla or bladder (Fig. 36*B*). Ampullae seem to occur only in fresh-water representatives of marine Turbellaria.

In the Catenulida there is a single median protonephridium doubled on itself and with a posterior nephridiopore (Fig. 29*A*). It has been claimed that the Catenulida have no flame bulbs; but Kepner, Carter, and Hess (1933) and Hess (1937) saw them in *Stenostomum*. Other rhabdocoels have a pair of protonephridia that run the body length and turn back on themselves at one or both ends (Fig. 36*A*, *B*). Where the nephridiopores are centrally located, each tubule commonly soon divides into an anterior and a posterior branch, each of which doubles back at the body ends (Fig. 36*A*). Distally the main tubules may fuse to a common tubule and pore or separately or after fusion may join the pharyngeal cavity (Fig. 36*A*) or the genital antrum. In the typhloplanine and mesostomine rhabdocoels the two tubules enter a so-called excretion beaker that is interpolated between the pharyngeal cavity and the mouth (Fig. 33*B*) or may be considered part of the pharyngeal cavity.

In alloeocoels the system is similar to that of rhabdocoels, but there may be two or three main stems on each side, and often additional nephridiopores occur (Fig. 36*F*).

Flame bulbs of *Mesostoma* in front and side view showing shape of the flame (*after Reisinger*, 1923). *F*. Excretory system of the plagiostomid alloeocoel *Hydrolimax grisea* (*after Hyman*, 1938). 1, brain; 2, zoochlorellae; 3, protonephridium; 4, rosulate pharynx; 5, excretory beaker; 6, subitaneous eggs; 7, proboscis; 8, intestine; 9, single testis; 10, sperm duct; 11, ovary; 12, seminal bursa; 13, prostatic vesicle; 14, single yolk gland; 15, penis stylet and sheath; 16, ampulla; 17, nephridiopore; 18, flame bulb; 19, nucleus; 20, lateral flame; 21, flame; 22, variable pharynx; 23, accessory nephridiopores; 24, branches of protonephridum; 25, capillary.

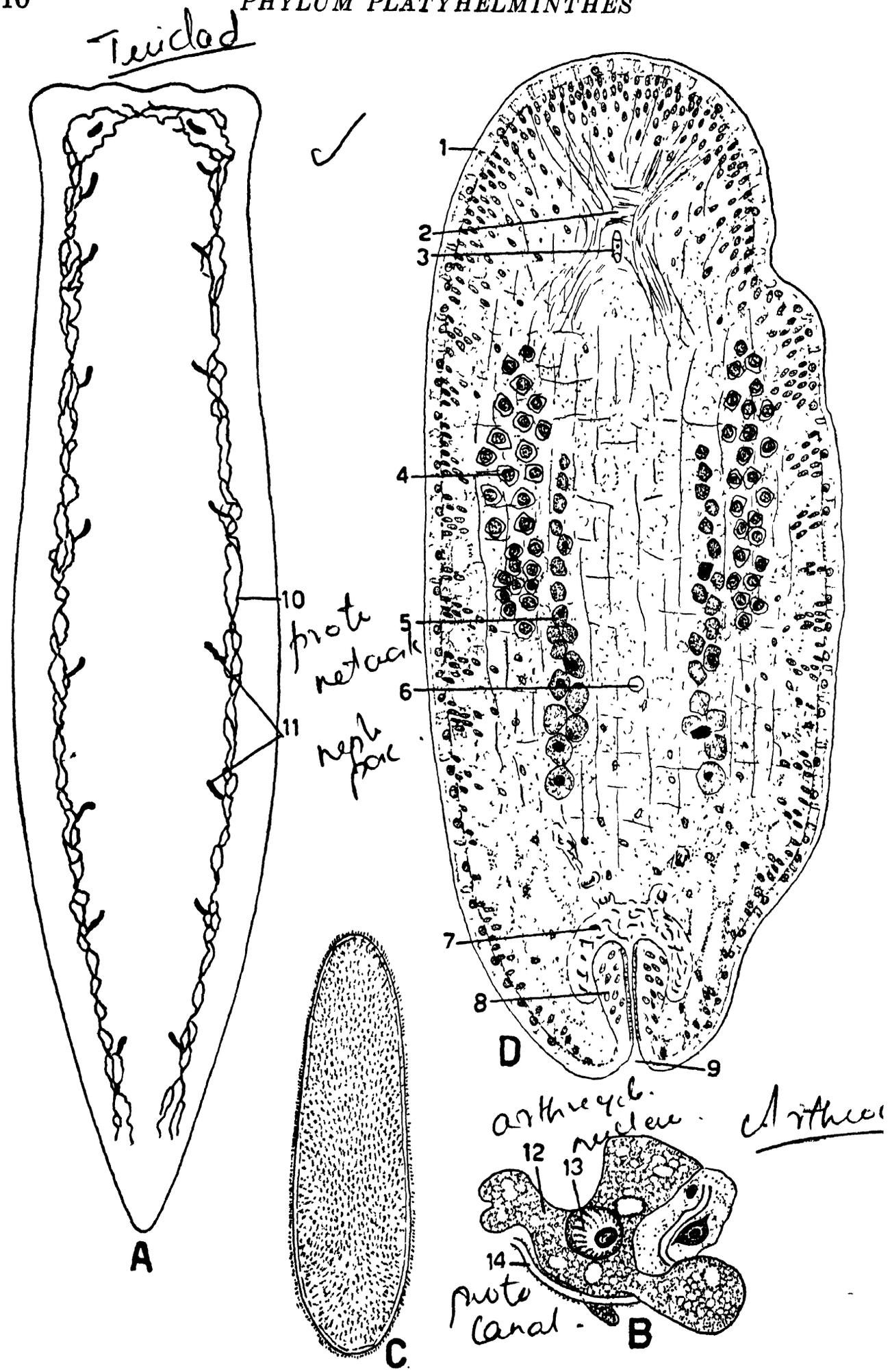

FIG. 37.—Excretory system (continued). Reproductive system. *A*. Triclad *Dendrocoelum lacteum*, showing excretory system (*after Wilhelmi*, 1906). *B*. Athrocyte wrapped around an excretory canal of *Rhynchomesostoma* (*after Luther*, 1904). *C*. Acoel *Afronta aurantiaca*, family Proporidae, from life, Main Coast. *D*. Frontal section of *Afronta* (*after Hyman*. 1944), showing simplest type of reproductive system found among the Turbellaria;

In triclads there are usually one to four tubules on each side, and these are commonly anastomosed into a network or if single broken up into a network, with numerous nephridiopores (up to several hundred). There may be two dorsal and two ventral pairs of tubules or one dorsal and one ventral pair or one or two dorsal pairs without ventral pairs (Fig. 37*A*). The tubules are located just beneath the epidermis and open on the nearest adjacent surface so that there may be both dorsal and ventral pores.

Little is known of the nephridial system of polyclads beyond the fact that flame bulbs occur.

In a number of Turbellaria there have been noticed associated with the nephridial system large cells with conspicuous nuclei and vacuolated cytoplasm. These cells, termed *athrocytes* or *paranephrocytes*, occur singly or in clusters that may be anastomosed into a syncytium in the vicinity of or wrapped around nephridial tubules (Fig. 37*B*). They are assumed to be of excretory nature from the fact that they readily take up vital dyes and so may be made conspicuous in small and more or less translucent turbellarians by immersing these in solutions of vital dyes.

13. Reproductive System.—The Turbellaria are hermaphroditic with very few exceptions, that is, each individual contains a complete male and a complete female reproductive system. These may be wholly separate, each with its own gonopore, or their terminal parts may join to form a common antrum and pore. The Cercyrinae, a subfamily of the marine triclad family Procerodidae, tend to dioeciousness, and to date two dioecious species of this group have been discovered [*Sabussowia dioica* (Claparéde) 1863 and *Cercyra teissieri* Steinmann 1930]. Reisinger (1924a) failed to find any male system in *Rhynchoscolex simplex* and believes permanent parthenogenesis obtains in this and some other Turbellaria (*Bothrioplana semperi*, *Graffilla parasitica*).

The sex cells of the Turbellaria come from the free cells of the mesenchyme that migrate to appropriate locations and undergo gametogenesis. In primitive forms as the Acoela there are no definite gonads but the gametogonia lie free in the mesenchyme mostly arranged in longitudinal strands, with the spermatogonia lateral to the ovogonia (Fig. 37*D*). But in most Turbellaria there are definite gonads more or less distinctly bounded from the mesenchyme. They may be rounded, oval, elongated, lobed, or branched. When numerous small gonads are present, the condition is spoken of as *follicular*. The polyclads have numerous testes and ovaries, the triclads and alloeocoels commonly possess a few to many

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lacks all female ducts; male system consists of seminal vesicle and male canal (penis). 1, epidermis; 2, brain; 3, statocyst; 4, spermatogonia; 5, ovogonia; 6, mouth; 7, seminal vesicle; 8, penis; 9, male gonopore; 10, protonephridial network; 11, nephridiopores; 12, athrocyte; 13, its nucleus; 14, protonephridial canal.

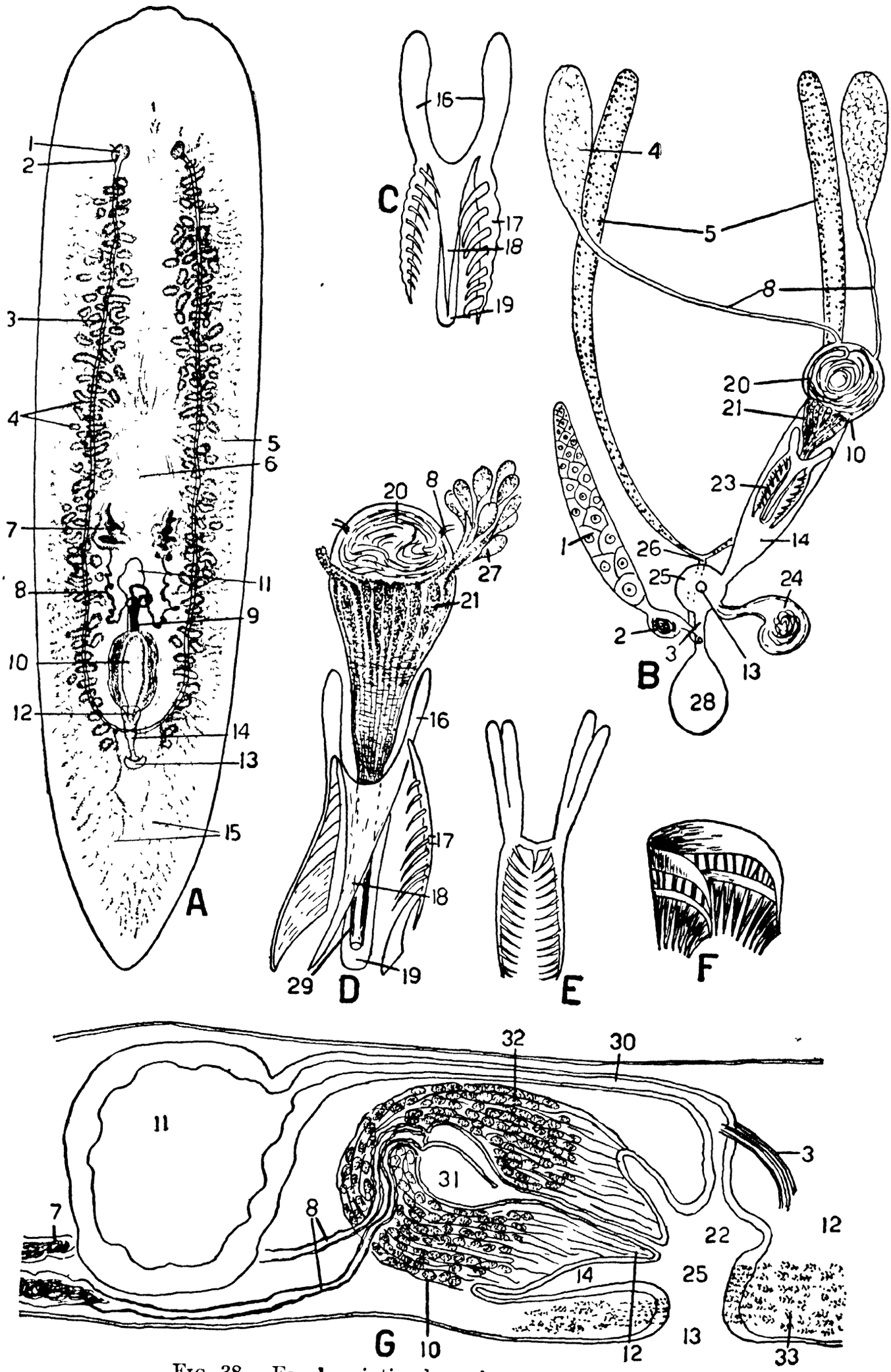

FIG. 38.—For descriptive legend see opposite page.

testes and one pair of ovaries, and in rhabdocoels there are usually present one pair of testes and one or two ovaries. The process of gametogenesis is the same as in other animals (Fig. 41*A*).

The copulatory complex of the Turbellaria can attain a high degree of complexity, but this complexity has evolved within the class and hence cannot be taken as indicative of the degenerative descent of the flatworms from some higher phylum. The copulatory complex is usually located posteriorly behind the pharynx or the intestinal sac but may have any other location.

a. Male Reproductive System.—There is only one pair of sperm ducts regardless of the number of testes but only one duct when the testis is single and several pairs in cases of multiple copulatory complexes (Fig. 40*A*). When numerous testes are present each connects with the sperm duct of that side by a minute *sperm ductule.* The sperm ducts may or may not unite to a *common sperm duct* before entering the copulatory complex. On approaching the latter, each duct or the common duct may present a tubular or sacciform expansion, the *spermiducal vesicle* (old name, *false seminal vesicle*), serving to store ripe sperm. This may have a thick muscular wall but usually is thin-walled. The sperm ducts or common duct open into the male copulatory complex, the lumen of which, termed *ejaculatory duct,* is the final part of the common sperm duct.

The male copulatory complex of the Turbellaria rings innumerable changes on a few fundamental parts. It is impossible here to give a detailed account of these variations. The main parts of the complex are the *seminal vesicle* and the *penis,* but in most Turbellaria there is also present a gland complex, the *prostatic* apparatus.

The seminal vesicle is a rounded, pyriform, or tubular structure usually with a thick muscular wall; it receives the sperm from the sperm ducts, stores them, and helps propel them onward during ejaculation. A worm may have both spermiducal and seminal vesicles (Fig. 51*D*), but generally when one is present the other is lacking. In the absence of a

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FIG. 38.—Reproductive system (continued). *A. Procotyla fluviatilis,* to show reproductive system of a fresh-water triclad. *B.* Reproductive system of *Dalyellia* (*after Graff,* 1911); note seminal vesicle and prostatic vesicle end to end in the penis bulb. *C–F.* Penis stylet of various species of *Dalyellia* to show a few of its many variations. *C. Dalyellia rossi,* eastern United States (*after Graff,* 1911). *D. Dalyellia sillimani,* eastern United States (*after Graff,* 1911). *E. Dalyellia viridis,* cosmopolitan (*after Graff,* 1882). *F. Dalyellia ornata,* Europe (*after Hofsten,* 1911). *G.* Copulatory complex of *Dugesia* in sagittal section; the entrance of the ovovitelline ducts into the curve of the bursal canal is diagnostic of the genus *Dugesia* (= *Euplanaria*). 1, ovary, 2; seminal receptacle with mass of sperm; 3, ovovitelline duct; 4, testes; 5, yolk glands; 6, pharynx; 7, spermiducal vesicle; 8, sperm duct; 9, common sperm duct; 10, penis bulb; 11, copulatory bursa; 12, penis papilla; 13, common gonopore; 14, male antrum; 15, accessory yolk ducts; 16, main stems of stylet; 17, distal stems bearing spines; 18, median dorsal piece; 19, median ventral piece; 20, seminal vesicle; 21, prostatic vesicle; 22, female antrum; 23, penis stylet; 24, seminal bursa; 25, common antrum; 26, common yolk duct; 27, bundle of prostatic glands; 28, uterus; 29, ejaculatory duct; 30, bursal canal; 31, bulbar lumen; 32, gland cells of penis bulb; 33, cement glands.

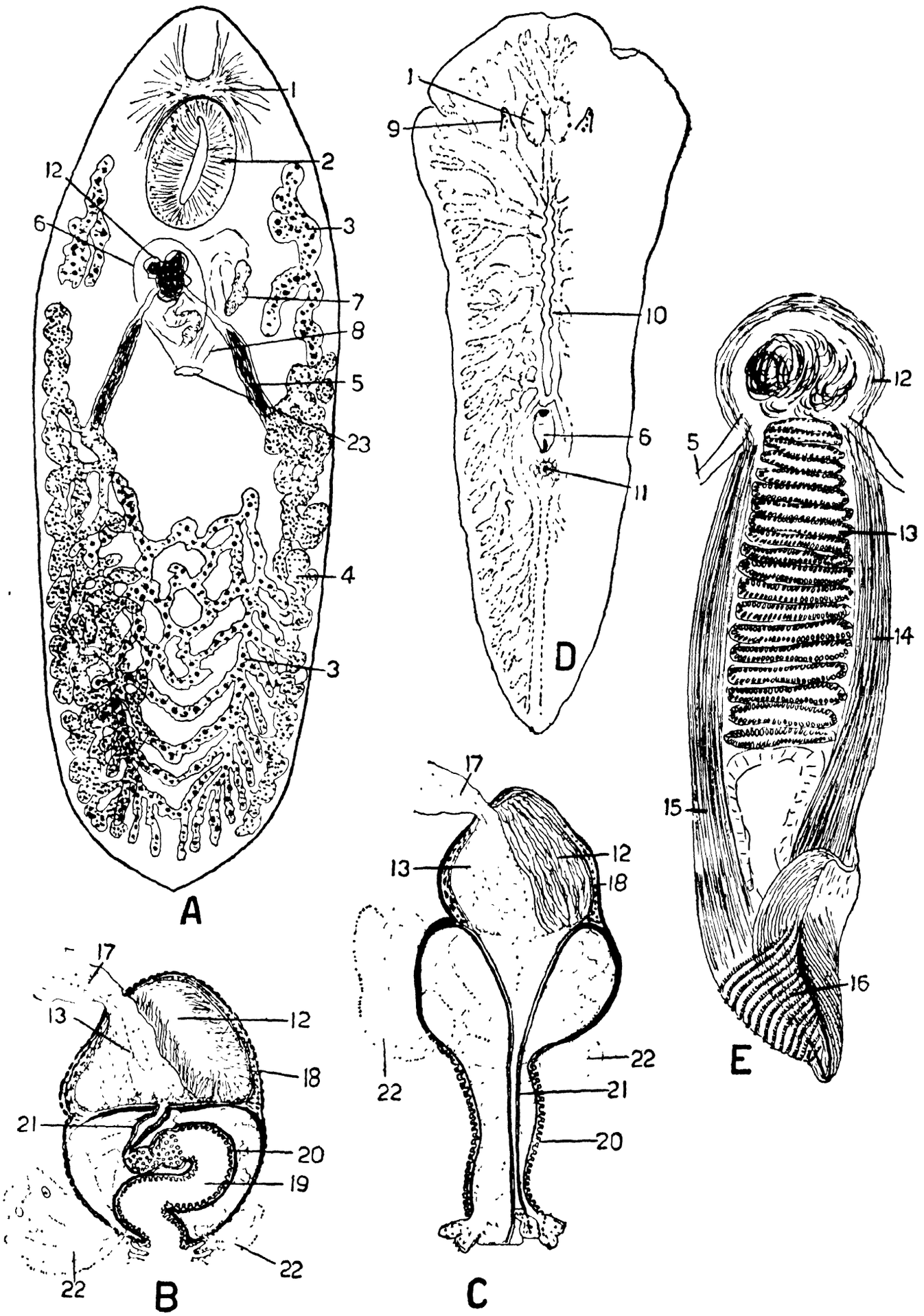

FIG. 39.—Reproductive system (continued). *A. Phaenocora kepneri*, typhloplanid rhabdocoel of the eastern United States (*from slide, courtesy Prof. U. Dahlgren*). *B.* Cirrus of *P. kepneri* in the resting state; note seminal and prostatic vesicles side by side in the penis bulb. *C.* Cirrus everted to form a copulatory organ. (*B, C after Gilbert*, 1935.) *D. Gnesioceros sargassicola*, family Planoceridae, pelagic polyclad common on the floating *Sargassum*, from life, Bermuda. *E.* Male copulatory complex of *G. sargassicola*, showing

seminal vesicle the sperm ducts or duct open directly into the prostatic apparatus or into the penis.

The prostatic apparatus in its simplest form consists of a group of gland cells, the *prostatic* or *granule glands,* that open into the ejaculatory duct or the penis base. Usually, however, they open into a special vesicle, the *prostatic vesicle,* that may be *interpolated* (Fig. 64*B*) between the seminal vesicle and the penis or may be incorporated within a common muscular wall with the seminal vesicle or may connect with the ejaculatory duct by a special *prostatic duct.* In the last case the prostatic vesicle is said to be "free" (Fig. 63*C*). The prostatic vesicle is a rounded, oval, or tubular body with a thick muscular wall. The gland cells may open into the vesicle from without or may be buried in its walls. The prostatic glands produce a granular secretion, or in some forms two kinds of secretion, coarsely and finely granular, of unknown nature and function; but it seems evident that the secretion, which is discharged in the ejaculate, must be of importance to the health and vitality of the sperm. A typical prostatic vesicle and glands are lacking in the triclads but are of general occurrence in other Turbellaria; but probably what is called penis bulb in the triclads is really a prostatic vesicle.

The penis or last part of the male copulatory complex is in its simplest state as seen in some Acoela and Alloeocoela (Fig. 37*D*) merely the terminal part of the male canal with or without a special thickened wall. Usually, however, the wall of the male canal is evaginated to form a muscular conical projection, the *penis papilla,* traversed by the final section of the ejaculatory duct (Fig. 38*G*). The male canal containing the papilla is then usually widened to a chamber termed the *male antrum.* The relations of the penis papilla to the male antrum are the same as those of the plicate pharynx to the pharyngeal cavity, i.e., the penis papilla is protruded by muscular elongation. The penis papilla may be armed with thorns or spines or with a long or short *stylet;* in some cases such a stylet may take the place of the papilla. The stylet is usually a straight or curved hollow tube; but in some rhabdocoels, notably the genus *Dalyellia* (Fig. 38*B–F*), the stylet consists of a complicated array of bars and teeth that differs for each species and constitutes a diagnostic taxonomic character. Quite commonly that part of the male apparatus supporting the penis papilla is formed into a highly muscular rounded body termed the *penis bulb,* considered to be a part of the penis. This bulb may incor-

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the cirrus of toothed bands; contraction of retractor muscle pulls bands to inside contraction of protractor muscle pulls them to the exterior (*after Hyman,* 1939). 1, brain; 2, rosulate pharynx; 3, yolk glands; 4, testes (incomplete on right side); 5, sperm ducts; 6, male copulatory complex; 7, ovary; 8, female canal; 9, tentacles; 10, pharynx; 11, female gonopore; 12, seminal vesicle; 13, prostatic vesicle; 14, retractor of cirrus; 15, protractor of cirrus; 16, cirrus; 17, ducts of prostatic glands; 18, penis bulb; 19, ejaculatory duct constituting the cirrus; 20, teeth of same; 21, noneversible part of ejaculatory duct; 22, cytoplasmic lobes, unknown function; 23, common gonopore.

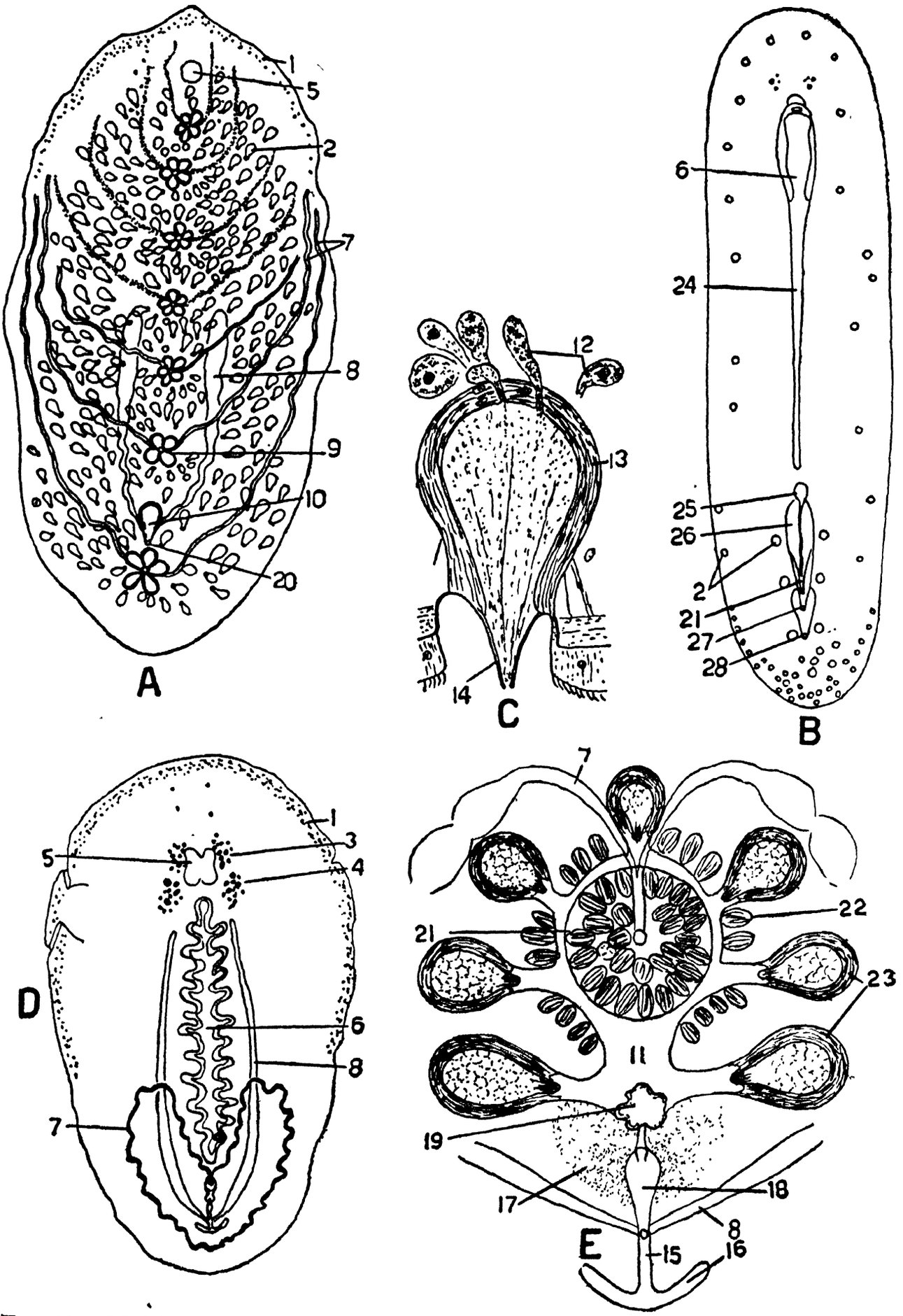

FIG. 40.—Multiplication of male parts. *A*. Pelagic polyclad of the family Polyposthiidae, Straits of Karimata (*after Palombi*, 1924), with multiple sperm ducts, male copulatory apparatus, and prostatoids. *B*. *Apidioplana mira*, polyclad from the Fiji Islands (*after Bock*, 1926) with numerous prostatoids. *C*. Prostatoid of *Apidioplana*, enlarged (*after Bock*, 1926). *D*. *Coronadena mutabilis*, family Discocelidae, Atlantic Coast of United States. *E*. Copulatory complex of *Coronadena*, with large prostatoids in pockets around the male antrum, and smaller ones in the penis papilla and wall of antrum (*after Hyman*,

porate either the seminal vesicle or the prostatic vesicle or both side by side or end to end (Figs. 38*D*, 54). A penis bulb is particularly characteristic of triclads and also occurs in many rhabdocoels.

Some Turbellaria, e.g., the rhabdocoel genus *Phaenocora* (Fig. 39*A–C*) and the polyclad family Planoceridae (Fig. 39*D*, *E*), have a cirrus instead of a penis. The cirrus is the terminal part of the ejaculatory duct generally lined with spines, thorns, etc., that is eversible to the exterior to act as a copulatory organ.

Multiplication of the male copulatory apparatus or parts thereof is very common among the Turbellaria. Thus among the acoels, *Childia* has two and *Tetraposthia* (Fig. 23*A*) four male apparatus composed of seminal vesicle and penis stylet. The alloeocoel *Multipeniata* has a series of male apparatuses in graded stages of development (Nasonov, 1927). Such multiplication is particularly common among polyclads. The male complex is paired in *Thysanozoon* and some species of *Pseudoceros*, and there is a curved row of male apparatus on each side in *Anonymus* (Lang, 1884). Several male apparatus occur around the antrum in *Cryptocelides* and *Polyposthia*, and in some other Polyposthiidae there is a median row of such clusters (Fig. 40*A*, Palombi, 1924). Even more common, also especially among polyclads, is the presence of multiple prostatic apparatus; these have been called by various names such as *pyriform organs*, *apioid organs*, *musculo-glandular organs*, etc., but *prostatoid* seems a convenient name for them. They consist of a pyriform body with a thick muscular wall, attached glands, and pointed tip, often hardened (Fig. 40*C*). These prostatoids may occur in numbers around the male antrum as in the Discocelidae (Fig. 40*E*) and *Boninia* (Bock, 1923), or they may be scattered throughout the ventral surface as in *Apidioplana* (Fig. 40*B*, *C*, Bock, 1926). Similar bodies, termed *adenodactyls*, occur in the wall of the common antrum in some fresh-water (Fig. 45*C*, *D*) and land triclads, and are also found among the Acoela. The purpose of this multiplication in the male system has not been ascertained, but it is usually supposed that the extra parts act as stimulators in copulation.

The male antrum either joins the female antrum to form a common antrum opening below by the common gonopore, or it opens independently by a male gonopore. However, it is not uncommon for the male apparatus to open into the pharyngeal cavity (Fig. 59*C*).

The sperm of the Turbellaria resemble those of other animals. They

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1940). 1, marginal eyes; 2, prostatoids; 3, cerebral eye cluster; 4, tentacular eye cluster; 5, brain; 6, pharynx; 7, sperm ducts; 8, oviducts (uteri); 9, cluster of male copulatory apparatus; 10, female antrum; 11, male antrum; 12, prostatic gland; 13, muscular wall of prostatoid; 14, tip of prostatoid with cuticularized surface; 15, bursal canal; 16, seminal bursa (Lang's vesicle); 17, cement glands; 18, vagina (female canal); 19, common gonopore; 20, female gonopore; 21, penis papilla (seen from above) full of prostatoids; 22, small prostatoids in antral wall; 23, large prostatoids.

are usually long and filamentous and are provided with two flagella or two bristles (Fig. 41*C*, *D*), or tapering at one or both ends to a flagella-like filament. The alloeocoel genus *Plagiostomum* has characteristic broad sperm with wing-like lateral extensions (Fig. 41*C*). In some genera the

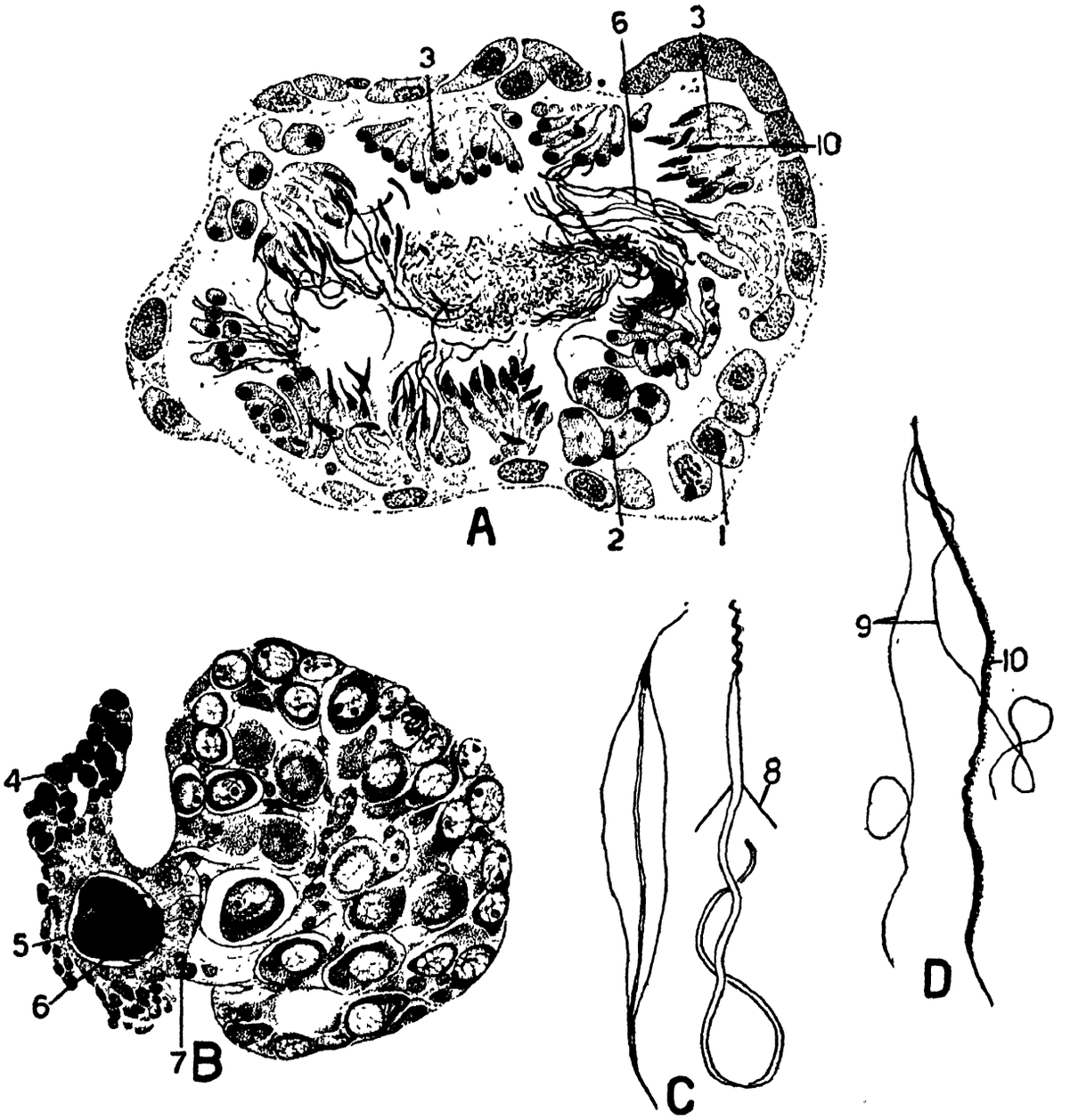

FIG. 41.—Reproductive system (continued). *A*. Testis of a fresh-water planarian, showing spermatogenesis. *B*. Ovary of a fresh-water planarian, showing also seminal receptacle with sperm mass at head of ovovitelline duct. (*A*, *B after Hyman*, 1925b.) *C*. Sperm of *Plagiostomum* (left) and *Macrostomum* (right). *D*. Sperm of *Dendrocoelum lacteum* (*after Hammerschmidt*, 1908). 1, spermatogonia; 2, spermatocytes in reduction division; 3, spermatids in various stages of transformation to sperm; 4, most anterior yolk glands; 5, seminal receptacle; 6, mass of sperm; 7, closing membrane of ovary; 8, bristles; 9, flagella; 10, nucleus.

sperm are aggregated into packets termed *spermatophores* that are discharged into the fellow copulant.

b. Female Reproductive System.—This system may be even more complicated and variable than the male system. Primitively as in many acoels there are no female ducts at all (Fig. 37*D*), and the eggs discharge either through the mouth or by rupture. The beginning of the female system appears to be the formation of a tube, the female canal or *vagina*,

leading inward from the gonopore. The distal part of this canal may enlarge to become the female antrum, and various other differentiations then ensue. The female antrum and gonopore may be distinct from the male ones or fuse with them to a common antrum and pore. In the Acoela the female gonopore is nearly always anterior to the male pore, but in most other Turbellaria the reverse is the case.

The Platyhelminthes are unique among animals in that the yolk supplies of the egg are usually not stored in the egg itself but in special cells, the *yolk* or *vitelline cells*, considered to be altered ovocytes. This state of affairs has arisen within the Turbellaria. Yolk cells are lacking, and the eggs store their own yolk as in other animals in the Acoela, the Polycladida, and the catenulid and macrostomid Rhabdocoela; however, in *Polychoerus* and a few other acoels, the ovocytes lie in a nutritive tissue differing in appearance from the rest of the mesenchyme. The first step toward the evolution of yolk glands is seen in the alloeocoel group Lecithoepitheliata in which some of the ovocytes become eggs and the others differentiate into follicle cells that embrace each growing ovocyte and pass food supplies into it (Fig. 43). Such an ovary therefore consists of a proximal germinal part producing ovocytes and a series of follicles that gradually increase in size toward the oviduct (Figs. 42*B*, *F*, 59*B*). Next the ovary differentiates into yolk-producing and egg-producing regions (Fig. 42*C*). Such sex glands are termed *germovitellaria* and exist in several types as illustrated in Fig. 42*B*, *C*, *G*, *H*. Finally as in most Turbellaria there is a complete separation of the yolk-producing part to form the *yolk glands* or *vitellaria* (Fig. 42*D*, *E*). These may be elongated, lobed, or branched bodies, or may consist of numerous scattered clusters of yolk cells, a condition termed follicular. The yolk glands may discharge directly into the oviducts as in triclads, in which case the oviducts are more properly termed *ovovitelline* ducts, or there may be special *yolk ducts* leading from the yolk glands to the oviducts.

Among the rhabdocoels and alloeocoels, the ovary-yolk-gland complex seems to have been derived from an originally tetrapartite condition (Fig. 42). No turbellarian is known that has a tetrapartite ovary (theoretical stage in Fig. 42*A*), but an alloeocoel *Gnosonesima* has been described by Reisinger (1926) from the antarctic that has a tetrapartite germovitellarium with follicles (Fig. 42*B*). In most present rhabdocoels and alloeocoels the condition shown in Fig. 42*D*, *E* obtains, i.e., there is a pair of yolk glands and one or two ovaries.

When the ovary is single there is a single oviduct; otherwise there are two oviducts to which, in the case of numerous ovaries, connection is made by minute *oviductules*. The Acoela and some primitive Alloeocoela lack oviducts altogether, and this condition is undoubtedly primitive. Following the entrance of the yolk cells, the oviduct becomes an ovovitelline

duct (old name, *ductus communis*), and proceeds toward the female copulatory complex. This is very variable in different Turbellaria so that general statements are impractical. A typical part of the apparatus is a sac for receiving sperm from the fellow copulant. This sac is termed

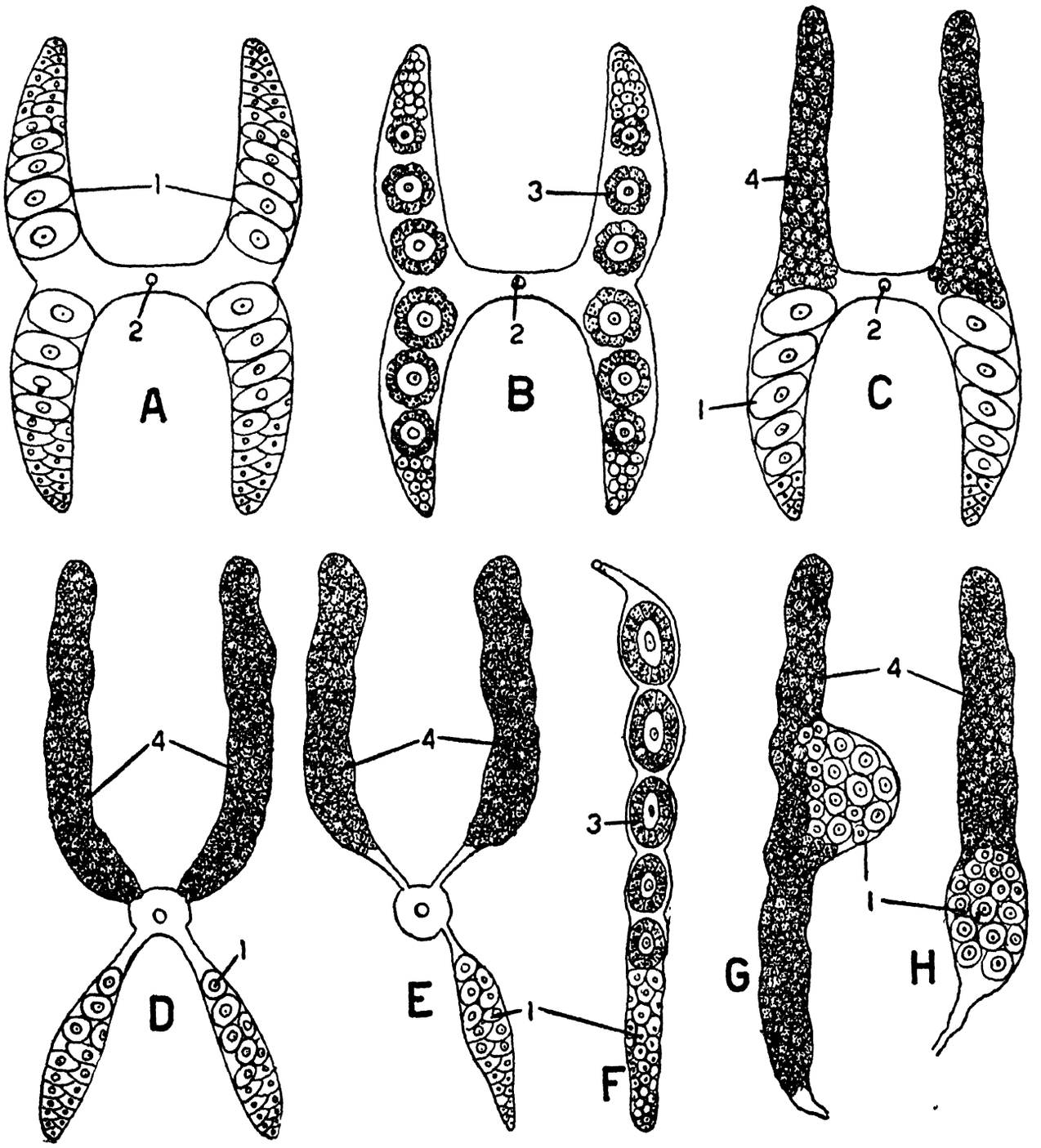

FIG. 42.—Evolution of ovary–yolk gland complex in rhabdocoels and alloeocoels. *A*. Hypothetical ancestral stage with tetrapartite ovary. *B*. Condition in *Gnosonesima* with tetrapartite germovitellaria composed of follicles. *C*. More usual type of germovitellaria with ovarian and vitelline regions. *D*, *E*. Usual condition of the female system in rhabdocoels and alloeocoels: two yolk glands and one or two ovaries. *F*. Condition in the Prorhynchidae, with one germovitallarium composed of follicles. *G*, *H*. Other types of germovitellaria. 1, ovary; 2, gonopore; 3, follicle; 4, yolk gland.

copulatory bursa (*bursa copulatrix*) when it retains the sperm for only a brief period, *seminal bursa* (*bursa seminalis*) when it keeps them a longer time, and *seminal receptacle* (*receptaculum seminis*) when it is the permanent abiding place of the sperm. The last is frequently merely a widened place in the oviduct; the other two are frequently set off from the antrum

by a *bursal canal.* A given worm may have both copulatory or seminal bursa and seminal receptacle as *Mesostoma* (Fig. 54) or *Dalyellia* (Fig. 38*B*). The copulatory or seminal bursa may open to the exterior by a *bursal* pore independent of the regular genital pore and sometimes not in the median line (Figs. 61*A*, 62*E*). The canal leading from the bursa to this bursal pore may be termed *copulation canal* (sometimes called *ductus vaginalis*) since it presumably serves for copulation. The bursa may also have special *insemination* canals (old name, *ductus spermaticus*) through which the sperm reach the oviducts, and these may occur in addition to the regular bursal canal (Figs. 53*A*, *B*, 61*A*). In the marine triclads *Bdelloura* and *Uteriporus*, the paired or single seminal bursa opens directly to the exterior (Fig. 61*A*) and is connected with the rest of the

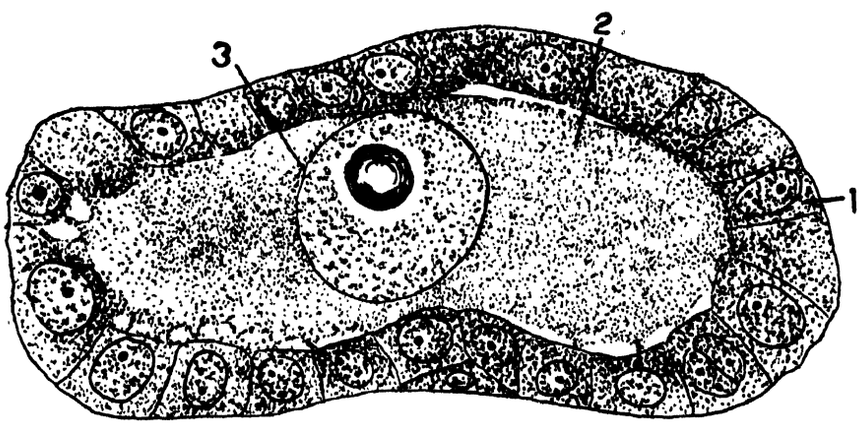

FIG. 43.—A follicle of the germovitellarium of *Prorhynchus*, showing maturing ovum surrounded by a follicle of nurse cells, presumed to be altered ova. 1, follicle; 2, egg; 3, nucleus of egg.

female system only by delicate insemination canals. Most Acoela lack all female parts, but the family Convolutidae is characterized by the presence of one to many seminal bursae. These are glandulo-muscular bodies connected or not with the vagina and provided with one or more nozzles (page 129) through which the sperm received at copulation exit into the mesenchyme. Various relations of vagina and seminal bursa in the Acoela are shown in Fig. 44.

In some Turbellaria, especially polyclads, the oviducts serve as storage places for large accumulations of ripe eggs and are then expanded as uteri. But as most Turbellaria lay their eggs singly or a few at a time a uterus is not necessary. However, in some rhabdocoels there is a single or paired uterus in the form of a blind sac or tube extending from the female or common antrum; the shelled eggs singly or a few at a time are held in this before laying, and it seems to play some role in the formation and particularly in the shaping of the shell. More often the shell is formed in the male or female antrum.

Large numbers of eosinophilous gland cells are usually associated with the female complex, opening into the bursal canal or the terminal parts of the oviducts, or the wall of the antrum, or the body wall around the

gonopore. They were formerly considered to be shell glands, but it is now known that the shell is formed from droplets present in the egg or in the yolk cells, and the glands are mostly of the nature of *cement* glands that secrete the material uniting the eggs into cakes or ribbons (Acoela, Polycladida) or fastening them to objects by means of stalks and filaments.

The oviducts or ovovitelline ducts may or may not unite to a common duct before entering the female copulatory complex. They may open into the bursal canal or into the male, female, or common antrum.

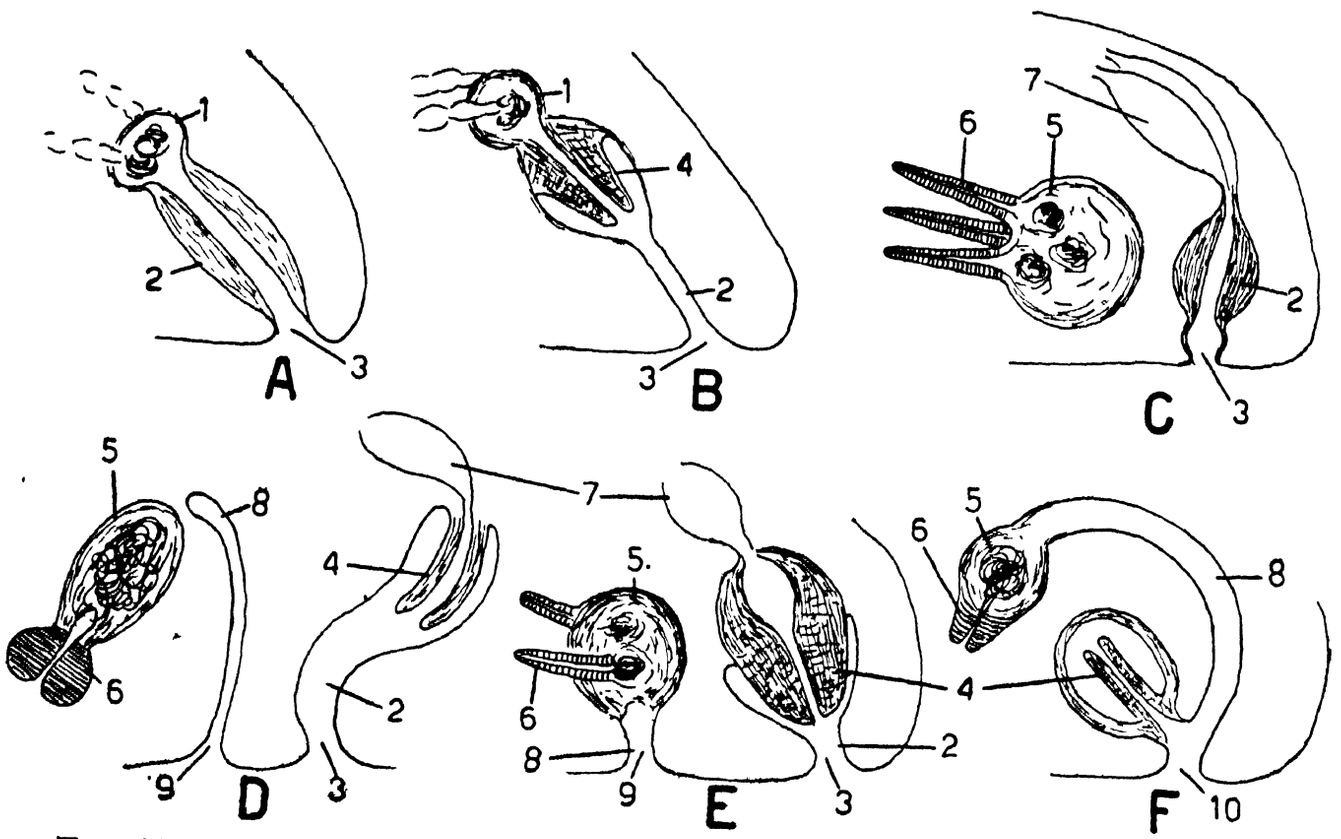

FIG. 44.—Diagrams of the reproductive system of various Acoela, based chiefly on Luther, 1912. *A. Afronta*, with male canal, no female parts. *B. Proporus*, similar, but with penis papilla in the male canal. *C. Palmenia*, similar to A, but with seminal bursa not connected to the gonopore. *D. Convoluta*, with vagina leading toward but not connected with seminal bursa. *E. Amphiscolops*, vagina connected with seminal bursa. *F. Otocelis*, similar to *E* but with common gonopore. 1, seminal vesicle; 2, male canal; 3, male gonopore; 4, penis papilla; 5, seminal bursa; 6, nozzles of bursa; 7, spermiducal vesicles; 8, vagina; 9, female gonopore; 10, common gonopore. In *F*, the penis papilla is everted into the male canal.

The parts of the female system are lined with a one-layered epithelium that varies greatly in height in different regions or in different states of activity. It may be ciliated in certain areas or glandular, either through the presence in it of cells of secretory granules or through being penetrated by the outlets of gland cells situated in the adjacent mesenchyme. In some groups all the gland cells associated with egg laying enter one particular region which is then termed *glandular duct* or *cement sac* (Figs. 62*D*, 65*D*). All parts of the female system except the ovaries are underlain by a muscular stratum usually of both circular and longitudinal fibers. This is often very thick around the terminal parts of the female system where it may form sphincters.

The eggs of the Acoela and Polycladida enclosed in delicate capsules are laid embedded in gelatinous material. In the other orders they are enclosed singly or severally in a hard shell, here termed *capsule* (also called *cocoon*). In those forms with yolk glands, hundreds of yolk cells are included with the eggs inside the capsule. The capsule is formed in the antrum, most commonly the male antrum, sometimes at least in part in a special uterus. It is usually pale and soft at first, but becomes brown and hard after laying. During its passage through the gonopore, the capsule becomes coated with the adhesive secretion of the cement glands, and this secretion may be drawn out into a stalk fastening the capsule to an object. During the breeding season, each worm usually copulates repeatedly and lays a succession of capsules, one at a time, at intervals of a few days. These hatch in a few weeks to complete tiny worms; free-swimming larvae occur only in some polyclads. In some species the eggs develop to young worms in the parent body, either in the uteri (Fig. 45*A*) or in the mesenchyme (Fig. 36*A*) or even in the lumen of the intestine (*Bresslauilla*). Such young escape by mouth or gonopore or through rupture and death of the parent.

A relatively common feature of the female system among the Turbellaria is a connection with the intestine, the *genito-intestinal canal* (Fig. 59*C*) or aperture; this is sometimes paired. Usually it is the seminal or copulatory bursa or its equivalent that opens into the intestine; in polyclads the connection when present is between the vagina or oviducts and the intestine. Very great phylogenetic importance has been attributed to this genito-intestinal connection by some students of the Turbellaria. They regard its occurrence as proof that the eggs were originally discharged by way of the intestine and mouth with the connection constituting the primitive oviduct (Steinböck, 1924; Reisinger, 1930). They argue that, when the Acoela evolved into turbellarians with a hollow intestine, a definite passage formed for the discharge of eggs into the intestinal lumen. Great weight has been placed by Reisinger on the rhabdocoel *Bresslauilla* (Reisinger, 1930) which lacks all female parts except a pair of yolk glands and one ovary; these connect broadly with the intestine into which the eggs discharge and where they develop into young worms. Equally prominent students of the Turbellaria reject these ideas altogether (Bock, 1927; Meixner, 1938). Bock points out that the connection is rather too variable in its relationship to permit of any generalization and further emphasizes the general tendency already mentioned toward fusion of contiguous structures among the Turbellaria. The author is of the opinion that the original mode of discharge of turbellarian eggs was in fact the mouth but that the sporadic occurrence of a genito-intestinal connection cannot be taken as proof of this or as indicative that the original female canal ran from the ovaries into the intestine.

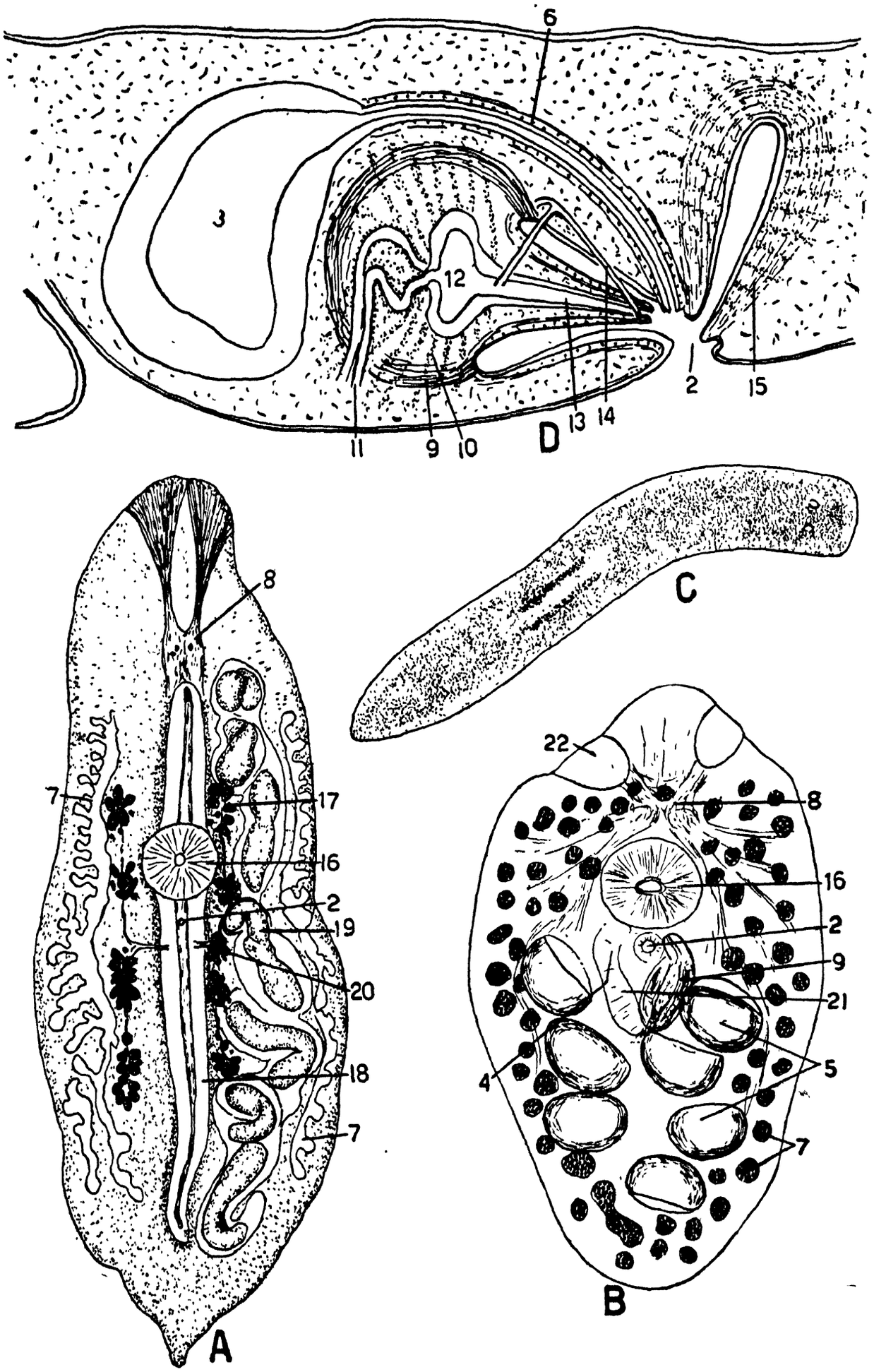

FIG. 45.—Reproductive system (continued). *A. Mesostoma ehrenbergii wardii* (*after Woodworth*, 1897), showing young worms developed from subitaneous eggs in the right uterus (left uterus not shown). *B. Mesostoma columbiana* with dormant hemispherical capsules (*after Hyman*, 1939). *C. Planaria dactyligera*, Virginia (*after Kenk*, 1935). *D.* Copulatory apparatus of *Planaria dactyligera* in sagittal view showing the adenodactyl

Conditions in the Acoela suggest on the contrary that the original female canal ran inward from the gonopore and had no direct connection with any other structure, serving only to receive the sperm of the partner. The impetus for the evolution of a female system appears to have been the desirability of safeguarding the sperm received in copulation.

A corollary of the genitointestinal theory is the intestinal derivation of the copulatory or seminal bursa, considered to be a sac cut off from the intestine. This idea is in the author's opinion acceptable although violently criticized by Meixner (1938). The bursa is usually lined by a tall bulbous epithelium closely resembling the intestinal epithelium and capable like the latter of intracellular digestion. One of the main functions of the bursa, in fact, is the digestion of excess sperm and prostatic secretion (Cernosvitov, 1931). The seminal bursa of the Acoela, however, appears to be of quite a different nature from that of other Turbellaria and is clearly unrelated to the intestine.

c. Copulation.—Internal fertilization is the rule among the Turbellaria, and for this purpose they are almost without exception provided with a copulatory apparatus. Although the Turbellaria are with few exceptions hermaphroditic and although the fertilization of the eggs by the sperm of the same animal would be anatomically possible, especially in those forms where both male and female ducts open into a common antrum, self-fertilization is of rare occurrence and is definitely absent in fresh-water planarians (probably all triclads) and polyclads. Isolated triclads may lay capsules, but these do not hatch as the contained eggs are unfertilized (Gelei, 1924; Goetsch, 1925). Self-fertilization fails to occur apparently because the sperm masses in the spermiducal or seminal vesicles are motionless and do not become motile until ejaculated along with necessary glandular secretions into another individual.

Two methods of cross insemination occur, hypodermic impregnation and regular copulation. In the former, practised among a few Acoela, Rhabdocoela, and Polycladida, one animal injects sperm through the epidermis of another at any place, mostly by means of an armed penis (Fig. 48*A*). The sperm so injected wander through the mesenchyme to the eggs. An ordinary copulation is, however, the rule and is probably the usual method even among the Acoela. This copulation is mutual, i.e., the protruded penis papilla or everted cirrus is inserted into the female or common gonopore of the partner by each copulant and each injects sperm into the other. The sperm are emitted directly into the copulatory or seminal bursa (Fig. 48*C*) when this structure is present;

characteristic of the genus *Planaria* (*after Kenk*, 1935). 1, mouth; 2, common gonopore; 3, copulatory bursa; 4, ovary; 5, dormant capsules; 6, bursal canal; 7, testes; 8, brain; 9, penis bulb; 10, glands of same; 11, sperm ducts; 12, bulbar lumen; 13, ejaculatory duct; 14, common ovovitelline duct; 15, adenodactyl; 16, rosulate pharynx; 17, yolk glands; 18, intestine; 19, young worms in uterus; 20, yolk duct; 21, oviduct; 22, sensory pits.

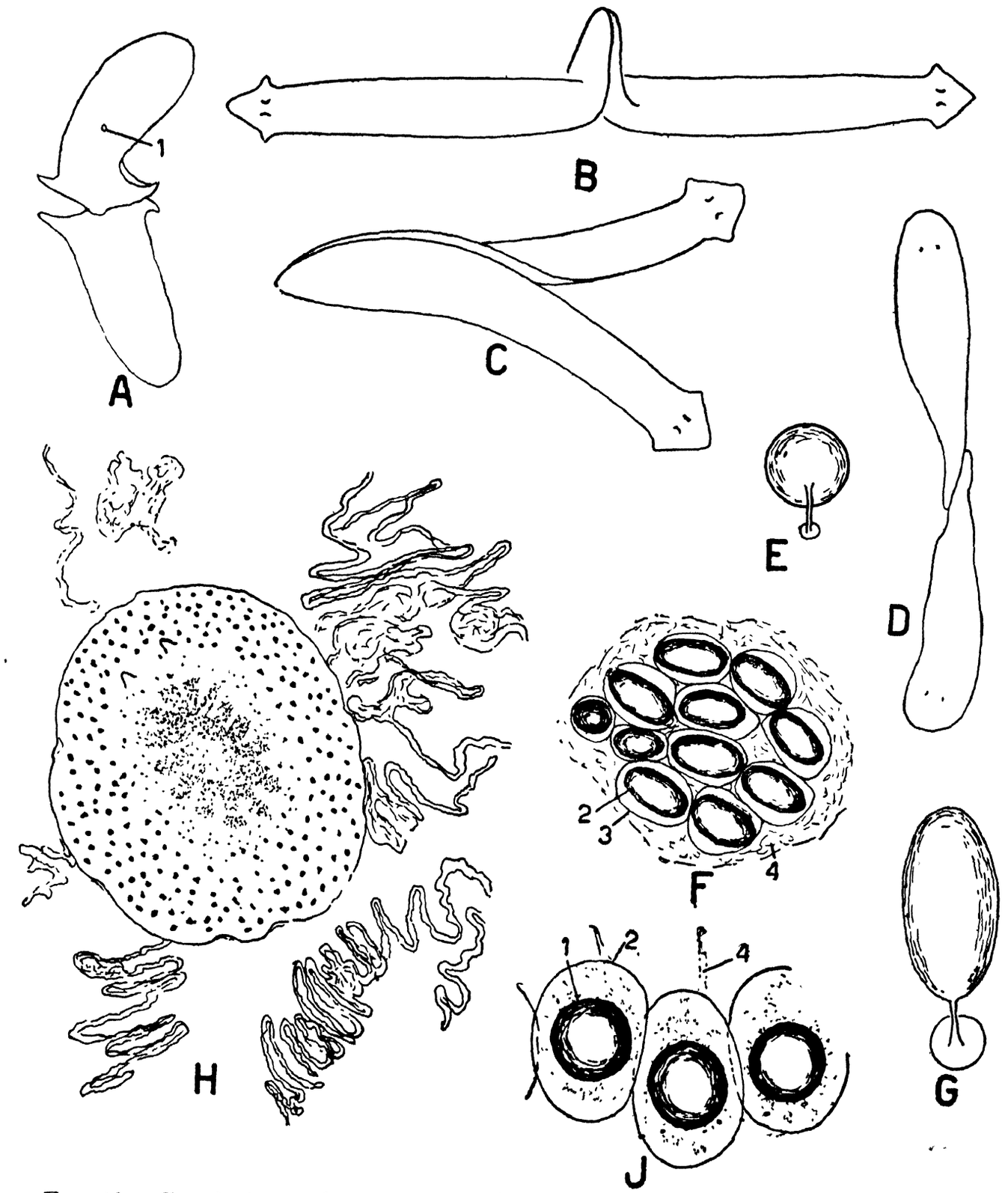

FIG. 46.—Copulation and egg laying. *A. Amphiscolops langerhansi*, acoel, in copulation, from life, Bermuda. *B* and *C*. Fresh-water planarians of the genus *Dugesia* in copulation, from life. *D*. Rhabdocoel *Macrostomum* in copulation, from life. *E*. Stalked capsule of *Dugesia*, from life. *F*. Egg mass of *Amphiscolops*, from life. *G*. Egg capsule of *Bdelloura*, marine triclad commensal on *Limulus*, from life; the capsules are fastened to the gill lamellae. *H*. Polyclad *Stylochus* in process of laying egg ribbons. *J*. Part of the ribbon, showing each egg enclosed in a capsule. (*H, J after photographs by Kato*, 1940.) 1, mouth; 2, egg; 3, capsule; 4, jelly.

otherwise they find their way into the oviducts or seminal receptacle. The copulation of the Acoela is of interest as these are the most primitive animals in which this process occurs. The details have been ascertained for only one species, however, *Amphiscolops langerhansi*, in which it was possible to section copulating pairs (Hyman, 1937). Here the penes

grasp each other and the sperm, guided by a body projection, pass into the seminal bursa (Fig. 47).

Copulation is generally preceded by a brief "courtship" consisting of head or body contacts. The copulatory attitude is similar throughout the class. Usually the copulants face more or less away from each other with genital regions pressed together and often elevated, rest of body

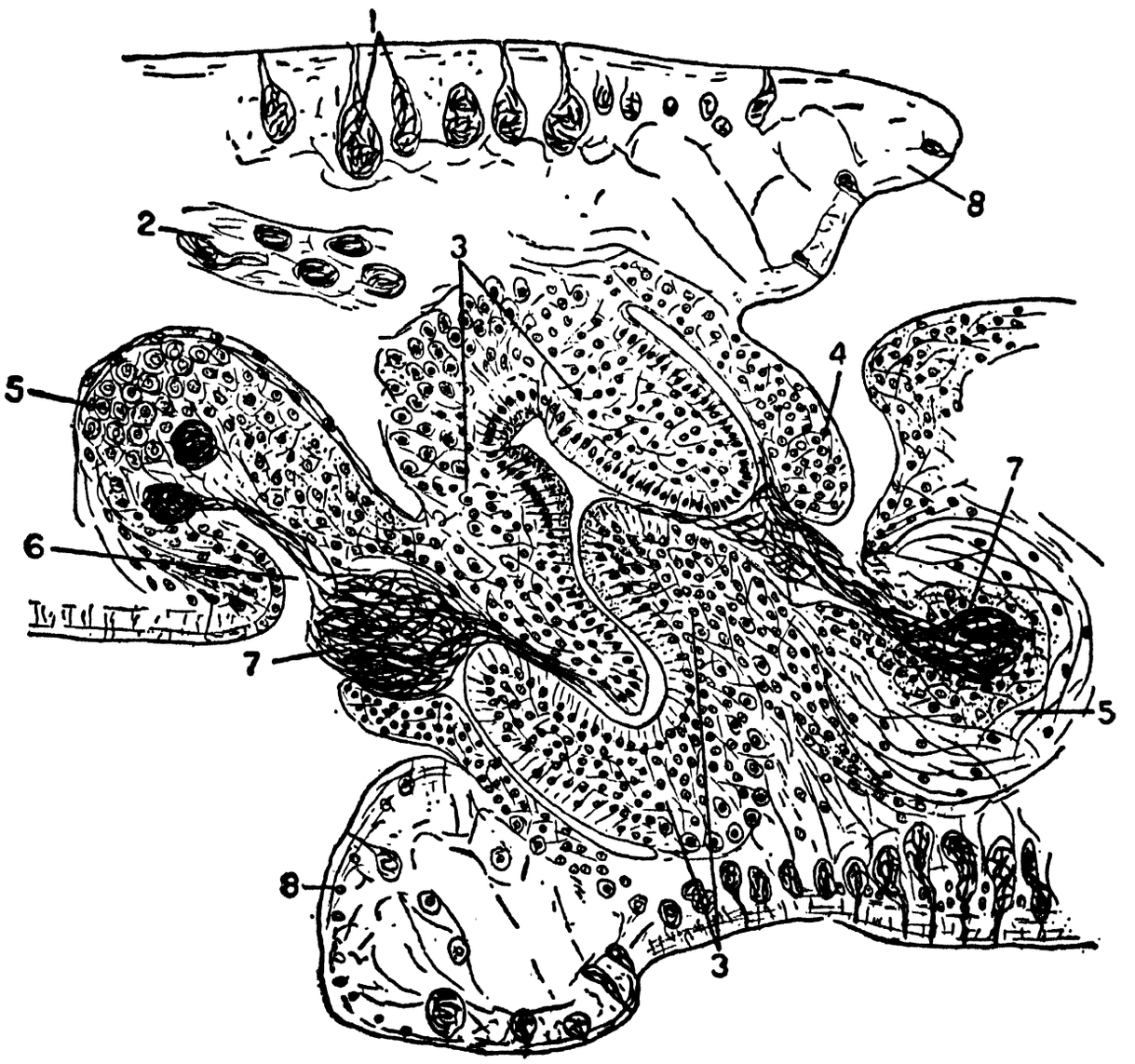

FIG. 47.—Sagittal section through the rear ends of a copulating pair of the acoel *Amphiscolops langerhansi*, showing penes interlocked and stream of sperm pouring into the seminal bursa of each copulant; sperm guide prevents dispersion of sperm into the water (*after Hyman*, 1937). 1, gland cells; 2, sperm duct; 3, penis papilla; 4, sperm guide; 5, seminal bursa; 6, vagina; 7, mass of sperm; 8, tail end of animal.

attached to substratum (Fig. 46*A–D*). A parallel position, however, is not infrequent in the same species. Copulation is generally of brief duration, a few minutes or less, but in the acoel mentioned above lasted 40 to 60 minutes and in polyclads may last an hour or more (Kato, 1940). During the breeding season any one individual copulates repeatedly. Adhesive secretions probably aid the copulatory process.

14. Order Acoela.—The Acoela are a group of small worms ranging mostly from below one millimeter to several millimeters in length; the largest known species is the 12-mm. *Anaperus sulcatus* from the Caspian

Sea (Beklemischev, 1914). The Acoela are mostly of plump, broad to elongate, oval form, of inconspicuous white or drab coloration, except when colored brown or green by symbionts. The contour is simple except for a pair of caudal lobes in *Amphiscolops* and *Polychoerus* (Fig. 13*D*, *E*) plus a tail filament in the latter. The characters of the epidermis are described above (page 68). There are nearly always present a statocyst (sometimes double) and a cluster of frontal glands opening by a pore or infrequently numerous pores at the anterior tip. Eyes are frequently wanting, but some have two or rarely four eyes. The eyes of *Otocelis rubropunctata* are pigment-spot ocelli, but those of other Acoela are of the usual pigment-cup type, of one to a few pigment and retinal cells. The nervous system in the most primitive forms (*Tetraposthia*, *Nemertoderma*) is epidermally located but in most Acoela is a submuscular plexus with three to six pairs of longitudinal strands (page 83, Fig. 23). The mouth, usually located near the middle or in the anterior half of the ventral surface, rarely at the posterior end (*Diopisthoporus*, Westblad, 1940), opens directly into the mesenchyme or into a long or short pharynx simplex, sometimes provided proximally with extra musculature. A digestive cavity is lacking (except *Nemertoderma*, see below), and mouth or pharynx lead directly into a syncytial vacuolated mass that fills the interior. The digestive phagocytic cells or areas of this are either scattered or aggregated into a central digestive zone in which temporary spaces form around the digesting food. The Acoela are totally devoid of an excretory system.

The reproductive system starts from simple conditions and concentrates on the development of male and female copulatory mechanisms. The sex cells originate directly from mesenchymal cells mostly in paired dorsolateral regions, sometimes in a median region; the male cells are lateral to the female ones (Fig. 37*D*). In some species there is a median common source of both eggs and sperm. As the sex cells ripen, they proceed posteriorly, forming longitudinal tracts of eggs and sperm (Fig. 37*D*). There may be single or paired seminal or spermiducal vesicles or both in which sperm collect and which lead into the penis. This is primitively simply a canal with or without special muscular wall (Fig. 37*D*), but in many Acoela a conical muscular penis papilla, sometimes armed with one or more hard stylets, projects into the male canal from its proximal end. Prostatic glands usually open into the penis base, and sometimes there is a vaguely indicated prostatic vesicle. There may be two or four penes (page 117). The male canal leads to the male gonopore usually at or near the posterior end, or it may join the female canal. All Acoela lack oviducts, and the more primitive members also lack all other female parts (*Nemertoderma*, *Diopisthoporus*, family Proporidae). The family Convolutidae has a female canal (vagina) springing from the

common antrum or opening by a separate female gonopore anterior to the male pore (Fig. 44). This family also usually has one to many (to 64 in *Anaperus*, Fig. 49*B*) seminal bursae connected or not with the vagina (Fig. 44). The seminal bursa may be merely a mesenchymal space in which received sperm accumulate (Fig. 23*A*) but usually is a glandulo-muscular body with a poor lumen and one to many nozzles by which the sperm exit to fertilize the eggs. These nozzles consist of flat disk-like cells whose centers, perforated by a canal, are cuticularized and of a yellow color (Fig. 49*C*). The Acoela are hermaphroditic; but protandry seems to be of common occurrence, and in *Diopisthoporus*, male, female, and hermaphroditic specimens may occur simultaneously (Westblad, 1940).

Although hypodermic impregnation certainly occurs among the Acoela, copulation is the rule (Fig. 47, page 125). The sperm pass directly from the vagina into the bursa or reach this through the mesenchyme or in the absence of a bursa wander through the mesenchyme to the eggs. After once attaining mature size, the Acoela appear to remain permanently in a sexual state and probably breed throughout the year in warmer waters, seasonally in colder zones. The eggs are laid through the mouth or gonopore or by body rupture. A few to many eggs are enclosed in a thin gelatinous capsule or in a rounded to cake-like gelatinous mass stuck to objects (Fig. 46*F*). This gelatinous material is secreted by gland cells opening into the antrum or onto the general body surface. In *Amphiscolops langerhansi*, observed by the author in tanks at Bermuda, copulation and laying of flat cakes of 3 to 16 eggs (Fig. 46*F*) occurred at frequent intervals in the same individuals; the eggs were laid between midnight and dawn (Hyman, 1937). The eggs of the Acoela develop in a few days directly into young worms that escape from the jelly.

The Acoela are exclusively marine, living under stones, among algae, and most commonly on the bottom mud from the littoral zone to rather deep waters. Several species, mostly of the genus *Haplodiscus* (Fig. 49*A*), of flat, broadly oval shape and translucent texture, are pelagic; but as they are known only from townet collections, their habits have not been observed (Böhmig, 1895; Löhner and Micoletzky, 1911). *Amphiscolops sargassi* lives on the floating *Sargassum* (Hyman, 1939).[1] The curious *Ectocotyla paguri* with a caudal adhesive disk (Fig. 13*F*) is ectocommensal on a hermit crab off the coast of Maine. There are also a number of entocommensal species, inhabiting the intestine of echino-

[1] The *Sargassum* is a seaweed, belonging to the brown algae, that floats loose in the Atlantic Ocean, being most abundant in a stagnant region to the northeast of Bermuda, termed on this account the Sargasso Sea. The *Sargassum* is inhabited by a number of animals that do not occur elsewhere and that are often notable for adaptive resemblance to the seaweed in color and shape.

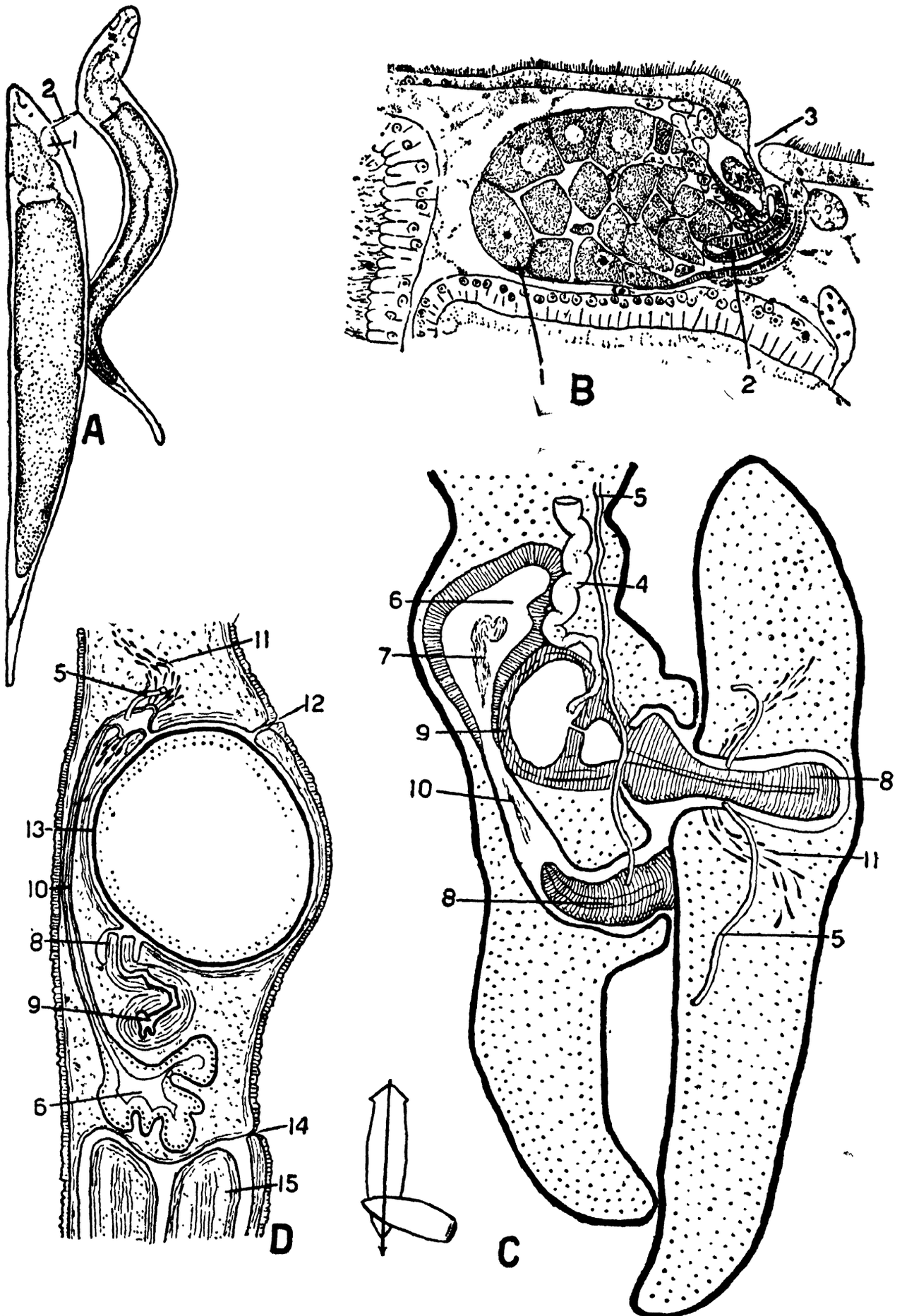

Fig. 48.—Copulation (continued). *A*. *Stenostomum* in process of hypodermic impregnation. *B*. Sagittal section through the male system of *Stenostomum*. (*A*, *B after Kepner, Carter, and Hess*, 1933.) *C*. Section through a copulating pair of *Dugesia gonocephala* (*after Burr*, 1912) showing penis papilla inserted into bursal canal; small figure below to left gives plane of section. *D*. Sagittal section of the copulatory complex of *Dugesia polychroa* (*after Burr*, 1912) showing capsule forming in the male antrum. 1, testis; 2, penis papilla (introverted in *B*); 3, male gonopore (dorsal); 4, sperm duct; 5, ovovitelline duct; 6, copulatory bursa; 7, mass of sperm; 8, penis papilla; 9, penis bulb; 10, bursal canal; 11, cement glands; 12, common gonopore; 13, capsule; 14, mouth; 15, pharynx.

derms: *Avagina incola* in a heart urchin (Leiper, 1904) and *Otocelis chirodotae*, *Aphanostoma pallidum* and *sanguineum*, and *Aechmalotus pyrula* from sea cucumbers on the Murman coast (Beklemischev, 1915). Although the Acoela occur in tropical and subtropical waters (chiefly as pelagic types), they reach their greatest abundance in temperate and arctic zones. Curiously, nearly all the known species come from the

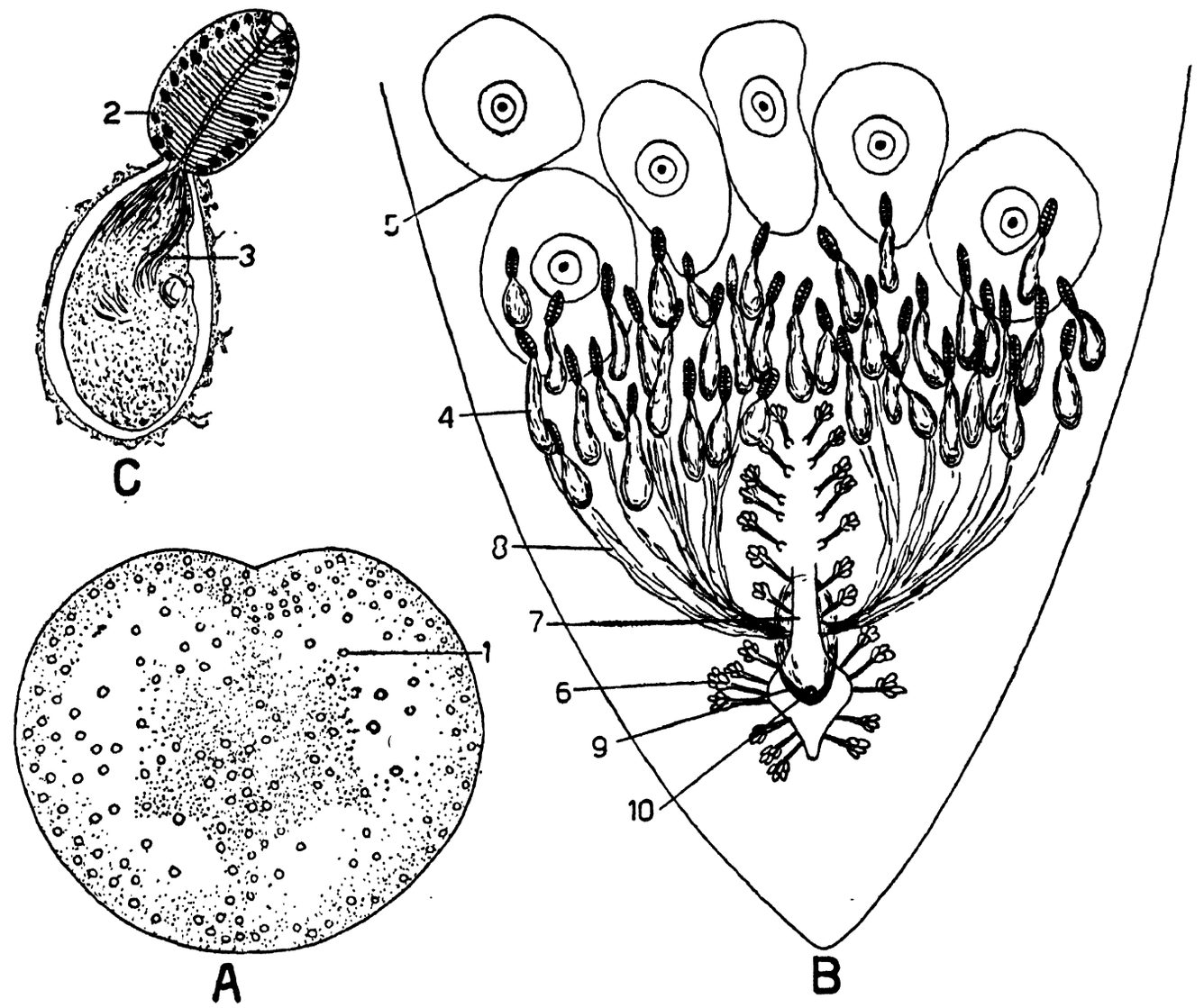

FIG. 49.—Acoela. *A*. Pelagic acoel, *Haplodiscus piger*, Bahamas (*after Böhmig*, 1895). *B*. Rear end of *Anaperus gardineri*, Massachusetts Coast (*after Graff*, 1911) with numerous seminal bursae and adenodactyls. *C*. A bursa enlarged. 1, zooxanthellae; 2, nozzle; 3, mass of sperm; 4, seminal bursa; 5, eggs; 6, adenodactyls; 7, female canal; 8, sperm tracts; 9, penis papilla; 10, common gonopore.

North Atlantic and its adjuncts as the Mediterranean, Caspian Sea, Baltic Sea, Finnish bays, Scandinavian fiords, Murman Coast, etc. Many interesting species were taken on the coasts of Greenland by a collecting expedition in 1926. Several species inhabit the New England coast. Scarcely any acoels are known from Pacific shores (two at Monterey Bay, California, a pelagic species off the Philippines). However, the Acoela have been so insufficiently collected that little weight can be placed on the known distribution.

The taxonomy also suffers from an insufficient knowledge of the group. The known species are arranged in five families, three of which

comprise a single species each: *Nemertoderma bathycola*, *Diopisthoporus longitubus*, and *Ectocotyla paguri*. The first, originally dredged off Greenland at 250 m. (Steinböck, 1931), was later found in numbers in shallow water on the Scandinavian Coast (Westblad, 1937). It combines primitive (epidermal nerve plexus, no female ducts, no penis papilla) and advanced (definite intestinal lumen, well-defined testes) characters (Fig. 23*C*, *D*). *Diopisthoporus* from the Scandinavian Coast has posterior mouth and male pore, long pharynx, no penis papilla, and no female ducts. *Ectocotyla* (Fig. 13*F*) is unique among acoels in its plicate pharynx and caudal adhesive disk. All other acoels that lack female ducts are grouped into the family Proporidae that includes the genera *Proporus* (Fig. 44*B*), *Rimicola*, *Haplodiscus* (Fig. 49*A*), *Avagina*, *Achoerus*, *Afronta* (Fig. 37*D*), *Childia*, and several of the new Greenland genera. Acoela with one or more seminal bursae, female or common gonopore, and vagina fall into the family Convolutidae with genera *Otocelis* (Fig. 44*F*), *Aphanostoma*, *Aechmalotus*, *Convoluta* (Figs. 13*B*, 44*D*), *Amphiscolops* (Figs. 13*D*, 44*E*, 46*A*, *F*, 47), *Polychoerus* (Figs. 13*E*, 24*D*), *Monochoerus*, *Palmenia* (Fig. 44*C*), *Tetraposthia* (Fig. 23*A*), *Anaperus* (Fig. 49*B*), and others. The first three are entocommensals of echinoderms. *Convoluta* with many species, some green from algal symbionts, some with the habit of rolling up like a cornucopia (Fig. 13*B*, *C*), is one of the best known acoels. *Amphiscolops langerhansi*, originally from the Madeira and Canary Islands, has become established in tanks at Bermuda and made the object of several studies (Welsh, 1936; Hyman, 1937). The genus *Polychoerus*, orange-red worms with a tail filament (Fig. 13*E*) and one bursa with many nozzles, is limited to North American coasts, having one species *caudatus* (Mark, 1892) off Cape Cod, and another, *carmelensis* (Costello, 1938b) off California. *Anaperus* and *Monochoerus* are provided with one or more prostatoids along the male canal (Fig. 49*B*).

15. Order Rhabdocoela.—The rhabdocoels are small worms, ranging mostly from 0.3 to 2 or 3 mm. in length, although larger forms, to 15 mm., occur. The body is of elongated slender to plump shape, of simple contour, without tentacles or projections, except that some genera (*Rhynchoscolex*, *Alaurina*, Figs. 32*B*, 50*A*) have a narrowed snout, and the Temnocephalida (Figs. 57, 58) are provided with 2 to 12 tentacles. Most are colorless or faintly colored and more or less transparent, but some are green from symbiotic algae (Fig. 36*A*) or brown. The body is clothed in a cellular or syncytial epidermis usually completely ciliated; dorsal ciliation is reduced or absent in sand-dwelling and terrestrial rhabdocoels, and ciliation is scanty or wholly lacking in the ectocommensal Temnocephalida. Ciliated pits and grooves are common among the lower rhabdocoels. The epidermis is usually strewn with bundles of rhabdites, and rhammite tracks leading to the anterior tip are often

present, notably in the mesotomine and temnocephalid groups. The group as a whole is rather lacking in adhesive organs, although adhesive areas (Fig. 51*C*) are characteristic of certain genera (*Dalyellia*, *Macrostomum*) and of ectocommensal (Figs. 57, 58) and sand-dwelling types

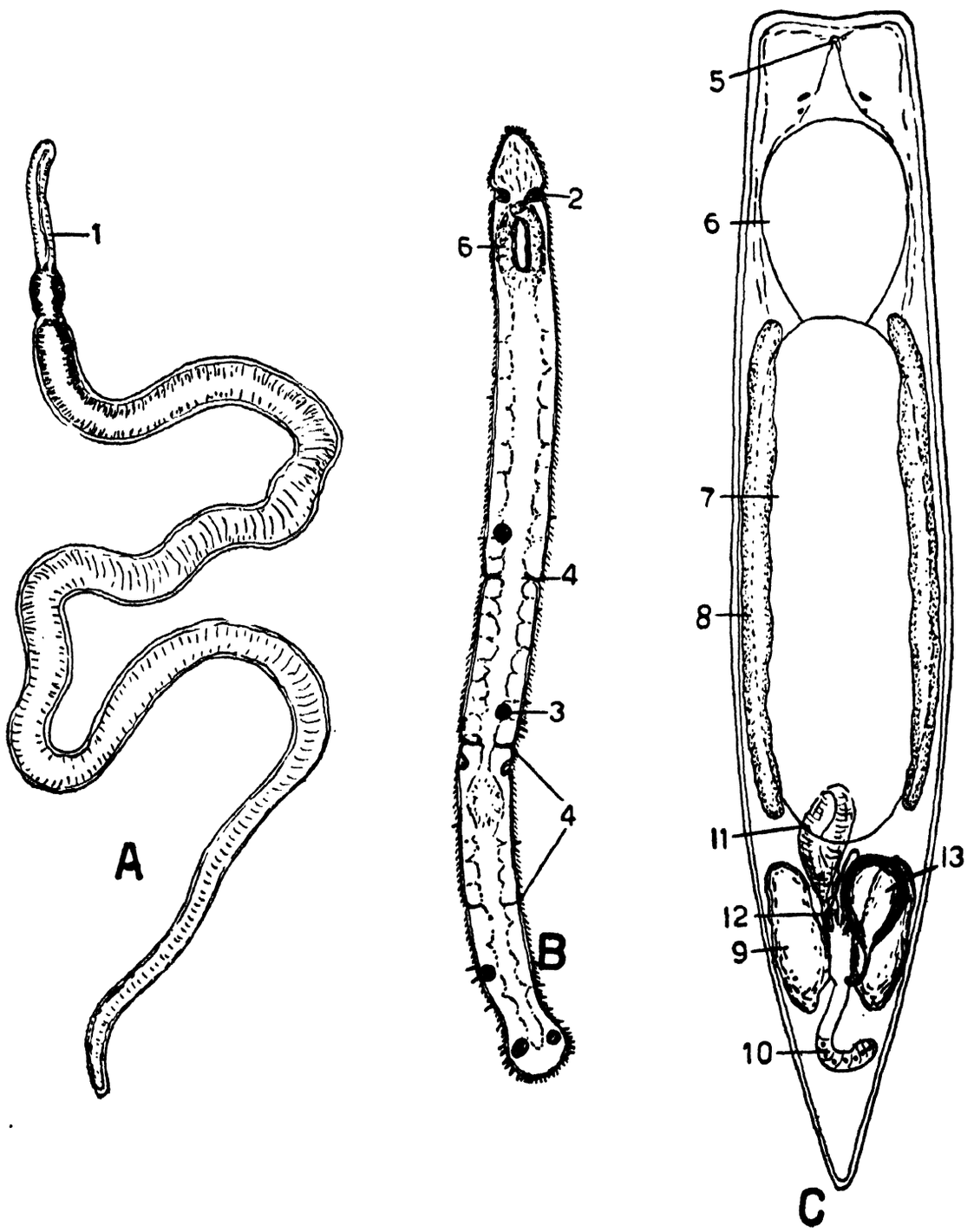

FIG. 50.—Rhabdocoela. *A. Rhynchoscolex* (*after Reisinger*, 1924a). *B.* A marine *Microstomum*, from life, California. *C. Castrella marginata*, family Dalyelliidae, from life, New York. 1, snout; 2, ciliated pits; 3, cluster of nematocysts; 4, fission plane; 5, mouth; 6, pharynx; 7, intestine; 8, yolk glands; 9, testes; 10, ovary; 11, copulatory bursa; 12, penis stylet; 13, stalked egg capsule forming in uterus.

(Fig. 76). Adhesive papillae are probably responsible for the adhesive power of these areas. The rhabdocoels lack the cluster of frontal glands common among the Acoela although a few such gland cells are sometimes present in the anterior end. The surface usually bears sensory spines, hairs, and bristles. A statocyst occurs only in a few of the lower genera (*Catenula*, Fig. 29*D*). Most of the rhabdocoels have a pair of

eyes, sometimes one eye, sometimes four (*Castrella,* Fig. 50*C*). The eyes are of the epidermal pigment-spot type in *Microstomum* and *Alaurina* (Fig. 32*C*); otherwise they are of the pigment-cup type with one pigment cell and one to three retinal cells. There is mostly a paucity of mesenchymal gland cells apart from those connected with adhesive areas or with the reproductive system. The brain is either a bilobed mass or a broad band passing in front of the eyes; into it stream sensory nerves from the anterior margin and from it a pair of strong ventral cords proceeds caudad. Primitive members (*Rhynchoscolex,* Reisinger, 1924a) may have four pairs of longitudinal cords, and a few others may have short dorsal, sometimes also lateral, cords; but in general rhabdocoels have only the ventral cords and are also poor in transverse connectives (Fig. 24*C*). Usually there is a nerve ring around the pharynx (Fig. 51*A*) or a strong connective behind it (Fig. 24*C*), or a pair of nerves from the ventral cords branches into the pharynx. The digestive system consists of a simple or bulbous pharynx and a blind sacciform to elongate intestine, mostly of simple contour, although sometimes lobulated. There is present a pair of protonephridia except in the Catenulida which have a single median nephridium (Fig. 29*A*). The reproductive system comprises usually a pair of well-delimited testes, sometimes broken up into lobes or separated follicles, one ovary or a pair of ovaries, a pair of yolk glands (lacking in the lower orders), and the copulatory complex. This on the male side often includes seminal and prostatic vesicles varyingly related to each other and to the penis, and a penis that may be a muscular papilla or a cuticularized structure varying from a simple tube to a complicated array of rods and teeth (Fig. 38*B–F*). Some genera have a cirrus (Fig. 39*A–C*). The female apparatus may include a seminal or copulatory bursa, seminal receptacle, single or paired uterus, and a variety of gland cells (Fig. 38*B*).

Copulation with mutual insemination (Fig. 46*D*) is the rule among the rhabdocoels. The eggs are generally laid singly, each enclosed in a rounded, oval, or hemispherical albuminoid shell, which will be termed *capsule;* this is formed from droplets stored in the periphery of the ripe egg (Fig. 51*E*) or in the yolk cells. In some species, two or three or even several eggs may be enclosed in the capsule. The lower rhabdocoels lack yolk glands, and hence only the egg or eggs occupy the interior of the capsule, but in the higher groups a number of yolk cells is included. The capsule may have a stalk or filament or disk for attaching it to objects, and there may be a preformed circular seam along which the capsule springs open at hatching. When not attached, the capsules simply lie among bottom debris. After attaining sexual maturity, the rhabdocoels probably continue to reproduce throughout the remainder of their rather brief existences, but some fresh-water forms show definite cycles related to habitat. Particularly inhabitants of temporary ponds,

alpine pools, and arctic and subarctic ponds where the brief season necessitates rapid reproduction, as species of *Dalyellia* and *Mesostoma*, hatch in spring from dormant overwintering eggs, quickly attain sexual maturity, produce a number of thick-shelled eggs, and die as the water dries up or freezes. The eggs can survive freezing and drying, although these are probably not prerequisite to hatching, and hatch the following spring as the ice melts or water again fills the ponds.

It is characteristic of many members of the family Typhloplanidae, as *Mesostoma*, *Typhloplana*, *Bothromesostoma*, etc., that they produce two kinds of eggs, thin-shelled or *subitaneous* and thick-shelled or *dormant* eggs. The former are smaller with a thinner capsule and fewer yolk cells than the latter and develop immediately without passing through a dormant period (Fig. 36*A*). The thick-shelled eggs are the same as the regular eggs of other rhabdocoels and in the typhloplanids probably must lie dormant for some time. The subitaneous eggs appear to be an adaptation for quickly increasing the number of individuals during the summer. Any one worm may produce first subitaneous, then dormant eggs, or may lay only the latter from the start. There is a tendency for the greater production of subitaneous eggs early in the season and for increasing numbers of dormant eggs toward autumn, until finally only the latter are formed. According to Bresslau (1903), subitaneous eggs are produced before the animal has attained full sexual maturity, and this accounts for the thin shell and paucity of yolk cells. The subitaneous eggs are fertilized by the individual's own sperm (this appears to be one of the very few authentic cases of self-fertilization among the Turbellaria) and develop inside the mother, either in the uteri (Fig. 45*A*) or in the mesenchyme (Fig 36*A*), into young worms that escape mostly by rupture and death of the parent. The dormant eggs are cross-fertilized.

The rhabdocoels are common throughout the world in standing fresh waters and the littoral zone of ocean shores, chiefly on sandy and muddy bottoms. They also occur sparingly in flowing fresh waters and in damp terrestrial habitats (Reisinger, 1924b). Species of *Alaurina* are pelagic, and one of these (Fig. 32*B*) has long bristles, presumably for buoyancy. Rhabdocoels also inhabit hot springs as *Macrostomum thermale* in hot salt springs (45°C. 3 per cent salt content) in western Java (Reisinger, 1933). Although ordinary rhabdocoels often get into cave waters, there appears to be a genuine cave rhabdocoel, white and eyeless, "*Vortex*" *cavicolens* Packard 1883, in streams in one of the Kentucky caves.[1] Fresh-water and marine species may spread into brackish waters, and some species appear to be equally at home in salt, brackish, and fresh water as *Macrostomum appendiculatum* and *Gyratrix hermaphroditus* (Fig. 36*B*). *Phae-*

[1] The generic name *Vortex* is invalid for turbellarians, and it is impossible to determine the genus of this worm without further study.

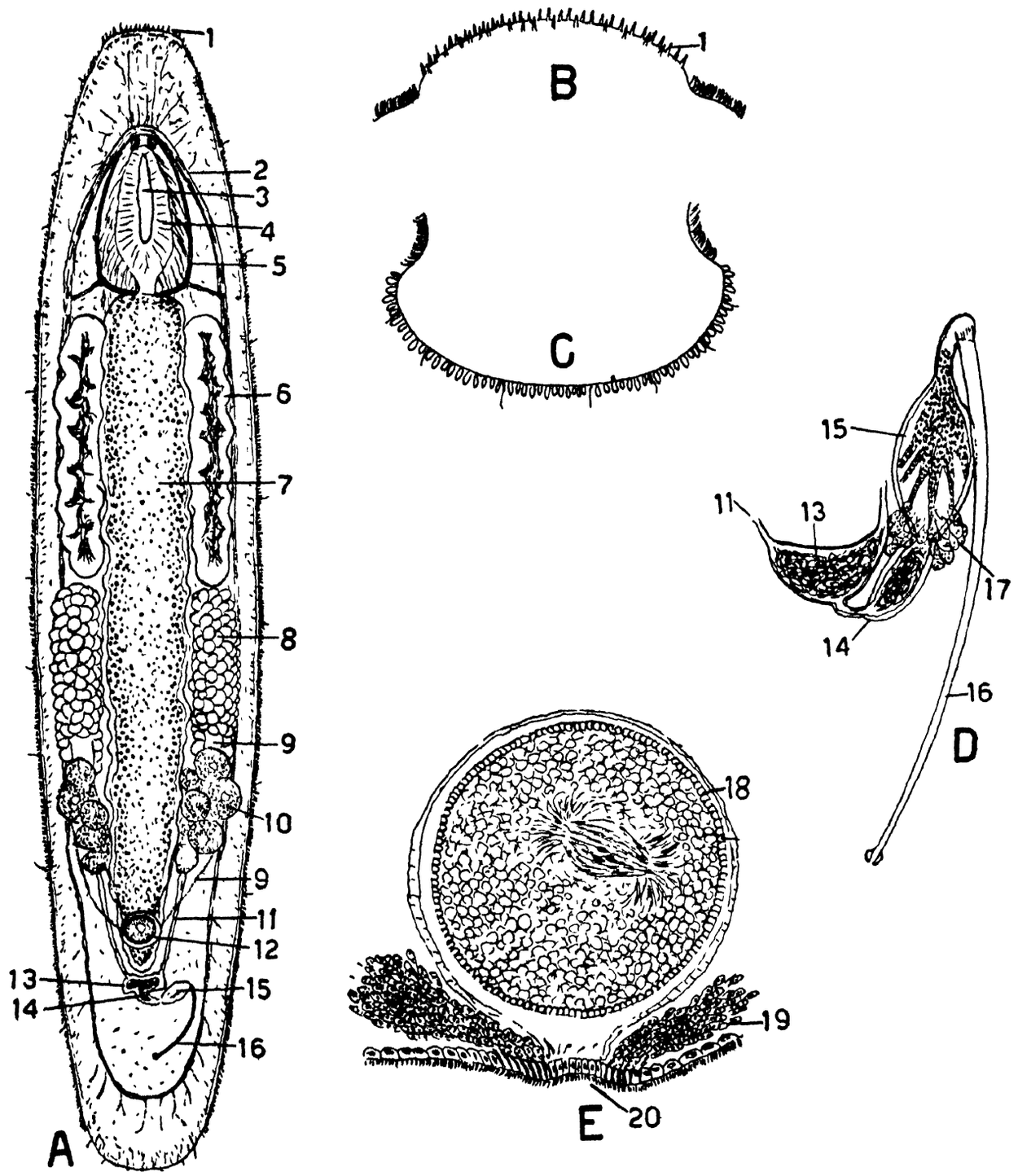

FIG. 51. Rhabdocoela (continued). *A. Macrostomum gigas.* *B.* Anterior end of same, showing sensory spines. *C.* Posterior end of same, showing protrusible adhesive papillae. *D.* Male copulatory apparatus of same. *E.* Section through the female antrum of the same, showing shell-forming droplets in periphery of the egg. (*All after Hyman*, 1943.) 1, sensory spines; 2, ventral nerve cords (confluent at rear); 3, mouth; 4, pharynx simplex; 5, nerve ring around pharynx; 6, testes; 7, intestine; 8, ovary; 9, oviduct; 10, ripe eggs in oviduct; 11, sperm duct; 12, egg in female antrum; 13, spermiducal vesicle; 14, seminal vesicle; 15, prostatic vesicle; 16, penis stylet; 17, prostatic glands; 18, shell-forming droplets; 19, cement glands; 20, female gonopore.

nocora (?) *salinarum* occurs in salt pits of high salt content near Trieste. A number of rhabdocoels, chiefly dalyellioids, inhabit the digestive tract or body spaces of mollusks, echinoderms, and crustaceans; they are probably commensal rather than parasitic except *Fecampia* (see below). There are a number of rhabdocoels with ectocommensal or epizoic habits, and these are generally provided with one or more adhesive areas for clinging to the host animal. They belong to the suborder Temno-

cephalida, discussed later, except *Typhlorhynchus nanus*, a typhloplanoid species, with a tactile snout and posterior adhesive region, inhabiting the parapodia of the polychaete *Nephthys* (Laidlaw, 1902).

Although the rhabdocoels are among the most common animals of fresh water and the ocean littoral, they have been poorly studied outside of Europe and Asia, greatly neglected in the western hemisphere, and but little investigated in tropical and subtropical regions. The indications are that both fresh-water and marine species are much more numerous in temperate and cold zones than in warmer regions. In the United States, rhabdocoels have been made the object of particular study only in a few eastern states and their coasts, chiefly under the leadership of Kepner of the University of Virginia, and undoubtedly rich material awaits study in other areas. The genera known to occur in the United States have been arranged in key form by Ruebush (1941), but many additional genera will certainly be discovered in the future. Many fresh-water species are cosmopolitan, and others are undoubtedly polytypic with many geographical races and varieties. Thus the cosmopolitan *Mesostoma ehrenbergii* exists in the United States as a subspecies *wardii* (Fig. 45*A*), differing from the European type in size, form and number of chromosomes, and some details of the copulatory apparatus (Husted and Ruebush, 1940). One must beware, however, of facile identification of American rhabdocoels with Eurasian species.

a. Suborder Notandropora or Catenulida.—This group includes only a few fresh-water genera with simple pharynx, single median protonephridium, and four pairs of longitudinal nerve cords. The gastrodermis is ciliated. Reports that the protonephridium lacks flame bulbs are clearly mistaken as Kepner, Carter, and Hess (1933) saw them in *Stenostomum* and Marcus (1945) recorded them throughout the Catenulida. The principal genera are: *Catenula* (Fig. 29*D*) with a statocyst, *Rhynchoscolex* (Fig. 50*A*) with a long snout, *Stenostomum* (Fig. 29*A*) with ciliated pits, and *Suomina* (= *Fuhrmannia*) with a transverse ciliated groove around the base of the head. Excellent work has been done on the Catenulida by Marcus (1945), who divides the order into three families and reports two new genera, *Chordarium* with brain at the anterior tip and *Dasyhormus*, similar to *Catenula*. *Stenostomum* with many species, most of them cosmopolitan, is one of the most common invertebrates, found everywhere in standing waters and protozoan cultures, and is probably the most familiar and investigated rhabdocoel. The Catenulida reproduce asexually by transverse fission, forming chains of zooids (Figs. 9, 29, 32*B*) and are seldom seen in the sexual state. Sexual conditions are best known for *Stenostomum* (Sabussow, 1897; Sekera, 1903, 1906; Van Cleave, 1929; Nuttycombe, 1932; Kepner *et al.*, 1933; Marcus, 1945) but have also been described for other genera by Marcus. *Stenostomum* is

markedly protandrous, developing testes in early fall, ovaries later. From a single testicular mass dorsal to the pharynx a short male canal having a muscular penial thickening leads to a dorsal gonopore (Fig. 48*B*). The female system consists in its entirety of one to several

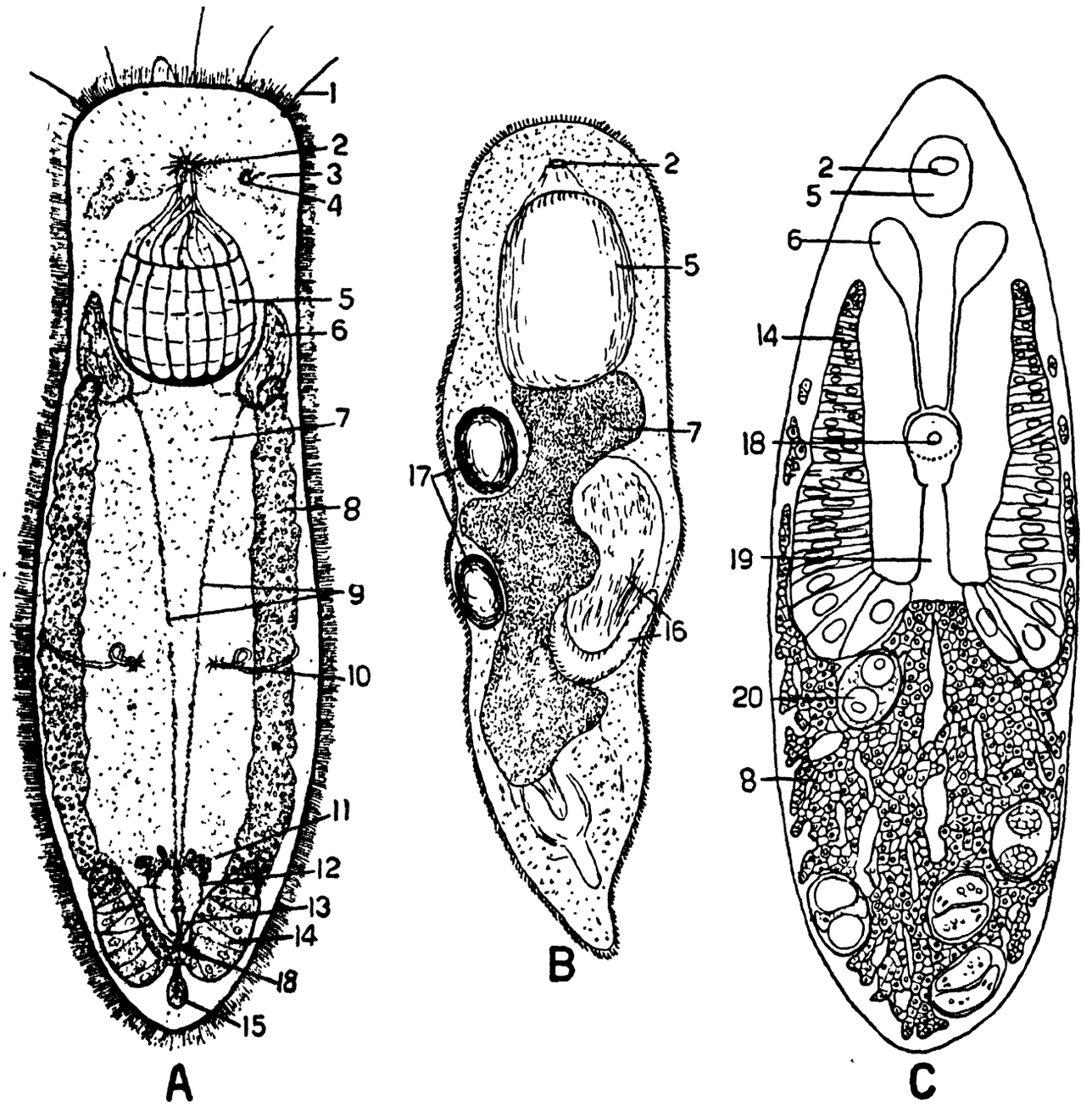

FIG. 52.—Rhabdocoela (continued). Dalyellioida. *A. Provortex* (*after Ruebush*, 1935a). *B. Plagiostomum* infested with two specimens of *Oekiocolax plagiostomorum* (*after Reisinger*, 1930). *C. Paravortex gemellipara* (*after Ball*, 1916) from the clam *Modiolus*. 1, sensory hairs; 2, mouth; 3, brain; 4, eye; 5, pharynx; 6, testes; 7, intestine; 8, yolk gland; 9, sperm ducts; 10, nephridiopore; 11, prostatic glands; 12, penis bulb; 13, penis stylet; 14, ovary; 15, seminal receptacle; 16, parasite; 17, eggs of parasite; 18, common gonopore; 19, female antrum; 20, capsules containing two embryos.

ovaries, each of which matures one egg per season. Reisinger (1924a) failed to find any male system in *Rhynchoscolex* and claims parthenogenesis for this and other Catenulida; Sekera believed that self-fertilization obtains; but Kepner *er al.* saw hypodermic impregnation (Fig. 48*A*) in *Stenostomum* during the male phase, and this is probably the correct state of affairs, for this genus at least. The fertilized egg enclosed in a capsule is released by rupture, and thereafter the female usually dies. The egg

hatches in the laboratory in 2 to 4 weeks but in nature probably remains dormant until spring. Asexual reproduction continues during the male phase but is inhibited and regenerative power lost during the female condition. Although external factors appear to control the onset of sexuality in *Stenostomum* in nature, no one has succeeded in inducing the sexual phase in laboratory cultures. Such cultures may run for years through hundreds of asexual generations or may continue indefinitely in the male phase.

b. Suborder Opisthandropora or Macrostomida.—This group has a simple pharynx, one pair of longitudinal nerve cords, and complete male and female systems with separate gonopores. The gastrodermis is ciliated as in the Catenulida, but there are the usual two protonephridia. The suborder comprises two families: Macrostomidae, without asexual reproduction, and Microstomidae, with zooid formation. In the former the principal genus is *Macrostomum* (Fig. 51) with many species and subspecies, common in fresh waters, and also extending into brackish and salt waters (Ferguson, 1939–1940). The rear end, often of spatulate shape, is adhesive. There is a pair of ovaries and oviducts connected to the female antrum and a pair of testes and sperm ducts connected to the male apparatus, which consists of spermiducal vesicle (not always present), seminal vesicle, prostatic vesicle, and tubular penis stylet of varying form (Fig. 51*D*). The Microstomidae comprise two genera, *Alaurina* with papillate snout and marine pelagic habits (Fig. 32*B*), and *Microstomum* (Fig. 50*B*) with ciliated pits and intestine extending anterior to the mouth. Both form chains of zooids as in *Stenostomum*. The nematocysts of *Microstomum* were discussed above (page 71). Most microstomids have eyes which may be of the pigment-spot type (Fig. 32*C*). Sexually mature specimens, probably related to environmental conditions, have seldom been seen. Marked protandry obtains; the sexual system differs from that of *Macrostomum* chiefly in that the ovary and oviduct are single (Meixner, 1924a). The fertilized egg remains dormant until spring.

Both the Catenulida and Macrostomida lack yolk glands, and yolk and shell substance are stored by the egg's own activity. As the egg is about to be laid, its shell-forming spherules assemble at the egg periphery and fuse and harden to a capsule (Fig. 51*E*).

c. Suborder Lecithophora: Dalyellioida.—All the Lecithophora lack asexual reproduction and have one or two yolk glands that furnish yolk cells to be incorporated with the egg inside the capsule. The yolk gland is primitively continuous with the ovary forming the *germovitellarium;* but in most Lecithophora the two are distinct. The Lecithophora have a pair of protonephridia, and only the ventral nerve cords are well developed.

The dalyellioid Lecithophora are readily known by the doliiform pharynx leading inward from the anteriorly placed mouth (Fig. 34*D*). There are usually paired testes, an armed penis, single or paired germovitellaria or separate ovaries and yolk glands, often a seminal or copulatory bursa, uterus, and common gonopore (Fig. 38*B*). The Provorticidae, with posterior gonopore and mostly a tubular penis stylet include terrestrial (Reisinger, 1923, 1924c), marine, and fresh-water species, also the parasitic *Oekiocolax plagiostomorum*, Greenland, inhabiting the mesenchyme of the alloeocoel *Plagiostomum* in which it causes ovarian degeneration (Reisinger, 1930, Fig. 52*B*). *Provortex* (Fig. 52*A*) is the only member of this family that has been found in the United States (Ruebush, 1935a). The Graffillidae, with more anterior gonopore and unarmed penis, comprise three genera: *Bresslauilla* (see page 123), free-living, and the entocommensal *Graffilla* and *Paravortex*. *Graffilla*, with long tubular coiled ovaries, has three species inhabiting the viscera of marine snails and one species in the shipworm *Teredo*. *Paravortex*, with branched yolk glands, lives in the viscera or mantle cavity of marine bivalves; the thin capsules, containing usually two eggs and a mass of yolk cells, are given off into the mesenchyme where they develop into young worms that escape by rupture. *Paravortex gemellipara* (Fig. 52*C*) occurs on the New England Coast in the clam *Modiolus* (Linton, 1910; Ball, 1916). The Umagillidae with small rounded pharynx, posterior gonopore, and conspicuous yolk glands, often lobed or branched, all inhabit the coelom or digestive tract of other animals, chiefly echinoderms. In this family the female system has a tubular uterus in which the long-stalked egg capsules are formed (Fig. 53*B*). The genera are: *Anoplodium*, *Anoplodiera* (Fig. 53*A*), *Wahlia*, *Umagilla*, *Xenometra*, and *Cleistogamia* in holothurians; *Desmote*, *Bicladus* in crinoids; *Syndesmis*, *Syndisyrinx* (Fig. 53*B*) in sea urchins; *Collastoma* in sipunculoids (Wahl, 1906, 1909, 1910; Bock, 1925; Westblad, 1926, 1930; Ozaki, 1932; Baer, 1938; Lehman, 1946). Very little is known of the occurrence of these genera on American coasts except that *Syndisyrinx* (Fig. 53*B*) inhabits a Californian sea urchin. *Pterastericola fedotovi*, only member of its family, lives in sea stars of the genus *Pteraster* off north European coasts (Beklemischev, 1916). Whether the umagillids and graffillids are commensals or parasites is not determinable on available evidence, but probably they are harmless commensals. The Fecampiidae, known only from European coasts, are, however, definitely parasitic. The young *Fecampia* (Fig. 53*D*) has eyes, mouth, long buccal tube, pharynx, and intestine; it somehow enters the haemocoel of various marine crustaceans and there grows to sexual maturity, losing all these structures except the intestine (Fig. 53*C*, Caullery and Mesnil, 1903). It then leaves the host and secretes a bottle-shaped capsule in which it deposits clusters, each consisting of two eggs and many yolk

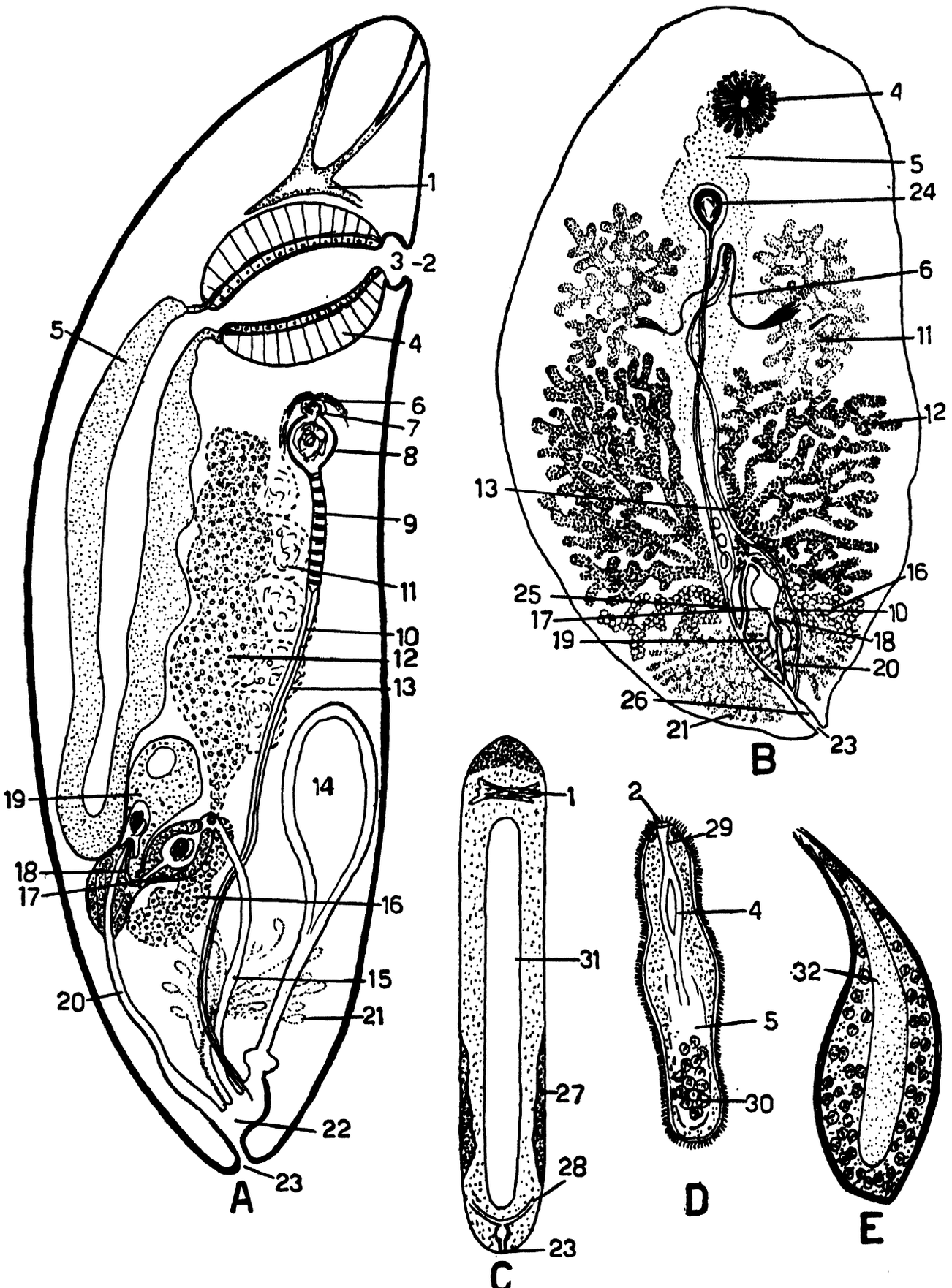

FIG. 53.—Dalyellioida (continued). Umagillidae, Fecampiidae. *A. Anoplodiera voluta* (*after Westblad*, 1930), from the gut of sea cucumbers, sagittal section. *B. Syndisyrinx* from the gut of California sea urchins, from life. *C–E, Fecampia*, (*after Caullery and Mesnil*, 1903). *C.* Adult without mouth or pharynx. *D.* Juvenile stage with digestive system and eyes. *E. Fecampia* secreting the capsule containing many clusters of eggs and yolk cells. 1, brain; 2, mouth; 3, pharyngeal cavity; 4, pharynx; 5, intestine; 6, sperm ducts; 7, spermiducal vesicle; 8, seminal vesicle; 9, penis bulb; 10, penis stylet; 11, testis (only one shown in *A*); 12, yolk gland (one shown in *A*); 13, ejaculatory duct; 14, uterus; 15, vagina; 16, ovary; 17, seminal receptacle; 18, insemination canal; 19, copulatory bursa; 20, bursal canal; 21, cement glands; 22, common antrum; 23, common gonopore; 24, long-stalked capsule in the uterus; 25, ovovitelline duct; 26, vagina; 27, hermaphroditic gonad; 28, gonoduct; 29, buccal tube; 30, yolk in intestine; 31, space; 32, worm inside capsule.

cells (Fig. 53*E*), thereupon dying. The related *Glanduloderma* (Jägersten, 1941), also lacking mouth and pharynx, inhabits the mesenchyme of myzostomids.

The Dalyelliidae, a family almost exclusively fresh-water, is distinguished by the cuticularized penis, composed of a complicated array of bars, rods, rings, and teeth (Fig. 38). The principal genus *Dalyellia* (old name, *Vortex*) is common everywhere in fresh waters, presenting numerous species and subspecies, differentiated by the details of the penial apparatus (Fig. 38*B–F*). Species and subspecies of *Dalyellia* in the United States have been discussed by Ruebush (1937) and Ruebush and Hayes (1939). A group of forms, exemplified by *D. viridis* with many geographical races, is green because of algal symbionts (see below).[1] Another dalyelliid genus found in the United States is *Castrella*, with four eyes and penial apparatus in a separate pocket (Fig. 50*C*).

d. Suborder Lecithophora: Typhloplanoida.—The typhloplanid rhabdocoels are distinguished by the rosulate pharynx (although a few species have a doliiform pharynx) and the more posterior mouth; there is a common gonopore or separate male and female pores. Besides the main family, Typhloplanidae, there are several other families of one to a few genera, chiefly of taxonomic interest. The Typhloplanidae are mainly fresh-water forms but also include most of the terrestrial rhabdocoels, which have obviously migrated from forest streams and pools into moist habitats of the forest floor. This is the largest rhabdocoel family, with numerous genera and species, arranged into several subfamilies based on the relative positions of testes and yolk glands and the location of the nephridiopores. The Protoplanellinae with ventral testes and surface nephridiopores include *Protoplanella*, *Amphibolella*, and several terrestrial forms (Reisinger, 1924b). The Typhloplaninae with ventral testes and nephridia opening into the pharyngeal cavity include *Strongylostoma*, *Typhloplana* with green symbionts (Fig. 36*A*), *Castrada*, and several others. *Rhynchomesostoma* with contractile snout and nephridia opening into the genital antrum is the sole genus of the Rhynchomesostominae. The Phaenocorinae are represented chiefly by *Phaenocora* (Fig. 39*A*) with greatly branched yolk glands, dorsal testes, cirrus, and surface nephridiopores. An admirable study of this genus in the United States has been made by Gilbert (1935, 1937, 1938). The Olisthanellinae have dorsal testes and surface nephridiopores but no cirrus; the chief genus *Olisthanella* is represented in the United States (Ruebush, 1935b). The Mesostominae are characterized by the dorsal or lateral testes, often

[1] Gieysztor (1938) has proposed that only these green forms retain the name *Dalyellia* and has created a new name, *Microdalyellia*, for nongreen species. The author is unable to grant generic significance to the presence or absence of zoochlorellae.

lobulated or subdivided into several masses, and the opening of the nephridia into the pharyngeal cavity (Fig. 33*B*). The chief genus *Mesostoma* (Fig. 45*A*, *B*) is one of the most common fresh-water rhabdocoels, with numerous species throughout the world, some cosmopolitan. The reproductive system of *Mesostoma*, with single ovary, seminal receptacle, copulatory bursa, long paired uteri, and penis bulb usually combining seminal and prostatic vesicles, is shown in Fig. 54. The uteri, containing the hemispherical, hard-shelled dormant eggs, are often conspicuous in the living animal. The known species of *Mesostoma* have been reviewed by Ferguson and Hayes (1941). *M. ehrenbergii*

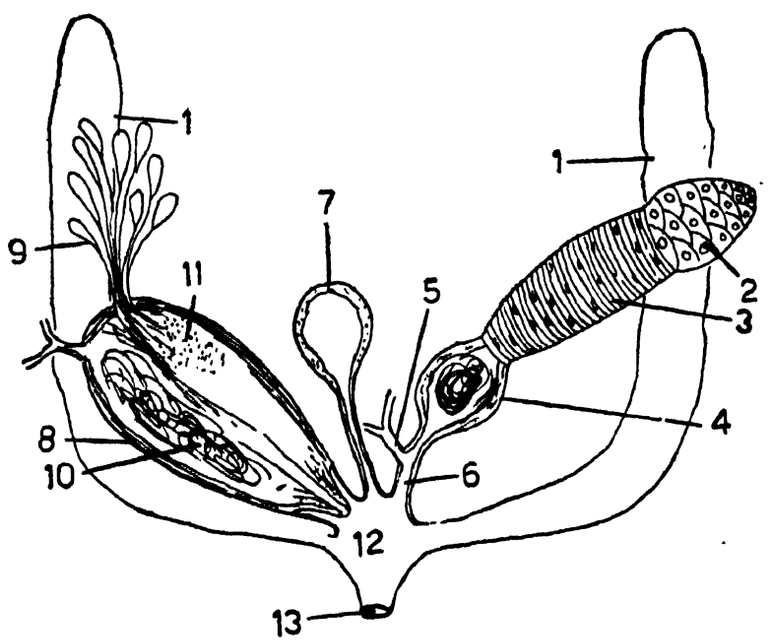

FIG. 54.—Typhloplanoida. Copulatory complex of *Mesostoma*, schematic. 1, uterus; 2, ovary; 3, oviduct; 4, seminal receptacle; 5, common yolk duct; 6, ovovitelline duct; 7, copulatory bursa; 8, penis bulb; 9, prostatic glands; 10, seminal vesicle in penis bulb; 11, prostatic vesicle in penis bulb; 12, common antrum; 13, common gonopore.

because of its large size (to 15 mm.) and broad, thin, transparent body is often selected as a textbook type; a variant of this species termed *wardii* (Fig. 45*A*) occurs in the United States and has proved amenable to laboratory cultivation. *Bothromesostoma* differs from *Mesostoma* in having a ventral pit and a canal connecting copulatory bursa and ovovitelline duct. Two other subfamilies need not be mentioned.

e. Suborder Lecithophora: Kalyptorhynchia.—The kalyptorhynchid rhabdocoels are readily recognized by the presence in the anterior end of a protrusible glandulo-muscular adhesive organ, usually termed proboscis (Figs. 55, 56), employed in the capture of prey. When the sensory bristles make contact with prey (chiefly copepods), the proboscis shoots out with lightning speed, secures the prey by the viscous secretion of its glands, and then bends around so that the food is brought in contact with the protruded pharynx (Meixner, 1925). The proboscis exhibits a great variety of structure and grades of complexity, some of which are shown in Figs. 55 and 56, and may be armed with hooks. The kalyptor-

hynchids are chiefly marine, inhabiting sandy bottoms of coastal waters, especially in bays, sounds, etc. Very few were known until recent years when new methods of collecting microscopic forms from such habitats revealed many new genera and species in such regions as the Bay of Kiel, Finnish Gulf, etc. (Meixner, 1923, 1924b, 1925, 1926, 1928, 1929,

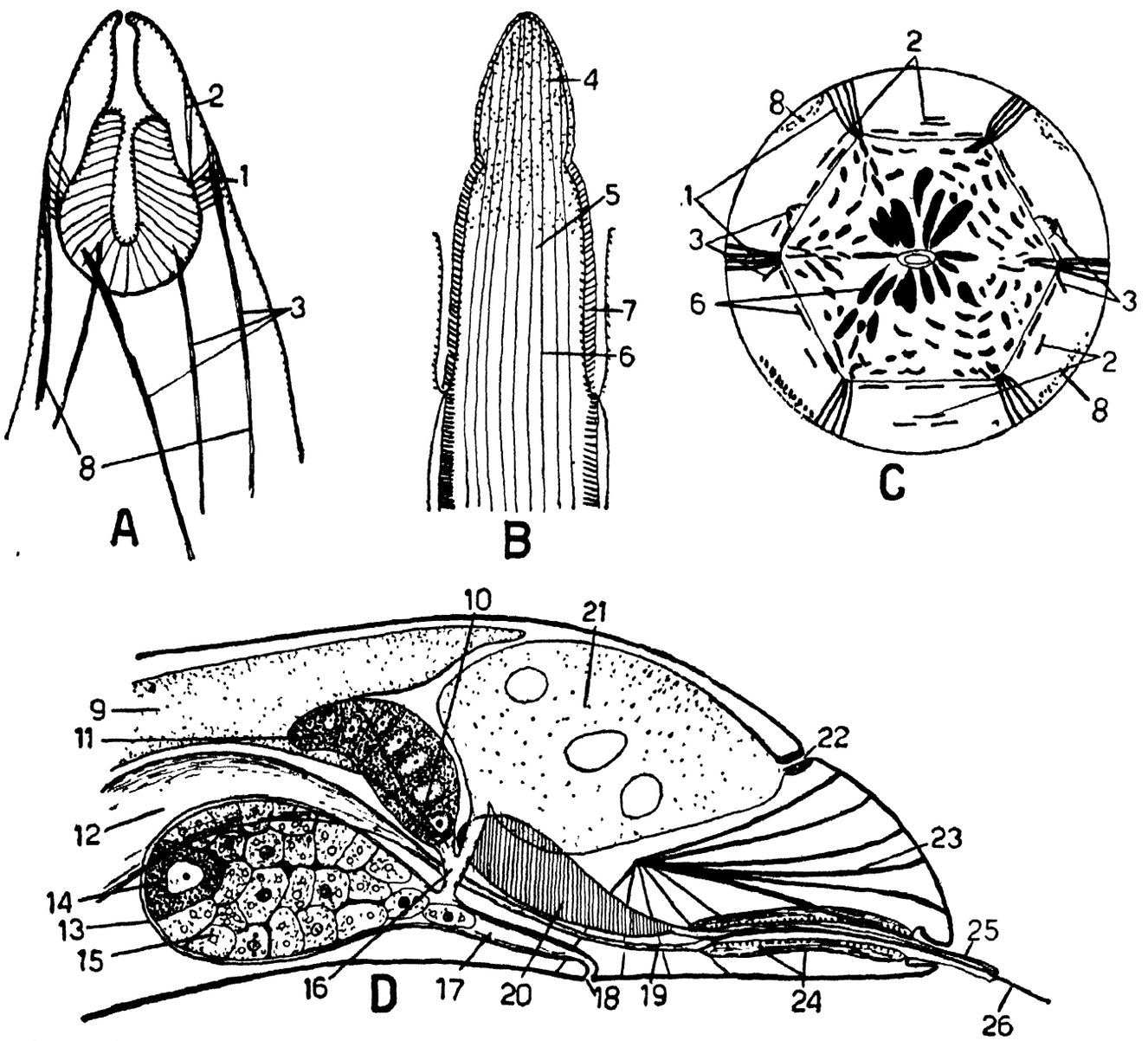

Fig. 55.—Kalyptorhynchia. *A–D. Gyratrix hermaphroditus* (*after Meixner*, 1915, 1929). *A*. Proboscis in resting state. *B*. Proboscis protruded. *C*. Cross section through the proboscis, showing its musculature. *D*. Copulatory complex, sagittal view. 1, fixators; 2, protractors; 3, retractors; 4, end cone; 5, muscle cone; 6, longitudinal musculature; 7, transverse musculature; 8, integumental retractors; 9, yolk gland; 10, yolk duct; 11, ovary; 12, seminal vesicle; 13, uterus; 14, egg; 15, yolk cells; 16, ovovitelline duct; 17, vagina; 18, female gonopore; 19, ejaculatory duct; 20, prostatic vesicle; 21, seminal bursa; 22, bursal pore; 23, protractors of the penis sheath; 24, penis bulb; 25, penis sheath; 26, penis stylet.

1938; Karling, 1931). The kalyptorhynchids are divided into two groups, the Eukalyptorhynchia with undivided proboscis (Figs. 55, 56) and the Schizorhynchia, in which the proboscis is bifurcated (Fig. 56*D*). The best known member of the former group is *Gyratrix hermaphroditus* (Figs. 36*B*, 55*A–D*), common throughout the world in fresh, brackish, and salt waters (see page 209). *Gyratrix* is unique among the flatworms in having chitin; the copulatory bursa has a chitinous lining (Flory and Showalter,

1930). Other well-known eukalyptorhynchids are *Acrorhynchus* (Fig. 56*A*) and *Polycystis* (Fig. 56*B*). The Schizorhynchia for years were known only by the genus *Schizorhynchus* (Fig. 56*D*), but recently many new genera were found and described (Meixner, 1928, 1938; de Beauchamp, 1927).

f. Suborder Temnocephalida.—The Temnocephalida, discovered in Chile in 1846, were first thought to be leeches, then regarded as trematodes, then for a long period made into a separate class Temnocephaloidea between Turbellaria and Trematoda. Their turbellarian nature was realized by Grobben in 1909 and has since been acknowledged by all students of the group. They are often considered to constitute a sixth order of Turbellaria, but their dalyellioid nature is now generally recognized and hence, following Fyfe (1942), they are here placed under Rhabdocoela as a suborder.

The Temnocephalida lead an ectocommensal existence on freshwater animals, chiefly crayfish, prawns, isopods, and other crustaceans, less often turtles and snails, occurring on the external surface or in the branchial chamber. They are limited to tropical and subtropical countries, and are most common in Australia, New Zealand, and South America, but species also occur in India, Balkan Peninsula, Central America, and various South Pacific islands. The Temnocephalida are obviously modified for an epizoic existence. They are small, flattened, mostly colorless and somewhat transparent worms, distinguished from other rhabdocoels by their tentacles and adhesive organs. The tentacles are typically 5, 6, or 12 finger-like anterior projections as in *Temnocephala* (Fig. 57*A*); but in *Scutariella*, *Monodiscus*, and *Caridinicola* (Fig. 58*C*), there are only 2 short stumpy tentacles, and *Actinodactylella* (Fig. 57*B*) has 12 distributed along the body. Tentacles are absent in *Didymorchis*, formerly placed in the Dalyelliidae. *Craspedella* (Fig. 58*A*) has papillate bands on the dorsal posterior region. All temnocephalids possess an adhesive disk at the rear end; except *Caridinicola* (Fig. 58*C*) in which there is instead a pair of adhesive pits. Some genera also have an anterior adhesive organ. The adhesive organ in no case has the structure of a true sucker such as is characteristic of trematodes. By alternately attaching tentacles and adhesive organ, the temnocephalids are able to move about over their hosts in a leech-like manner.

The syncytial epidermis usually has a clear border apparently cuticular and lacks cilia except in a few species that have a limited ciliation. Paired clusters of gland cells furnish adenal rhabdites to the anterior end and to the tentacles, and gland cells also supply the adhesive organs. The nervous system comprises a subepidermal and a submuscular net; in the latter are differentiated many sensory nerves from the tentacles into the brain and three pairs of longitudinal cords with transverse connec-

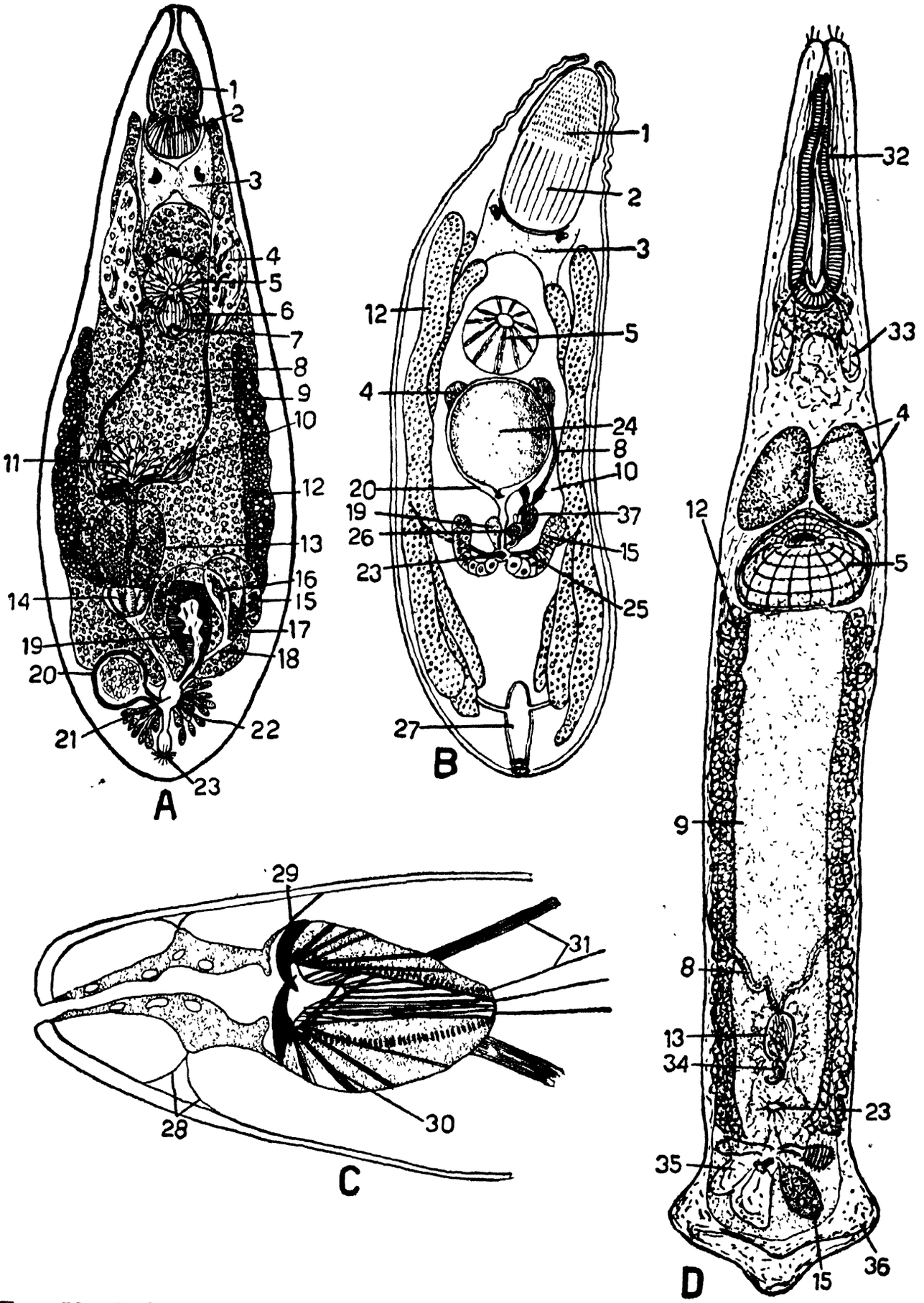

FIG. 56.—Kalyptorhynchia (continued). *A. Acrorhynchus* (*after Graff*, 1905). *B. Polycystis goettei* (*after Bresslau*, 1906). *C. Gnathorhynchus*, proboscis armed with hooks (*after Meixner*, 1929). *D. Schizorhynchus arenarius* (*after Beauchamp*, 1927). 1, end cone of proboscis; 2, muscle cone of proboscis; 3, brain; 4, testes; 5, pharynx; 6, pharyngeal cavity; 7, mouth; 8, sperm ducts; 9, intestine; 10, spermiducal vesicles; 11, prostatic glands; 12, yolk gland; 13, penis bulb; 14, penis papilla; 15, ovaries; 16, seminal receptacle; 17, common yolk duct; 18, ovovitelline duct; 19, seminal bursa; 20, uterus; 21, common antrum; 22, cement glands; 23, common gonopore; 24, capsule forming in uterus; 25, yolk duct; 26, prostatic vesicle; 27, excretory ampulla; 28, dilator muscles; 29, hooks; 30, flexors of hooks; 31, retractor muscles; 32, bifurcated proboscis; 33, proboscis glands; 34, penis stylet; 35, copulatory bursa; 36, caudal adhesive region; 37, seminal vesicle.

tions (Fig. 58*B*). The tentacles are undoubtedly tactile, and in addition tactile bristles and papillae may be present. Most species have a pair of eyes, each of which is double with a retinal cell at each end facing the central pigment cell. The digestive system is dalyellioid with doliiform pharynx and sacciform intestine. There is a protonephridium on each side (Fig. 58*C*) provided with terminal bulbs and lateral flames and opening anteriorly, mostly dorsally, by way of an excretory bladder. The nephridia of the two sides are confluent anteriorly and posteriorly, and from the anterior anastomosis branches proceed into the tentacles. Paranephrocytes are also present. The testes occur as one pair, or each is subdivided into two to six parts (Fig. 57). The male system includes a spermiducal vesicle, seminal vesicle, prostatic glands opening into the penis base or into a prostatic vesicle, and a cirrus or a penial cuticular apparatus varying from a simple stylet to a dalyelliid complex. There is a single ovary and a pair of yolk glands often much subdivided or forming an anastomosing net; these connect with the female canal which also usually bears a large seminal bursa and one or more small seminal receptacles. The seminal bursa is unusually active in digesting and absorbing excess sex products. The female antrum, often called uterus, is enlarged and thickened for the secretion of the egg capsule, and sometimes lined with teeth. There is a common antrum and gonopore. The oval capsules are fastened to the exterior of the host or to its gills.

Although the temnocephalids do not voluntarily leave their hosts, some species can live for weeks or months when removed from them; others die in a short time. The group is commensal, not parasitic, since the food consists of small animals and diatoms available in the habitat. The respiratory water currents maintained by the host animals are probably beneficial to the temnocephalids. *Scutariella didactyla* on a prawn in Montenegro apparently feeds on its host's body fluids and hence may be an ectoparasite (Mrazek, 1906).

16. Order Alloeocoela.—The Alloeocoela are a group difficult of precise definition, for the more primitive members grade into the Acoela, from which they differ chiefly in having a digestive cavity, and the higher members grade into the Tricladida.[1] Although some are minute, the alloeocoels are on the whole larger than the acoels and rhabdocoels, many ranging from 1 or 2 to 8 or 10 mm. in length, and some species are 15 to 25 mm. long. The largest member is *Baicalarctia gulo*, from Lake Baikal, 40 mm. in length (Friedmann, 1926). The alloeocoels tend to a cylindroid shape, plump to elongate; the group includes a number of long slender forms such as *Prorhynchus stagnalis* (Fig. 59*A*). Ciliated

[1] Meixner (1938), in recognition of this affinity, makes the triclads a section under the alloeocoel suborder Seriata. He also considers *Hofstenia* to be an acoel, but it would be preferable to transfer *Nemertoderma* to the alloeocoels.

pits and grooves are of common occurrence, and a caudal adhesive region with adhesive papillae is present in most Seriata (Fig. 29*C*). Reminiscent of the Acoela is the presence of a cluster of frontal glands in several genera (*Hofstenia, Enterostomula, Protomonotresis, Hydrolimax*, Fig. 18, *Bothriomolus, Baicalarctia*), and of a statocyst in some forms (*Hofstenia*, Fig. 31*F*, *Otomesostoma*, family Monocelididae, Fig. 29*C*). Many alloeocoels lack eyes but some have one or two pairs. The nervous

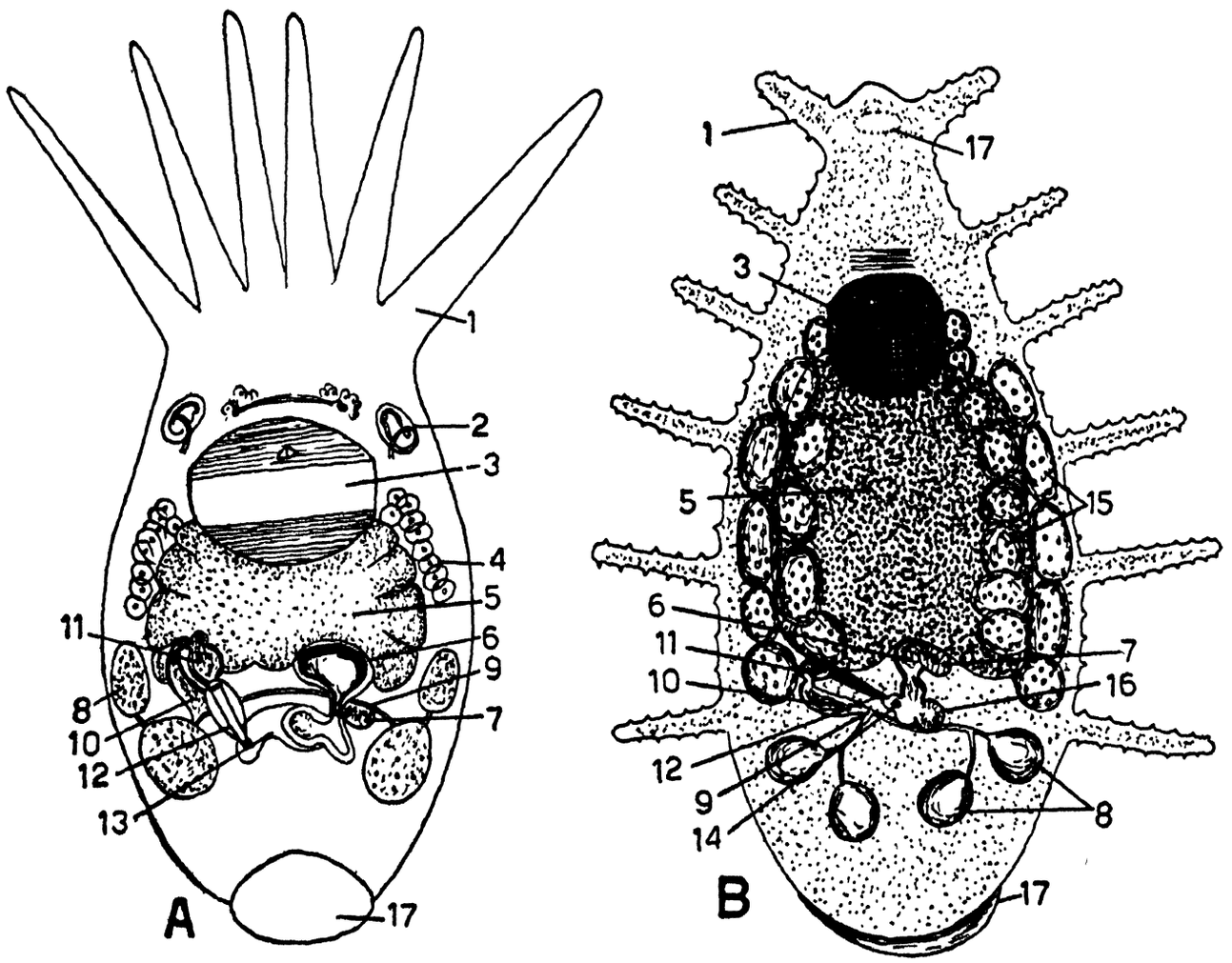

FIG. 57.—Temnocephalida. *A. Temnocephala* (*after Haswell*, 1893). *B. Actinodactylella* (*after Haswell*, 1893). 1, tentacles; 2, excretory ampulla; 3, pharynx; 4, tentacle glands; 5, intestine; 6, bursa; 7, ovary; 8, testis; 9, sperm duct; 10, seminal vesicle; 11, prostatic vesicle; 12, penis stylet; 13, common antrum; 14, common gonopore; 15, yolk glands; 16, uterus; 17, adhesive disk.

system is characterized by three or four pairs of longitudinal cords with transverse connections (Fig. 24*A*). There is a pair of protonephridia, but these often have two or three main branches on each side and a number of nephridiopores (Fig. 36*F*). The pharynx is of the simple, doliiform (variable), or plicate type and the intestine varies from a simply contoured sac to a considerably diverticulated organ, finally approaching the triclad condition as in *Bothrioplana* (Fig. 35*D*). There are usually several to many small testes and a pair of ovaries. The alloeocoels are predominantly marine, found in the littoral zone, among vegetation and especially on sandy and mucky bottoms; they also extend into brackish waters, and some occur in fresh water, especially *Otomeso-*

stoma, Bothrioplana, and members of the families Prorhynchidae and Plagiostomidae. Species of Prorhynchidae also extend into moist terrestrial habitats. Some alloeocoels have ectoparasitic or ectocommensal habits.

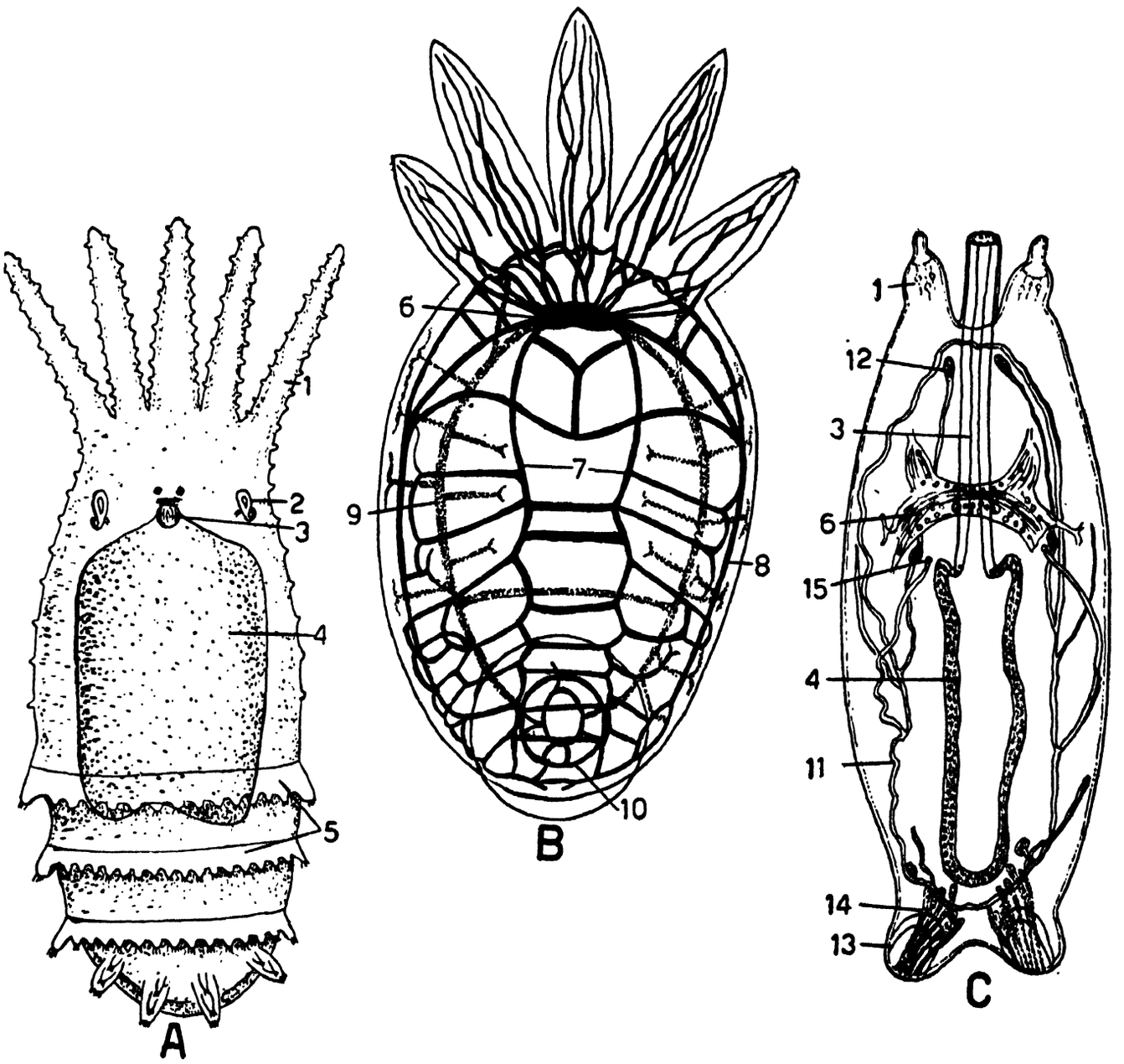

FIG. 58.—Temnocephalida (continued). *A. Craspedella* (*after Haswell,* 1893). *B.* Nervous system of *Temnocephala* (*after Merton,* 1913). *C. Caridinicola* (*after Plate,* 1914). 1, tentacles; 2, excretory ampullae; 3, pharynx; 4, intestine; 5, papillate bands; 6, brain; 7, dorsal cord; 8, lateral cords; 9, ventral cords; 10, nerve ring in adhesive disk; 11, protonephridial tubules; 12, athrocytes; 13, adhesive pit; 14, glands of same; 15, nephridiopore.

a. Suborder Archoophora.—This consists of the single species, *Proporoplana jenseni,* dredged off Greenland (Reisinger, 1935). The animal, 1 mm. long, has a frontal gland, buccal tube, plicate pharynx, no female ducts, and a simple male copulatory apparatus opening posteriorly. Although regarded by Reisinger as a rhabdocoel, the animal fits better into the Alloeocoela.

b. Suborder Lecithoepitheliata.—In this group there are no yolk glands, but the single or paired germovitellaria consist of loose clusters, each

composed of an ovocyte encircled by nutritive cells (Figs. 42*F*, 43). There is a simple female duct or none. There is generally a typical male apparatus armed with a penis stylet. This group comprises the already much-mentioned *Hofstenia* (Fig. 31*F*), marine, Japan (Bock, 1923), *Gnosonesima*, Antarctic (Reisinger, 1926, see page 119), and the Prorhynchidae, with one pair of ciliated pits and male apparatus opening into the buccal tube (Fig. 59). The prorhynchids (monographed by Steinböck, 1927), are common throughout the world in fresh and brackish waters, and also extend into moist terrestrial habitats. There are two genera, *Prorhynchus* with straight and *Geocentrophora* with curved penis stylet (Fig. 59*B*, *C*). *Prorhynchus stagnalis* (Fig. 59*A*), a slender white worm to 6 mm. long, is cosmopolitan, one of the commonest fresh-water turbellarians.

c. Suborder Cumulata or Holocoela.—In this suborder there are yolk glands more or less distinct from the ovaries, although the ovocytes may still be encircled by a nutritive zone. The intestine has a simple or slightly lobulated contour, and the penis is generally unarmed. In the Pseudostomidae (genera *Pseudostomum*, with ciliated groove (Fig. 60*E*) *Protomonotresis*, Reisinger, 1923, with plicate pharynx), the genital antrum joins the anteriorly placed pharyngeal cavity. In the Cylindrostomidae, with plicate pharynx, the common genitopharyngeal cavity is at the posterior end; here belong several marine genera such as *Cylindrostoma*, *Allostoma*, *Enterostomula* (Carolina Coast, Jones, 1941), and *Hypotrichina* (= *Genostoma*). *Cylindrostoma cyprinae* lives commensally on the gills of various marine bivalves on European coasts. Species of *Hypotrichina* (Fig. 60*C*) with anterior adhesive disk and scanty ciliation are ectoparasitic on the crustacean *Nebalia* in the Mediterranean. The Plagiostomidae (Fig. 60*A*, *B*) have an anterior mouth and posterior gonopore. The principal genus, *Plagiostomum*, with bulbous pharynx, comprises numerous marine species on North American and Eurasian coasts and one or two fresh-water species of which *Plagiostomum lemani*, in European lakes, ponds, and streams, is one of the best known alloeocoels (Hofsten, 1907). An interesting plagiostomid, *Hydrolimax grisea* (Fig. 18) inhabits fresh waters in Pennsylvania and adjacent states; it has a frontal gland and an enormous prostatic vesicle (Hyman, 1938). *Vorticeros*, marine, differs in the plicate pharynx and two tentacles (Fig. 14*C*). In the Multipeniatidae with the single genus *Multipeniata* (page 117), and the Baicalarctiidae with one genus *Baicalarctia*, mouth and gonopore are adjacent in the anterior part of the body.

d. Suborder Seriata.—The members of this group have a plicate pharynx directed backward, slightly or markedly lobulated intestine, and numerous yolk glands opening into a pair of yolk ducts. The principal family, Monocelididae, has a statocyst, caudal or lateral adhesive

area with adhesive papillae, and usually a seminal bursa. *Monocelis* (Fig. 29*C*), a slender white worm with separate bursal pore (hence three genital pores) has many species common along ocean shores. *Archiloa*, of which a species has been found along the Carolina Coast (Stirewalt, Kepner, and Ferguson, 1940) differs in lacking a bursal pore. *Otoplana*, marine, has a pair of ciliated pits and conspicuous anterior tactile bristles (Fig. 60*D*) whereas *Bothriomolus* lacks these and instead possesses a frontal organ. The Otomesostomidae comprise the single species *Otomesostoma auditivum*, widely distributed in fresh water, with two pairs of ciliated pits and a statocyst but no adhesive papillae. *Bothrioplana* (Reisinger, 1925), common in fresh water, the only genus of the Bothrioplanidae, has two pairs of ciliated pits and caudal adhesive papillae but no statocyst (Figs. 24*A*, 35*D*). Whereas in other Seriata, the intestine passes above the pharynx, in *Bothrioplana* it forks around the pharynx (Fig. 35*D*) as in triclads, although single behind this organ.

17. Order Tricladida.—The triclad Turbellaria, commonly known as planarians, are familiar objects of classroom study and of zoological research. They are readily recognized by the plicate pharynx and three-branched intestine. They are of larger size than the preceding orders, ranging from 2 or 3 mm. to over 50 cm. in length. They are of elongated form, usually with strongly flattened but sometimes cylindroid body, of solid consistency and coated with slime. Adhesive organs of the glandulo-muscular type are of common occurrence, located usually on the ventral side of the anterior end; a marginal adhesive zone also occurs in fresh-water and marine triclads (page 74). The epidermis is usually ciliated only ventrally and is abundantly supplied with rhabdites, probably all of the adenal type. There are two to many pigment-cup ocelli with numerous retinal and pigment cells, attaining their greatest complexity in land planarians (page 94, Fig. 32*F*). Eyes are lacking in cave planarians of the family Kenkiidae and in some other forms. The triclads lack frontal glands and a statocyst but are well provided with chemo-, tango-, and rheoreceptors such as the auricular grooves (page 91), sense margins and auricles. The mouth, situated near the body middle, leads into the pharyngeal cavity containing the plicate pharynx, usually cylindrical and attached anteriorly, sometimes (some land planarians) ruffled and attached dorsally. From it extends the highly diverticulated intestine with one main anterior branch proceeding forward and two posterior branches passing backward one to either side of the pharyngeal cavity (Fig. 35*E*). Secondary fusions and anastomoses of the diverticula are of common occurrence. Polypharyngy obtains in a number of species (page 101). The nephridia consist of a network on each side with numerous nephridiopores (page 111). There is a single pair of small ovaries usually near the anterior end, from each of which an

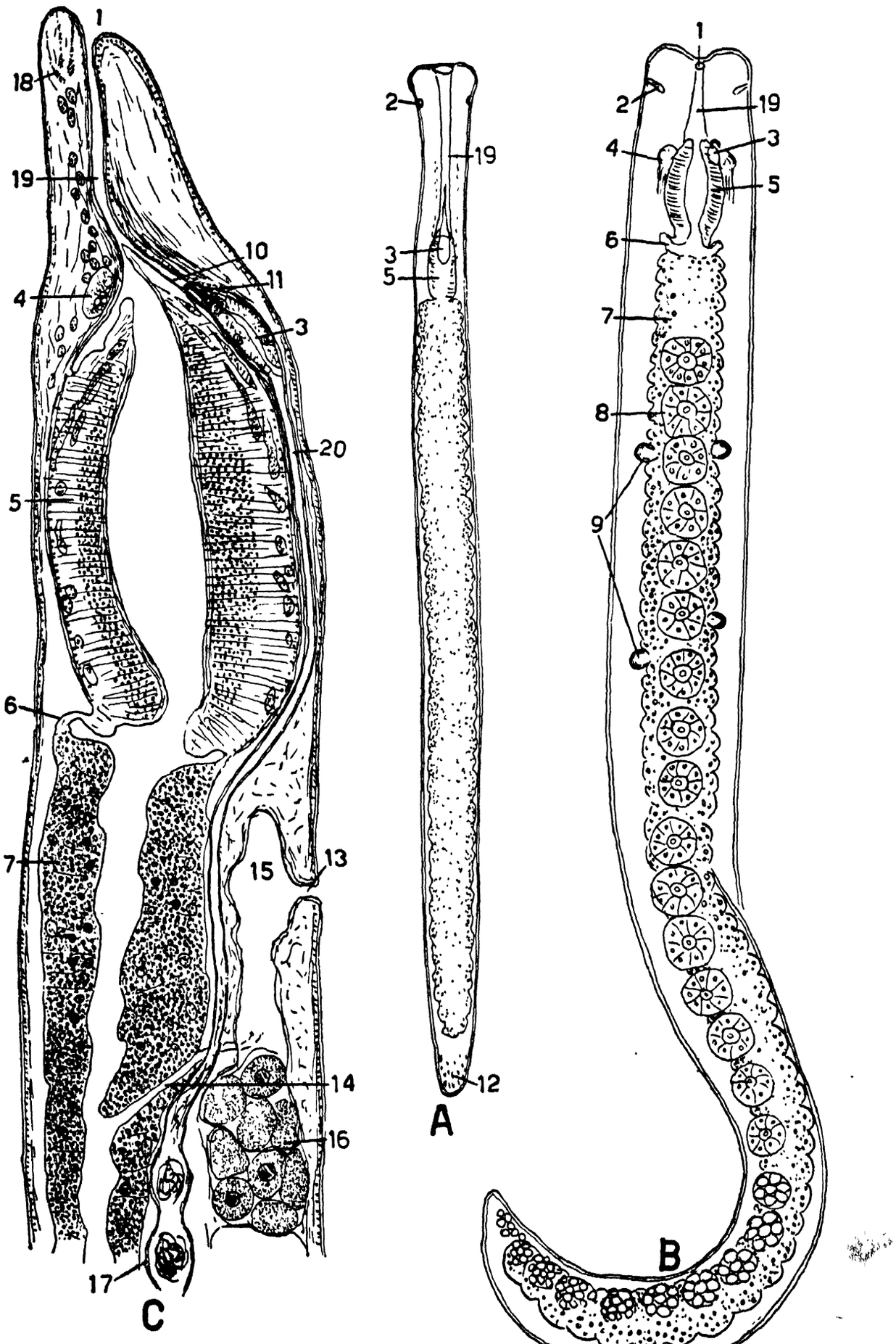

FIG. 59.—Alloeocoela: Prorhynchidae. *A. Prorhynchus stagnalis*, from life, New York State. *B. Geocentrophora tropica*, Canal Zone (*after Hyman*, 1941a). *C.* Sagittal section through the anterior end of *Geocentrophora tropica* (*after Hyman*, 1941a). 1, mouth; 2, ciliated pits; 3, penis; 4, brain; 5, pharynx; 6, esophagus; 7, intestine; 8, follicles of germovitellarium; 9, testes; 10, male canal; 11, penis stylet; 12, adhesive papillae; 13, female gonopore; 14, genitointestinal canal; 15, female antrum; 16, ripe eggs; 17, seminal vesicle; 18, frontal glands; 19, buccogenital canal; 20, ejaculatory duct.

ovovitelline duct proceeds posteriorly collecting from the numerous clusters of yolk glands (Fig. 38*A*). There are several to many testes (rarely, one pair), prepharyngeal in position or strewn along the body length. They connect by sperm ductules with a pair of sperm ducts that as they approach the copulatory complex enlarge to form tubular or rounded spermiducal vesicles packed with masses of sperm. The sperm ducts, singly or after fusion, enter the penis bulb, a spherical or oval muscular and glandular structure, often considered to be a seminal vesicle (Fig. 38*G*). However, it never stores sperm and appears rather to be of the nature of a prostatic vesicle. The triclads lack a typical prostatic apparatus. The penis bulb is continuous with the penis papilla, a conical muscular projection, sometimes lacking, sometimes armed with thorns. This lies in the male antrum continuous with the common antrum receiving the female antrum from behind and opening below by the common gonopore situated posterior to the mouth (Fig. 38*G*). The female system usually includes a copulatory or seminal bursa (sometimes two).[1] The relations of bursa, ovovitelline ducts, and female antrum differ in different groups of triclads and are of taxonomic importance.

Copulation with mutual insemination is the rule among the triclads. In known cases, the sperm are ejaculated directly into the copulatory or seminal bursa (Fig. 48*C*). They soon leave this and travel up the ovovitelline ducts to the ovaries where they collect in a small chamber acting as seminal receptacle and separated from the ovary by a membrane (Fig. 41*B*). The ripe eggs pass through this membrane, are immediately fertilized, and then travel posteriorly along the ovovitelline ducts, becoming mingled with yolk cells emitted into these ducts from the yolk glands. Eggs and yolk cells collect in the male antrum (Fig. 48*D*) where a capsule (also called cocoon) is formed around them from droplets present in the yolk cells. When completed, the capsule containing several eggs and hundreds of yolk cells is laid through the common gonopore, receiving an adhesive secretion from the cement glands opening into the antrum or some adjacent part of the female system. In some genera (*Dugesia, Curtisia*) this adhesive secretion becomes drawn out into a stalk as the capsule is laid, and this serves to attach the capsule to objects, chiefly the underside of stones (Fig. 46*E*). At ordinary temperatures, the capsules hatch in two or three to several weeks into minute fully formed worms.

The triclads inhabit fresh and salt waters and humid terrestrial regions. There is a correspondence between ecological habitus and taxonomic classification, something very unusual among animals. Con-

[1] Formerly erroneously called "uterus" and still so labeled in old figures copied into textbooks. The egg capsule is formed in the male antrum, and positively never in the bursa.

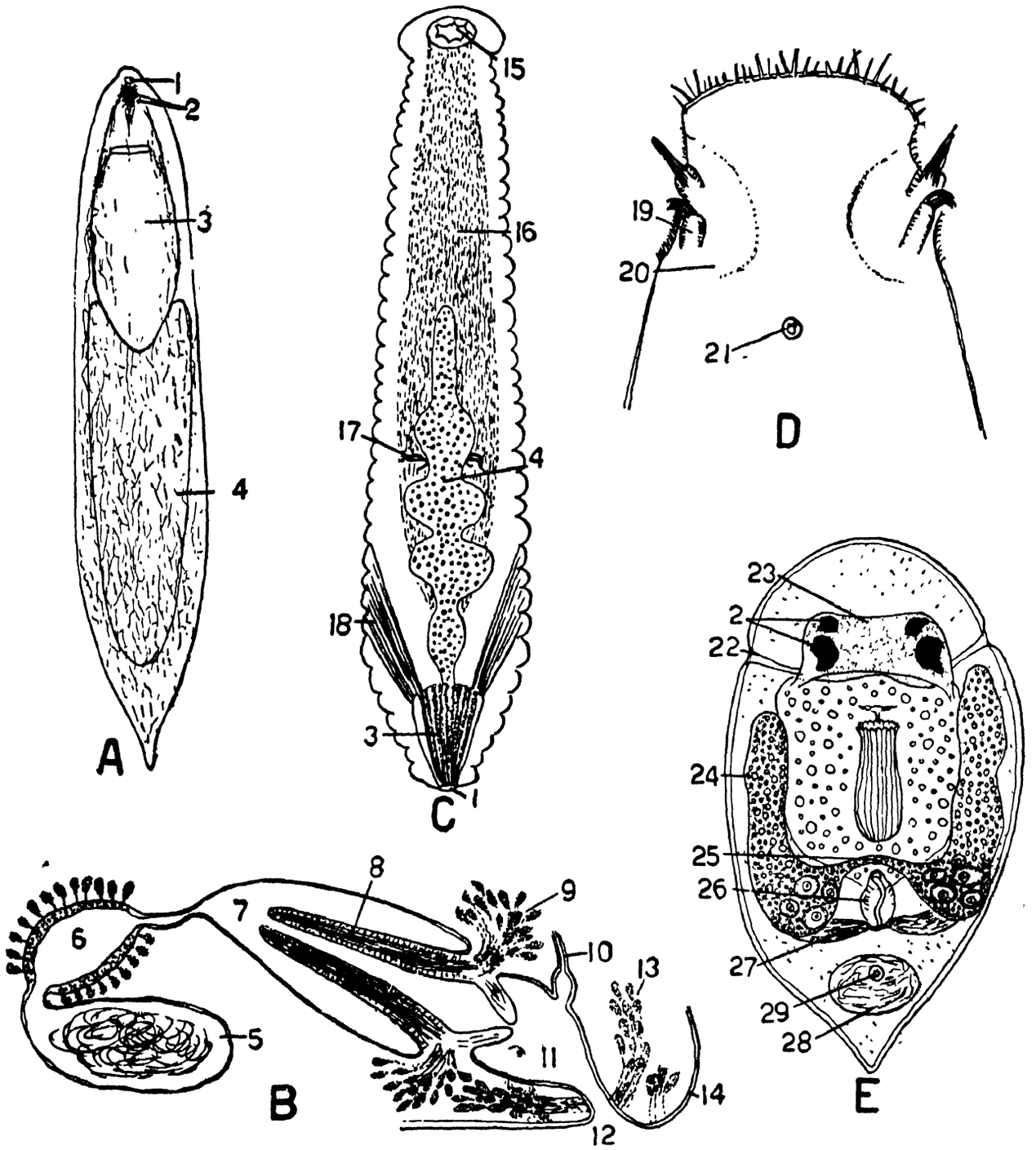

FIG. 60.—Alloeocoela (continued). *A. Plagiostomum album*, Maine (*after Hyman*, 1944). *B.* Scheme of the copulatory apparatus of the genus *Plagiostomum*. *C. Hypotrichina* (*after Graff*, 1903). *D.* Anterior end of *Otoplana intermedia* (*after Wilhelmi*, 1908). *E. Pseudostomum*, with ciliated groove (*after Graff*, 1882). 1, mouth; 2, eyes; 3, pharynx; 4, intestine; 5, seminal vesicle; 6, prostatic vesicle; 7, penis bulb; 8, penis papilla (introverted into bulb); 9, penis glands; 10, common ovovitelline duct; 11, common antrum; 12, common gonopore; 13, cement glands; 14, rear end of animal; 15, adhesive organ; 16, ciliated area; 17, excretory ampullae; 18, retractors of pharynx; 19, papillae bearing sensory bristles; 20, ciliated pits; 21, statocyst; 22, ciliated groove; 23, brain; 24, germovitellaria; 25, common gonopore; 26, penis; 27, spermiducal vesicles; 28, seminal bursa; 29, bursal pore.

sequently there are three suborders of triclads, marine, fresh-water, and terrestrial.

a. Suborder Maricola.—The marine triclads occur in the littoral zone, mostly on gravelly bottoms and under stones, in temperate and subpolar regions. The majority of the known forms are found along the Mediterranean, including the Black Sea, and in general the group prefers protected situations. Other localities where marine triclads occur

are north European coasts, the shores of Japan, the north Atlantic Coast of North America, and arctic and antarctic situations. These worms appear to be absent from tropical and subtropical shores, and none are known to occur on the Pacific coasts of Africa and the Americas.

The marine triclads are of moderate size, from 2 to 20 mm. in length, and are mostly white, gray, or brown. The anterior end varies from truncate with auricles to pointed (Fig. 19*D*, *F*). An adhesive zone with protrusible papillae encircles the ventral surface near the margin; other adhesive structures are lacking. There is a pair of eyes, and auricular grooves (page 91) appear to be of general occurrence in the group. The submuscular nerve plexus has dorsal, lateral or marginal, and ventral cords, connected by numerous ring commissures and also by direct connectives between the dorsal and ventral cords (Fig. 25*C*). The regular arrangement of the testes in some species has given rise to unwarranted phylogenetic theories (page 25). All forms have a typical penis papilla sometimes armed with a stylet. A large rounded copulatory bursa is generally present, lying *behind* the male apparatus and attached to the common antrum by a bursal canal, which receives the common ovovitelline duct. However, in the Uteroporidae, the single median, and in the Bdellouridae, the paired lateral bursae are situated anterior or lateral to the male apparatus, and each has its own bursal pore to the exterior, also connections with the ovovitelline ducts by insemination canals (Fig. 61*A*). The round to oval brown capsules, to 1.5 mm. in diameter, are fastened mostly without a stalk to stones, shells, etc., and hatch in a month or more to two or three young worms. Sexual reproduction seems to be somewhat seasonal. The marine triclads are incapable of asexual reproduction.

The Maricola have been monographed by Wilhelmi (1909), whose five families are now generally reduced to three. The Bdellouridae have two bursae each with a pore. Members of the genus *Bdelloura* (Figs. 19*D*, *E*, 61*A*) with pointed anterior end and adhesive zone expanded into a caudal adhesive disk are commensal on the horseshoe crab *Limulus* along the New England Coast. The oval capsules containing two eggs are attached by a stalk to the gill lamellae of the host (Fig. 46*G*). *Syncoelidium pellucidium*, without caudal disk, is also commensal on the gill lamellae of *Limulus* (Wheeler, 1894). *Synsiphonium*, Antarctic, South Africa, is peculiar in that the seminal bursae have the form of long canals that run forward from the bursal pores to open into the ovovitelline ducts near the ovaries (Hallez, 1913). The Uteriporidae comprise one species, *Uteriporus vulgaris*, Swedish Coast, in which the single bursa with separate pore lies anterior to the penis (Bergendal, 1890). The family Procerodidae includes the majority of marine triclads; the seminal bursa when present lacks a bursal pore and lies *behind*

the penis, opening into the female antrum by a bursal canal. The typical genus is *Procerodes* (includes *Gunda*, *Fovia*), with a number of species, small dark-colored worms with a truncate head and more or less evident auricles (Fig. 19*F*, *G*). The famous *Gunda segmentina* (page 25), notable for the regular repetitive arrangement of its testes, intestinal diverticula, etc., is really a species of *Procerodes*. *Foviella* differs in the reduced or absent bursa (Bock, 1925). *Ectoplana*, Japan, without adhesive disk, is commensal on *Limulus*. The cercyrine Procerodidae, including the genera *Cercyra* and *Sabussowia*, are notable among the Turbellaria in that some species are dioecious. *Micropharynx* is commensal on the back of skates in the North Atlantic (Jägerskiöld, 1896; Averinzev, 1925); it is a broad eyeless white worm adhering firmly to the host by the rear part of its adhesive zone. In recent years several new genera of marine triclads have been discovered, and undoubtedly much remains to be learned of this group of planarians.

b. Suborder Paludicola or Probursalia.—The fresh-water or paludicolous triclads are familiar inhabitants of streams, springs, ponds, and lakes throughout the temperate zones of the earth. Like the other groups of aquatic turbellarians, they appear to be scarce in tropical and subtropical regions. A particularly rich development of species is seen in Lake Baikal and the Balkan peninsula. The majority range from a few to 30 mm., but longer forms up to 10 cm. in length occur among the Lake Baikal planarians. The coloration is mostly plain, white, brown, gray, or black, sometimes streaked, spotted, or striped (Fig. 15*B*–*D*). The anterior end ranges in shape from triangular with projecting auricles to truncate with scarcely noticeable auricles (Figs. 15, 38*A*), and the elongated flat body generally tapers to a more or less pointed caudal end. An adhesive organ of the glandulo-muscular type is often present in the center of the anterior margin. The brain consists of two conjoined rounded masses or, in planarians with triangular head, of thick cords forming a V (Fig. 26). There is a pair of large ventral cords, but the other longitudinal cords are generally absent (Fig. 25*D*). The copulatory apparatus is of rather uniform construction throughout the group, presenting as its distinguishing character a large sacciform copulatory bursa situated *in front* of the penis and connected to the female antrum by a long bursal canal passing dorsal to the penis (Fig. 38*G*). The bursa may also be connected to the intestine. The bursa was formerly erroneously termed uterus and was supposed to be the site of fertilization and formation of the capsule. Numerous observations prove that the bursa functions only to receive the sperm at copulation and to digest excess sex products (Burr, 1912; Cernosvitov, 1931). Fertilization occurs at the head of the ovovitelline ducts (page 153), and the capsules are formed in the male antrum. The ovovitelline ducts enter the bursal canal or

the female antrum or most commonly the male antrum. The usual eosinophilous cement glands surround the terminal parts of the ovovitelline ducts and the antrum. The penis consists of a powerful bulb and usually also of a large muscular penis papilla, reduced or wanting in some genera. Not uncommonly one or more prostatoids, also called adenodactyls, are associated with the copulatory apparatus (Fig. 45*D*). The fresh-water planarians never fertilize themselves (Gelei, 1924; Goetsch, 1925). The spherical or oval brown capsules may or may not have an attachment stalk. They are usually to be found on the underside of stones and in many species are probably laid at definite seasons of the year. During the breeding season, each individual may copulate repeatedly and lays a succession of capsules at intervals of a few days. These hatch at ordinary temperatures in 2 or 3 weeks, cracking open to release several tiny worms.

The Paludicola have never been monographed, but valuable suggestions concerning their classification have been published by Meixner (1928) and Kenk (1930). They fall into three families, Planariidae, Kenkiidae, and Dendrocoelidae, distinguished by their adhesive organs and the arrangement of the muscle fibers of the inner wall of the pharynx (Fig. 61*D*, *E*). The Planariidae lack adhesive organs and are colored or white with triangular to truncate heads. Formerly it was usual to throw almost any two-eyed member of this family into the genus *Planaria*, but this genus has now been restricted according to taxonomic rules to that species to which the name was first applied (*Planaria torva* by O. F. Müller in 1776) and close relatives thereof. As *P. torva* happens to have a peculiar type of adenodactyl (Kenk, 1930), very few planarians remain in the genus *Planaria* (Fig. 45*C*, *D*). The typical textbook planarian with triangular head, projecting auricles, two eyes, and dark coloration belongs to the genus *Dugesia* (= *Euplanaria*) with many species, all of very similar appearance, in Europe, Asia, and the Americas (Fig. 15*B–D*). *Dugesia* reproduces by fission and is devoid of a reproductive system except during the seasonal breeding period. Some species are rarely found in the sexual state, and others have sexual and asexual races probably of genetic origin. *Dugesia tigrina* (= *Planaria maculata*) is the most common fresh-water planarian of the United States, found everywhere in streams and ponds (Fig. 15*C*, *D*), exhibiting considerable color variation. It breeds from early spring through summer, laying many stalked capsules under stones; the copulatory apparatus then disappears and the worms remain in a nonsexual state reproducing by fission until the following spring (Kenk, 1937, 1940). Sexuality is induced by a rising temperature following a sojourn at a cold temperature (Hyman, 1941b). This species is peculiar in that in some localities it remains permanently asexual (Curtis, 1902). The reason for this has not been

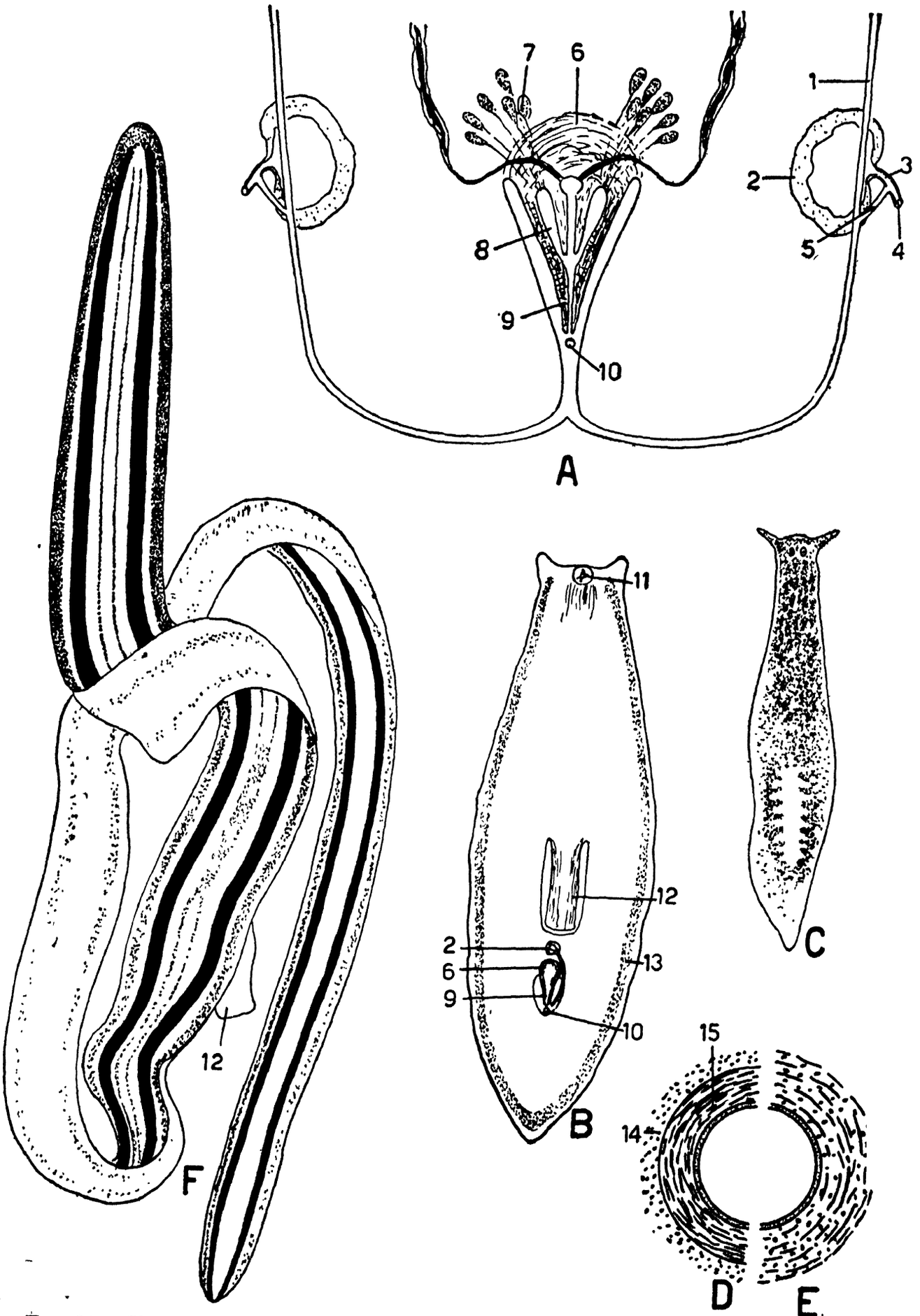

FIG. 61.—Tricladida. *A.* Copulatory apparatus of *Bdelloura candida*, with two bursae. *B. Sphalloplana percoeca*, white eyeless planarian of the family Kenkiidae, from Mammoth Cave. *C. Crenobia alpina*, European planarian of alpine streams (*after Micoletzky*, 1907). *D, E.* Diagrams of arrangement of fibers of the inner muscular zone of the pharynx to show diagnostic family characters. *D.* Arrangement in the families Planariidae and Kenkiidae, circular and longitudinal layers distinct. *E.* Family Dendrocoelidae, circular and longitudinal fibers intermingled. *F. Dolichoplana striata*, common land planarian of the Indo-

ascertained but Kenk (1941) was able to induce testes and the copulatory apparatus in the posterior two-thirds of an individual of such an asexual stock by grafting it to the anterior third of a sexual individual. *D. gonocephala*, a common Eurasian species, is very similar to *D. tigrina*, also occurring in sexual and asexual strains (Benazzi, 1936, 1937, 1938, 1940). It appears, however, that in *D. gonocephala* asexual individuals may arise from sexual stocks, and further that members of asexual stocks sometimes become sexual, although producing very few young. *D. dorotocephala* (Fig. 15*B*) is another common planarian of the United States, widely distributed in springs and spring-fed marshes. These species appear to be "polytypic," i.e., to occur in many geographical races. *Curtisia* with low triangular head and a few prepharyngeal testes has one species *C. foremanii* (= *Planaria simplissima*) in the eastern United States and some in South America. *Phagocata* (= *Fonticola*), with truncate head, common ovovitelline duct entering the male antrum, and spermatophores, comprises mostly rather small gray or white planarians, often found in mountain streams. Some are polypharyngeal (Fig. 34*C*). *P. velata* has an interesting life history (Child, 1913a, 1914; Castle, 1927, 1928; Castle and Hyman, 1934). In the spring the worms grow to 12 to 15 mm. in length, then gradually fragment into small pieces, each of which encysts in a mucous cyst. Within these cysts the pieces reorganize into minute worms that emerge in a few weeks if the cysts remain submersed. In habitats that dry up in summer, emergence may not occur until the following spring, and such an asexual cycle may continue indefinitely. In permanent waters, mostly spring-fed marshes, worms hatched from cysts in the fall become sexually mature and breed in winter. Similar fragmentation and encystment occur in some European *Phagocatas*. *Crenobia alpina* (Fig. 61*C*), a European planariid found in mountain streams, requires cold temperatures and is extremely reactive to water currents (page 213). *Polycelis*, with several Eurasian species, and one, *coronata* (Fig. 32*D*), in our western mountains, is characterized by the numerous eyes in a band around the anterior margin.

The Kenkiidae are a family of cave planarians peculiar to North America (Hyman, 1937, 1939c); they are white, eyeless, and have a glandulo-muscular adhesive organ in the center of the anterior margin, reaching an extreme development in *Kenkia rhynchida* (Fig. 22*B*, *C*). The Kenkiidae have the same pharyngeal structure as the Planariidae (Fig. 61*D*) and seem to be derived from the genus *Phagocata*. European cave planarians do not show any such peculiarities but are mostly eyeless

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Malay region. 1, ovovitelline duct; 2, copulatory bursa; 3, copulation canal; 4, bursal pore; 5, insemination canal; 6, penis bulb; 7, penis glands; 8, gland pockets in penis; 9, penis papilla; 10, common gonopore; 11, adhesive organ; 12, pharynx; 13, margin of rhabdite-forming glands; 14, longitudinal muscle fibers; 15, circular muscle fibers.

variants of epigean species. A number of species of the Kenkiidae have been found in our caves, and in fact there seems to be a different species in each locality. The best known kenkiid, *Sphalloplana percoeca* (Fig. 61*B*) from the Mammoth Caves, Kentucky (de Beauchamp, 1931), showed surprisingly little response to light, although killed by direct sunlight, or to temperatures warmer than those of cave waters (Buchanan, 1936).

The Dendrocoelidae are mostly white planarians with two to many eyes (or none) and truncate anterior end often with a central adhesive organ. This family is represented abundantly in Eurasia by *Dendrocoelum, Sorocelis, Bdellocephala,* and other genera, but is poorly exemplified in the Americas where in fact there is only one common dendrocoelid, *Procotyla fluviatilis,* the familiar white planarian of the northeastern United States (Figs. 21*C*, 22*A*, 38*A*). *Polycladodes* and *Sorocelis* have numerous eyes in two clusters; the latter, though mainly Asiatic, has one species in Oklahoma caves (Fig. 32*E*). *Dendrocoelum* and *Bdellocephala* are not represented in the Americas; the former has an adenodactyl, the latter lacks a penis papilla.

The foregoing classification does not take account of some of the remarkable Lake Baikal[1] triclads described by Korotneff (1912), for the information furnished about them is inadequate for taxonomic purposes. These planarians are not only larger than any other Paludicula, but they show an excessive development of sucker-like adhesive organs (page 82, Fig. 21*A*, *B*).

c. Suborder Terricola.—The land planarians inhabit the forest floor of tropical and subtropical jungles, although a few species occur in humid habitats in temperate zones. Although they require a highly humid environment, the land planarians cannot endure submersion in water. They have nocturnal habits, remaining under leaf mold, fallen logs, stones, etc., during the day and coming out at night to seek prey. Mucous secretion plays an important role in their activities, forming a slime trail for locomotion, slime threads by which they can cross spaces or drop from heights, and a protective coat against drying. The land planarians are mostly of long and slender form, varying from 10 mm. or less to over 60 cm. in length. They are usually colored, either more or less uniformly green, gray, brown, or black, less often blue or violet, or else striped or barred with contrasting colors. A very frequent color pattern consists of dark or black stripes or bars on a light, often yellow or orange,

[1] Lake Baikal, in the mountains of eastern Siberia, is the largest fresh-water lake in Eurasia, having an area about equal to that of Switzerland, and is the deepest lake in the world, being at some points nearly a mile in depth. It has a rich and highly peculiar fauna, mostly endemic and probably in many cases relicts of ancient forms.

ground or vice versa (Figs. 14*D*, 61*F*). There are two to many eyes and other sense organs in the form of ciliated grooves and a sensory margin. One or two adhesive cushions on the ventral surface of the anterior end occur in some genera, as *Cotyloplana*, *Artiocotylus*, and *Choeradoplana*. The peculiarities of the nervous system of the Terricola were noted above (Fig. 25*E*).

The Terricola were monographed by von Graff in 1899, and in this work beautiful colored plates showing the characteristic appearance and color patterns may be seen. There are three principal families, Geoplanidae, Rhynchodemidae, and Bipaliidae, and some minor ones. The Geoplanidae have a flattened body tapering to a narrowed anterior end and numerous eyes along the body margin. They creep upon the entire ventral surface as they lack a creeping sole. The chief genus *Geoplana* (Fig. 32*A*) without adhesive organs or prostatoids has hundreds of species, centering in the jungles of tropical South America. Two species brought in with tropical plants have become established in Californian gardens (Fig. 32*A*). The Rhynchodemidae have two eyes on the narrowed anterior end and lack adhesive organs. *Rhynchodemus* and the related genera *Dolichoplana* and *Platydemus* have slender more or less flattened bodies, strongly developed subepidermal musculature and simple copulatory apparatus. Species of *Rhynchodemus* occur sparingly in the United States (Fig. 62*C*, *D*) and Europe in moist woods and in gardens (Hyman, 1943), and large numbers are found in the tropics. *Dolichoplana striata* (Fig. 61*F*) to 20 cm. long, is one of the most common land planarians of the Indo-Malay region and may be introduced into greenhouses. Another group of rhynchodemids, exemplified by *Geodesmus* (= old *Rhynchodemus* in part) and *Diporodemus*, are of short plump cylindroid form with a creeping sole, weak subepidermal musculature, and complicated copulatory apparatus, often including a seminal bursa. Species of *Geodesmus* (Fig. 62*A*) are endemic to Europe and the United States; the best known one is *Geodesmus terrestris*, a plump black worm discovered in 1774. *Diporodemus*, with species in the Appalachians (Fig. 62*B*), Mexico, and the Canal Zone, differs in the separate external pore of the seminal bursa (Fig. 62*E*). The Bipaliidae are readily recognized by the expanded lunate head (Fig. 14*D*) having numerous minute eyes along its borders. There is probably but one genus *Bipalium* (includes *Placocephalus*) with numerous tropical species, especially in the Indo-Malay region. *Bipalium kewense* (Fig. 14*D*), a large worm to 25 cm. or more in length, with five dark stripes on a lighter ground, is the best known member of the genus. It was discovered in the greenhouses of the Kew Gardens, near London, by Moseley in 1878 and has since been found widely distributed in greenhouses in temperate regions and outdoors in many tropical and subtropical localities, having been carried

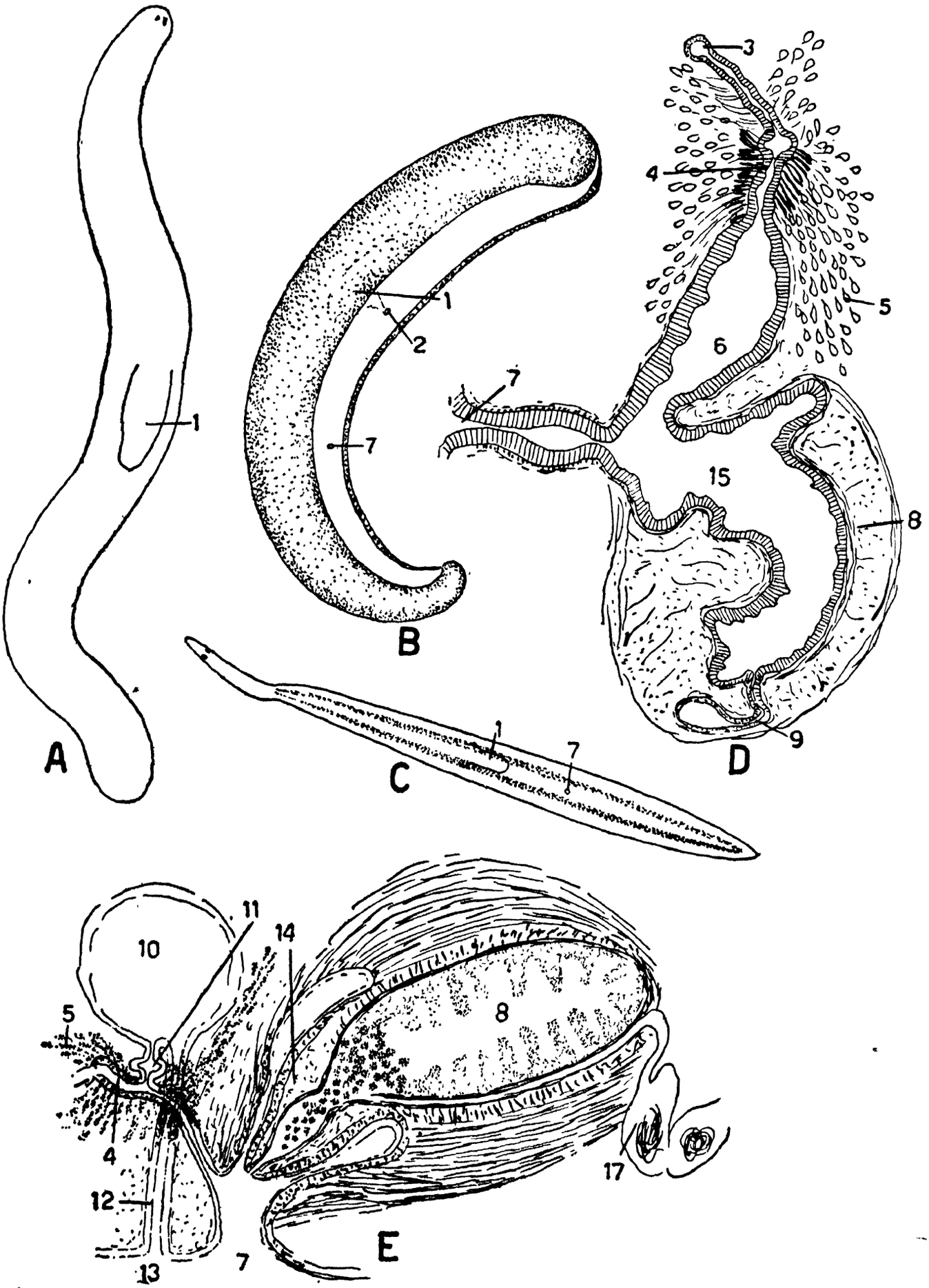

FIG. 62.—American land planarians. *A. Geodesmus atrocyaneus*, eastern United States. *B. Diporodemus indigenus*, Appalachians. *C. Rhynchodemus sylvaticus*, eastern United States. *D.* Sagittal section of the copulatory complex of *Rhynchodemus sylvaticus*. *E.* Sagittal section of the copulatory complex of *Diporodemus plenus*, Canal Zone. (*After Hyman*, 1941a, 1943.) 1, pharynx; 2, mouth; 3, common ovovitelline duct; 4, glandular part of female canal; 5, cement glands; 6, female antrum; 7, common gonopore; 8, penis bulb; 9, common sperm duct; 10, copulatory bursa; 11, bursal canal; 12, copulation canal; 13, bursal pore; 14, penis papilla; 15, male antrum; 16, common antrum; 17, spermiducal vesicle.

about the world at an early date with plant shipments. It is now established in gardens in California, Louisiana, Florida, and the West Indies. Its original habitat is unknown. It owes its colonizing success to extensive ability to propagate by fragmentation, for it never becomes sexual in temperate regions. In general, tropical land planarians are unable to mature sexually in temperate zones and hence soon die out unless they have some means of asexual propagation. Another *Bipalium*, *B. adventitium*, of unknown source, has become acclimated to Californian gardens where it breeds sexually (Hyman, 1943).

18. Order Polycladida.—The polyclads are common inhabitants of the ocean littoral in all zones of the earth. They are typically bottom dwellers, unable to swim or swimming only briefly, but some species are pelagic, having been taken from surface waters to depths of nearly 1000 m. Some of these apparently swim about freely in the open water whereas others are confined to the floating *Sargassum*. The group includes only one fresh-water species, *Limnostylochus borneensis* from Borneo (Stummer-Traunfels, 1902), although many endure some brackishness. There are no parasitic polyclads, but several species live in constant association with other animals, especially mollusks and hermit crabs.

The polyclads are mostly of considerable size, ranging from 2 or 3 mm. to several centimeters in length. They are greatly flattened animals and although sometimes of elongated form as *Cestoplana* (Fig. 35*G*) are mostly broadly oval, widest through the anterior third or the middle (Figs. 63*B*, 64*A*). The pelagic species tend to be translucent or transparent; the bottom dwellers are often white, brown, or gray, especially in northern waters, but bright colors and patterns also obtain, particularly in the polyclads of warmer waters and of coral reefs. Plates illustrating the colors may be seen in Lang's monograph (1884). The body contour is simple, although the margins may be ruffled, and the surface is generally smooth but there are a number of species with dorsal tubercles or papillae (Fig. 15*A*). Tentacles are frequent, either as a *nuchal* pair (Fig. 63*B*) over the brain region or a *marginal* pair at the anterior margin (Fig. 14*A*, *B*). The polyclads lack frontal glands, statocysts, and adhesive areas or organs except for the ventral disk of the Cotylea, the genital disk in *Leptoplana*, and adhesive cells in *Emprosthopharynx*. Numerous eyes are present, usually as a pair of cerebral clusters in the brain region and a tentacular cluster on or near each tentacle or at the sites where tentacles would be expected (Figs. 35*F–J*, 63*A*, *B*). Eyes may also occur strewn over the anterior end (Fig. 63*A*) or as a band along all or part of the body margin (Fig. 63*A*, *B*). The body is clothed in a completely ciliated cellular epidermis containing numerous gland and rhabdite-forming cells. Muscular and nervous systems were described above (pages 77, 85). The plicate pharynx is either an oval

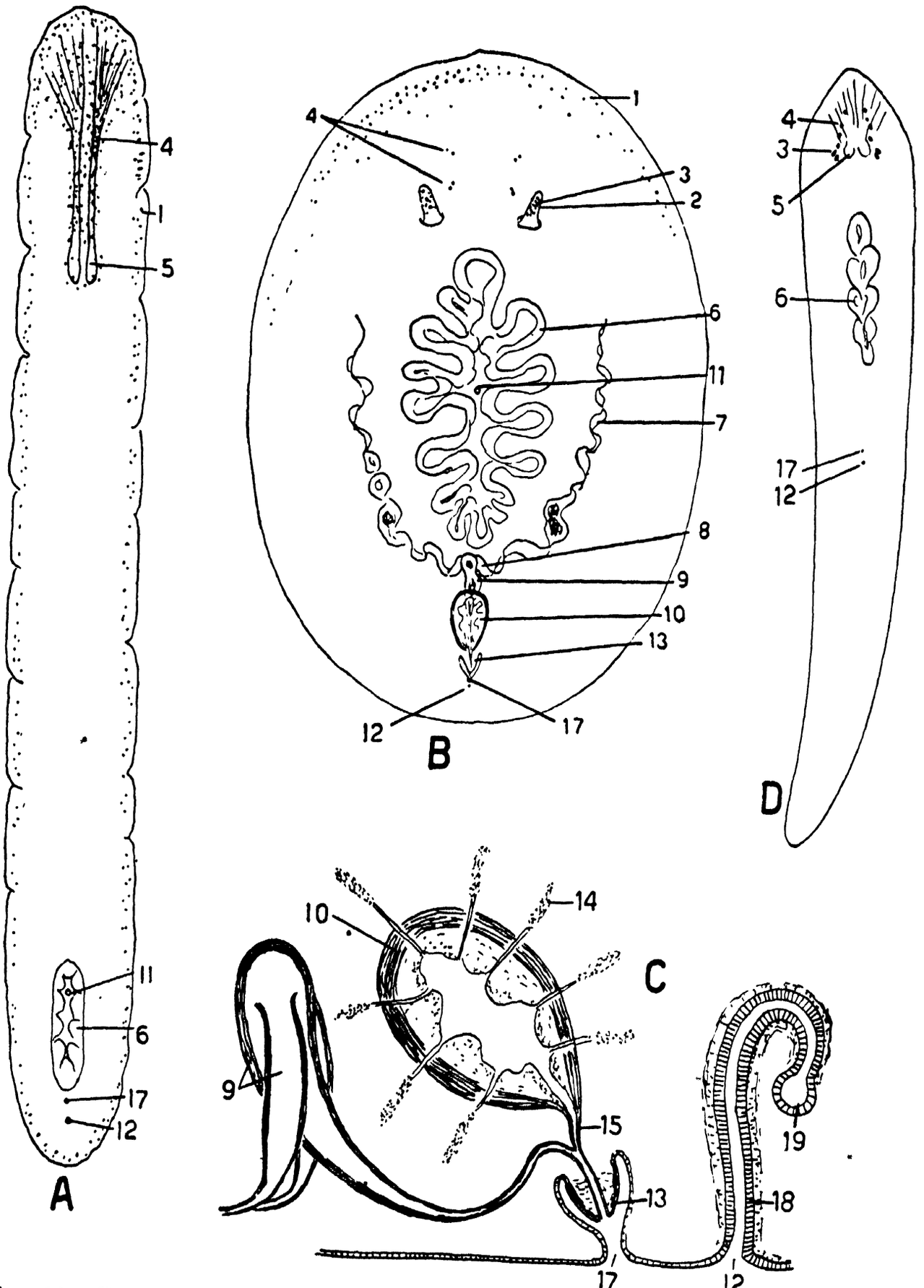

FIG. 63.—Polycladida. *A. Latocestus whartoni*, Florida. *B. Stylochus ellipticus*, most common polyclad of the United States Atlantic Coast. *C.* Schematic sagittal view of the copulatory apparatus of the genus *Stylochus*, illustrating free type of prostatic vesicle; simple vagina without bursa is diagnostic of the genus. *D. Euplana gracilis*, common leptoplanid polyclad of the United States Atlantic Coast. 1, marginal band of eyes; 2, tentacle; 3, tentacular eyes; 4, cerebral eyes; 5, cerebral ganglia; 6, pharynx; 7, sperm duct; 8, spermiducal vesicle; 9, seminal vesicle; 10, prostatic vesicle; 11, mouth; 12, female gonopore; 13, penis papilla; 14, prostatic glands; 15, prostatic duct; 16, ejaculatory duct; 17, male gonopore; 18, vagina; 19, entrance of oviduct into vagina.

ruffled curtain hung vertically or a cylindrical tube directed forward. The pharynx leads into a median main intestine lying above or behind it (Fig. 35*F–J*) and extending part or most of the body length. From this intestine branches radiate to the periphery, often subdividing and anastomosing. The form of the branching is correlated with body shape (Fig. 35*F–J*). Little is known of the excretory system beyond the fact that flame bulbs occur. There are numerous small ovaries and testes scattered throughout the lateral body regions; each ovary consists of ovocytes and nutritive follicle cells. Yolk glands are absent. The distal parts of the sperm ducts are usually expanded to form spermiducal vesicles, sometimes very muscular. Usually present are a muscular seminal vesicle and a large and muscular prostatic vesicle, of either the interpolated (Fig. 64*B*) or free type (Fig. 63*C*). When interpolated the prostatic vesicle may be incorporated into the muscular penis bulb (Fig. 39*E*) from which continues the penis papilla, often provided with a simple stylet, that is sometimes very long (Fig. 64*B*). Some polyclads, especially the Planoceridae, have a cirrus, often of complicated construction, instead of a penis (Fig. 39*E*). The frequent multiplication of male apparatus and prostatoids in the polyclads was noted above (page 117). The oviducts generally act as reservoirs of ripe eggs and hence are termed uteri; they sometimes bear uterine vesicles of unknown function (Pseudoceridae, Euryleptidae). The oviducts enter the terminal female canal or vagina, often very muscular, and usually having a glandular region or chamber (Fig. 65*D*) that receives the numerous cement glands. A seminal bursa termed Lang's vesicle is of common occurrence, opening from behind into the vagina by a long bursal canal (Fig. 64*B*). There is a common gonopore or separate male and female pores of which the latter is nearly always behind the former.

The polyclads practice both hypodermic impregnation and regular copulation; they do not fertilize themselves. In copulation, the sperm pass into the seminal bursa (Lang's vesicle) when this is present and later migrate up the oviducts, or they are ejaculated directly into the oviducts. Fertilization occurs in the oviducts or in the vagina, immediately before laying. In laying, a continuous adhesive gelatinous thread containing a row of eggs issues and is woven back and forth or in a spiral to make a gelatinous egg mass or ribbon (Fig. 46*H*). The sticky gelatinous material comes from the cement glands, and additional secretion is added from ventral mesenchymal glands (Kato, 1940). As soon as the egg reaches the exterior a surface layer of egg spherules coalesces to form a thin shell that elevates from the egg surface and hardens. This capsule encloses one egg (Fig. 46*J*) or sometimes several. Cleavage begins at once and hatching ensues in several days to weeks. In the northern hemisphere

breeding usually occurs in the summer months, and an individual may lay several egg masses, containing thousands of eggs.

The best modern work on the systematics of the polyclads is that of Bock (1913), who has corrected and extended the pioneer monograph of Lang (1884). Lang's work, further, was more or less limited to Mediterranean species. Although a large number of species have been described, the polyclads are as yet imperfectly known. The species of the Atlantic Coast of the United States have been treated by the author (Hyman, 1939a, 1940). Those of our Pacific Coast are poorly known, although several papers needing revision have been published about them (Boone, 1929; Freeman, 1930, 1933; Heath and McGregor, 1912; Plehn, 1896a, 1897). Japanese polyclads have been well studied by Kato (1934–1939) and Yeri and Kaburaki (1918). Pelagic polyclads have been the object of several papers (von Graff, 1892; Hyman, 1939b; Palombi, 1924; Plehn, 1896b). Very little has been issued of the projected account of the polyclads by Stummer-Traunfels (1933) in Bronn's *Klassen und Ordnungen des Tierreichs.*

a. Suborder Acotylea and Section Craspedommata.—The acotylean polyclads lack a glandulo-muscular adhesive disk behind the female pore. The pharynx is usually a vertical ruffled curtain, tentacles when present are of the nuchal type, and eyes never occur as a pair of clusters on the anterior margin. The copulatory apparatus lies posteriorly as a rule, and from it the oviducts (uteri) extend forward alongside the pharynx. The section Craspedommata includes those acotylean families that have eyes in a band around all or the anterior part of the body margin (in addition to cerebral and tentacular clusters). Of these the Discocelidae, Latocestidae, and Stylochidae tend to occur in warmer waters. The Discocelidae lack a typical prostatic vesicle, but the penis papilla and antral wall bear numerous small prostatoids (Fig. 40*D*, *E*). The Latocestidae, with numerous species in the main genus *Latocestus* (Fig. 63*A*), are of long slender form with posterior pharynx, long main intestine, and numerous small eyes strewn over the anterior end. The Stylochidae have thick oval or oblong bodies and a free prostatic vesicle (Fig. 63*B*, *C*). There are a number of genera (see Bock, 1925), of which *Stylochus* with prominent nuchal tentacles containing eyes and simple female apparatus is the most common and best known (Fig. 63*B*, *C*). Several species of *Stylochus* occur along the Atlantic Coast of the United States (described in Hyman, 1940) of which *S. ellipticus* is the most common (Fig. 63*B*). Another, *S. zebra*, with a pattern of alternate brown and flesh crossbars, often occurs inside shells inhabited by hermit crabs. *Stylochus* often feeds on oysters; and one species, *S. frontalis*, has this habit to such an extent that it is deleterious to the oyster industry on the Florida Coast, where it is known as the "oyster leech" (Pearse

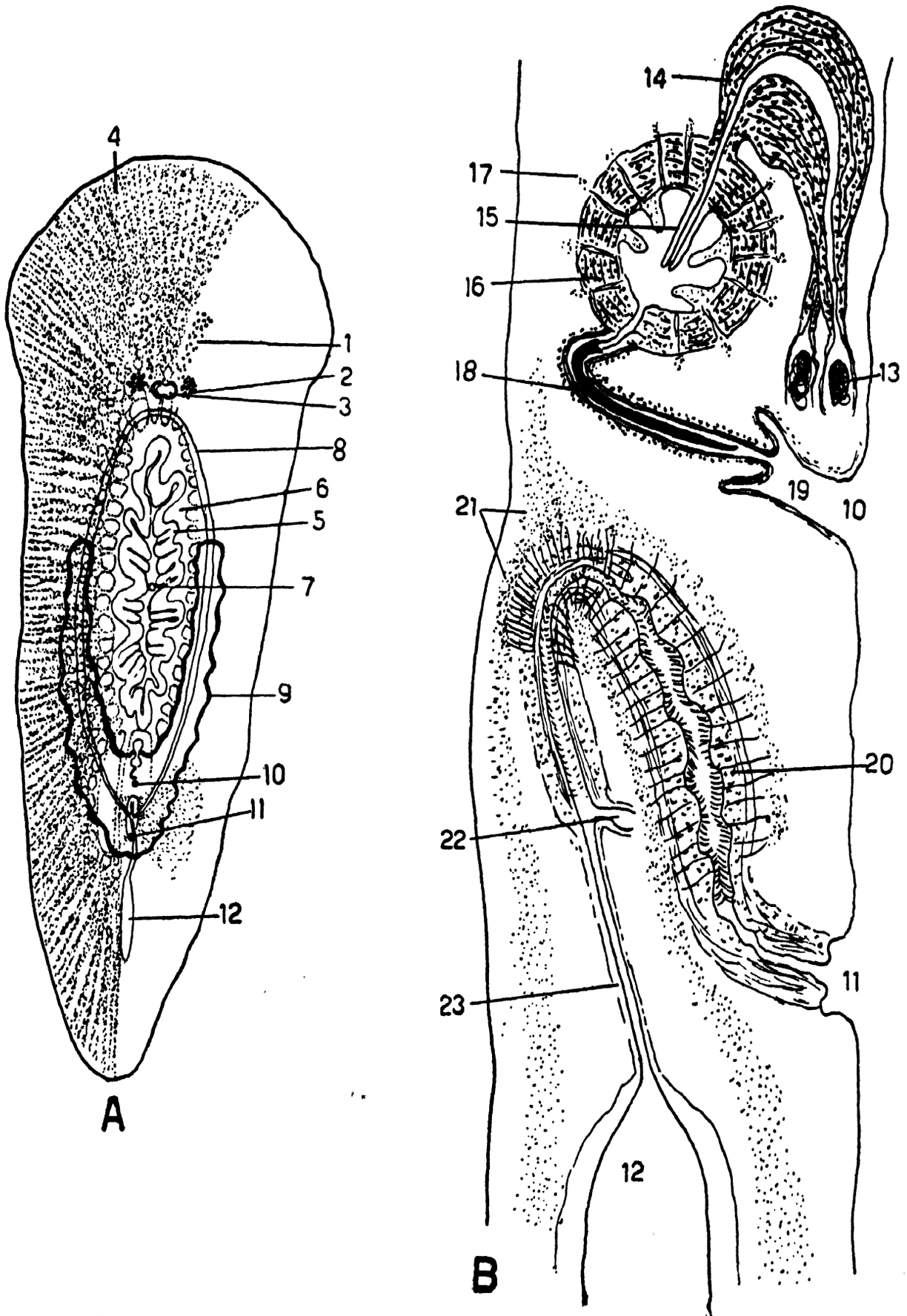

FIG. 64.—Polycladida: *Notoplana*. *A*. *Notoplana atomata*, common leptoplanid polyclad of North Atlantic shores. *B*. Sagittal view of the copulatory apparatus of *Notoplana atomata;* only distal part of the bursa is shown; projection of ejaculatory duct into the prostatic vesicle is diagnostic of the genus *Notoplana*. 1, cerebral eye clusters; 2, tentacular eye clusters; 3, brain; 4, intestinal branches; 5, pharynx; 6, main intestine; 7, mouth; 8, oviducts (uteri); 9, sperm ducts; 10, male gonopore; 11, female gonopore; 12, seminal bursa (Lang's vesicle); 13, spermiducal vesicles; 14, seminal vesicle; 15, ejaculatory duct; 16, prostatic vesicle; 17, prostatic glands; 18, penis stylet; 19, male antrum; 20, vagina; 21, cement glands; 22, entrance of oviducts into vagina; 23, bursal canal.

and Wharton, 1938). It creeps into the oyster while the latter's valves are open and gradually devours the oyster's flesh, although the latter may put up a defense by secreting chitinous partitions around the polyclad. Stylochids are often very large, and the largest polyclads of our coasts, broad flat forms over 50 mm. long, belong to this family: *Stylochus oculiferus*, Florida, and *Kaburakia excelsa*, Puget Sound.

Some other craspedommatous families are the Plehniidae and Polyposthiidae, characteristic of northern and boreal waters, and the Emprosthopharyngidae. The Polyposthiidae are mainly pelagic and have numerous penes or prostatoids (Palombi, 1924, 1929, Fig. 40*A*). *Emprosthopharynx opisthoporus*, Panama, commensal in shells occupied by hermit crabs, is unique among polyclads in having a marginal adhesive zone like that of triclads (Bock, 1925).

b. Suborder Acotylea: Section Schematommata.—The polyclads of this section lack marginal eyes and generally have four clusters of eyes in the brain region (Fig. 64*A*). The chief family, Leptoplanidae, comprises worms of moderate size, oval or oboval shape, and brown or gray coloration. Formerly it was customary to throw almost any schematommatous polyclad without tentacles into the genus *Leptoplana*, but this genus must be limited to the species first assigned to it and related species, characterized by a genital adhesive disk between the male and female pores and some other peculiarities. Most of the species formerly called *Leptoplana* fall into the genus *Notoplana*, a genus of many species common on all rocky shores and impractical to distinguish except by section of the copulatory apparatus (Fig. 64*B*). *Notoplana atomata* (Fig. 64*A*, *B*) occurs on North Atlantic shores from Massachusetts to Scandinavia, and many species are found on the Pacific Coast of North America. *Stylochoplana*, another common genus with many species, differs in a minor detail of the male apparatus; *S. parasitica* inhabits the mantle groove and gills of chitons on Japanese coasts (Kato, 1935a). *Euplana* (= *Discoplana*), devoid of a prostatic vesicle, is represented on the Atlantic Coast of the United States by the small planaria-like *E. gracilis* (Fig. 63*D*). *Euplana takewakii*, Japan, infests the genital bursae of serpent stars (Kato, 1935b). The Hoploplanidae, without seminal vesicle, have highly muscularized spermiducal vesicles and a penis stylet borne directly by the prostatic vesicle. *Hoploplana inquilina* (Fig. 65*A*), a small rounded polyclad, inhabits the mantle chamber of snails along the Atlantic Coast of the United States, and *H. grubei* is one of the common polyclads of the Sargassum. The Planoceridae usually have tentacles and are characterized by the cirrus armed with spines, teeth, etc. (Fig. 39*E*). They are often of thin transparent texture and pelagic habits, as exemplified by the widely distributed *Planocera pellucida*. *Gnesioceros* (= *Pelagoplana*) with conch-shaped cirrus armed

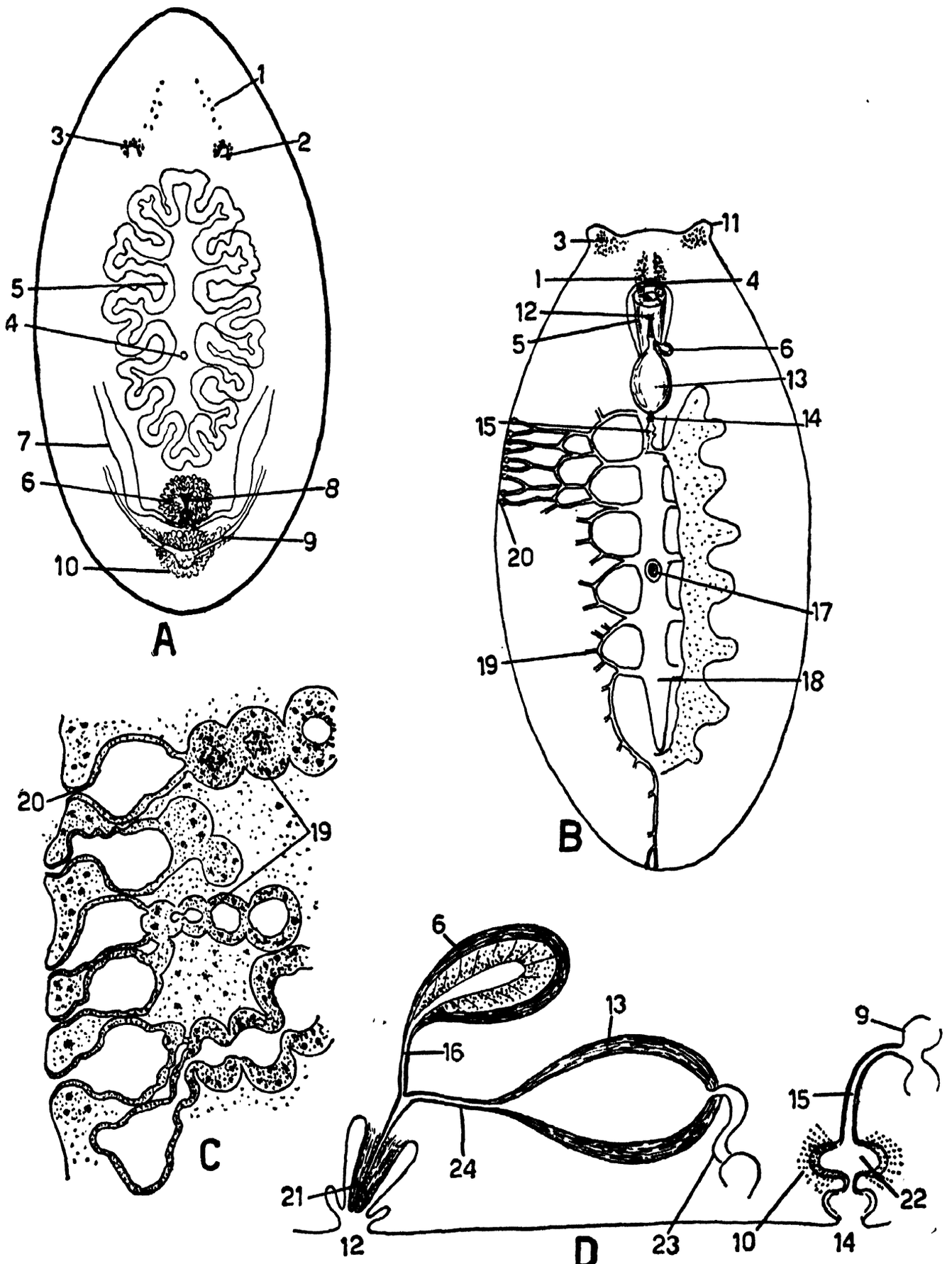

FIG. 65.—Polycladida (continued). *A. Hoploplana inquilina*, commensal in snail shells. *B. Cycloporus*, cotylean polyclad, simplified after Lang, 1884; has numerous anal pores around the margin. *C.* Part of margin of *Cycloporus*, showing anal pores (*after Lang*, 1884). *D.* Scheme of the copulatory apparatus of the Cotylea in general, with free prostatic vesicle. 1, cerebral eye cluster; 2, nuchal tentacle; 3, tentacular eye cluster; 4, mouth; 5, pharynx; 6, prostatic vesicle; 7, spermiducal vesicles; 8, penis stylet; 9, oviducts (uteri); 10, cement glands; 11, reduced marginal tentacles; 12, male gonopore; 13, seminal vesicle; 14, female gonopore; 15, vagina; 16, prostatic duct; 17, adhesive disk; 18, main intestine; 19, intestinal branches; 20, anal pores; 21, penis papilla; 22, cement pouch; 23, sperm duct; 24, ejaculatory duct.

with toothed bands (Fig. 39*E*) has one species, *sargassicola*, common on the *Sargassum* (Fig. 39*D*) and another, *floridana*, abundant among seaweeds on the south Atlantic Coast of the United States. In the Diplosoleniidae with free prostatic vesicle the most common genus is *Pseudostylochus* with several species in the North Pacific.

The two following schematommatous families have a tubular pharynx directed forward. The Apidioplanidae comprise only the curious species *Apidioplana mira* (Fig. 40*B*, *C*) with numerous prostatoids throughout the ventral surface, found on gorgonian colonies in the Fiji Islands (Bock, 1927). *Enantia*, sole genus of the Enantiidae, is unique among Turbellaria in having marginal spines (page 68, Fig. 17*A*, *B*).

c. Suborder Acotylea: Section Emprosthommata.—This section includes one family, Cestoplanidae, with one genus *Cestoplana* (Fig. 35*G*), very similar to *Latocestus* except that it lacks marginal eyes.

d. Suborder Cotylea.—The cotylean polyclads have a glandulomuscular adhesive organ, commonly but erroneously called sucker, behind the female gonopore. They have a pair of marginal tentacles bearing eyes (Fig. 35*H*) or else a cluster of eyes where such tentacles should be (Fig. 65*B*) or a band of eyes across the anterior margin (Fig. 35*J*). The pharynx is ruffled or tubular. A seminal bursa is absent, and the prostatic vesicle when present is of the free type (Fig. 65*D*). The cotyleans are most common in less cold waters and are often of striking form and coloration. The principal families are the Pseudoceridae, Euryleptidae, and Prosthiostomidae. The first are large, often brightly colored polyclads with a pair of marginal tentacles, ruffled pharynx, and net-like intestinal branches. *Thysanozoon* (Fig. 15*A*) is covered with papillae, each containing an intestinal branch; *Pseudoceros*, very similar, is smooth or tuberculate, but the tubercles contain no intestinal diverticulum (Fig. 14*A*). In the similar *Yungia* many of the intestinal branches open dorsally by anal pores. The Euryleptidae have a tubular pharynx directed forward. *Prostheceraeus* with numerous lateral anastomosing intestinal branches, and *Eurylepta* and *Oligocladus* with three to five nonanastomosing branches (Fig. 35*H*) are the chief genera with well-developed tentacles. *Stylostomum* and *Cycloporus* have reduced tentacles, and the latter has a number of anal pores along the dorsal periphery (Fig. 65*B*, *C*). *Acerotisa* (= *Aceros*) lacks tentacles altogether, having an eye cluster in place of each. This genus contains some very small polyclads, as *A. notulata*, from the Sargassum, barely 1 mm. long. Even smaller, however, is the curious *Graffizoon lobata*, California, which resembles a Müller's larva but is fully mature sexually (Heath, 1928); it is probably a neotenic larval stage of a euryleptid. The Prosthiostomidae are rather small polyclads of elongated form, with long tubular pharynx, no tentacles, and a band of eyes along the anterior

margin (Fig. 35*J*). The chief genus *Prosthiostomum* has numerous species in warmer waters, mostly pale or white, and very much alike externally. *Euprosthiostomum* differs in the posterior location of its adhesive disk, apparently as an adaptation to commensal life in the shells occupied by hermit crabs (Bock, 1925).

Some other cotyleans that may be mentioned are the Anonymidae with numerous copulatory apparatus in a curved row on each side and the Boniniidae in which many prostatoids encircle the male copulatory organ (Bock, 1923).

19. Embryology.—The embryonic development of the majority of the Turbellaria is modified by the fact that the yolk supply is contained in the yolk cells, not in the eggs. Hence for the study of the original, unmodified course of development, entolecithal eggs must be used. These occur in the Acoela and Polycladida, groups devoid of yolk glands. The development of polyclads is usually regarded as the original mode for the class and has been worked out in a number of species of different genera by Lang (1884), Surface (1907), Bresslau (1933), and Kato (1940). Practically nothing is known of the development of those Rhabdocoela and Alloeocoela that have entolecithal eggs.

a. Entolecithal Development of Polyclads.—In polyclads the cleavage is of the spiral determinate type and so closely resembles that of annelids and mollusks as to leave no doubt of some phylogenetic connection between these three groups. The egg undergoes total unequal spiral cleavage after the pattern described in Chap. IX (Fig. 3). Three quartets of micromeres are given off, and the macromeres then divide into a fourth quartet of large micromeres, and a quartet of small macromeres (4*A*–4*D*) that occupy the vegetal pole. Traces are sometimes seen of the rosette and the cross. The offspring of the first quartet of micromeres form the ectoderm of anterior dorsal regions and the pigment cells of the eyes and give off into the interior a mass of cells that differentiates into the brain and the entire nervous system (Fig. 66*D*, *E*). From the same invagination that produces the nervous system there is differentiated a cluster of frontal glands that in some species forms a long tuft of sensory hairs (Fig. 67). Although this frontal organ of polyclad larvae had been seen by earlier workers, it was first correctly interpreted by Kato (1940). It soon degenerates and no trace remains in the adult. It may be taken to correspond to the apical sense organ of some cnidarian larvae and of the trochophore. The descendants of the second quartet contribute to surface ectoderm, and some of them pass into the interior as the ectomesoderm from which the muscular and mesenchymal elements of the pharynx arise. The third-quartet cells also furnish surface ectoderm and may possibly contribute to the ectomesoderm. Three of the large yolky fourth-quartet cells, namely,

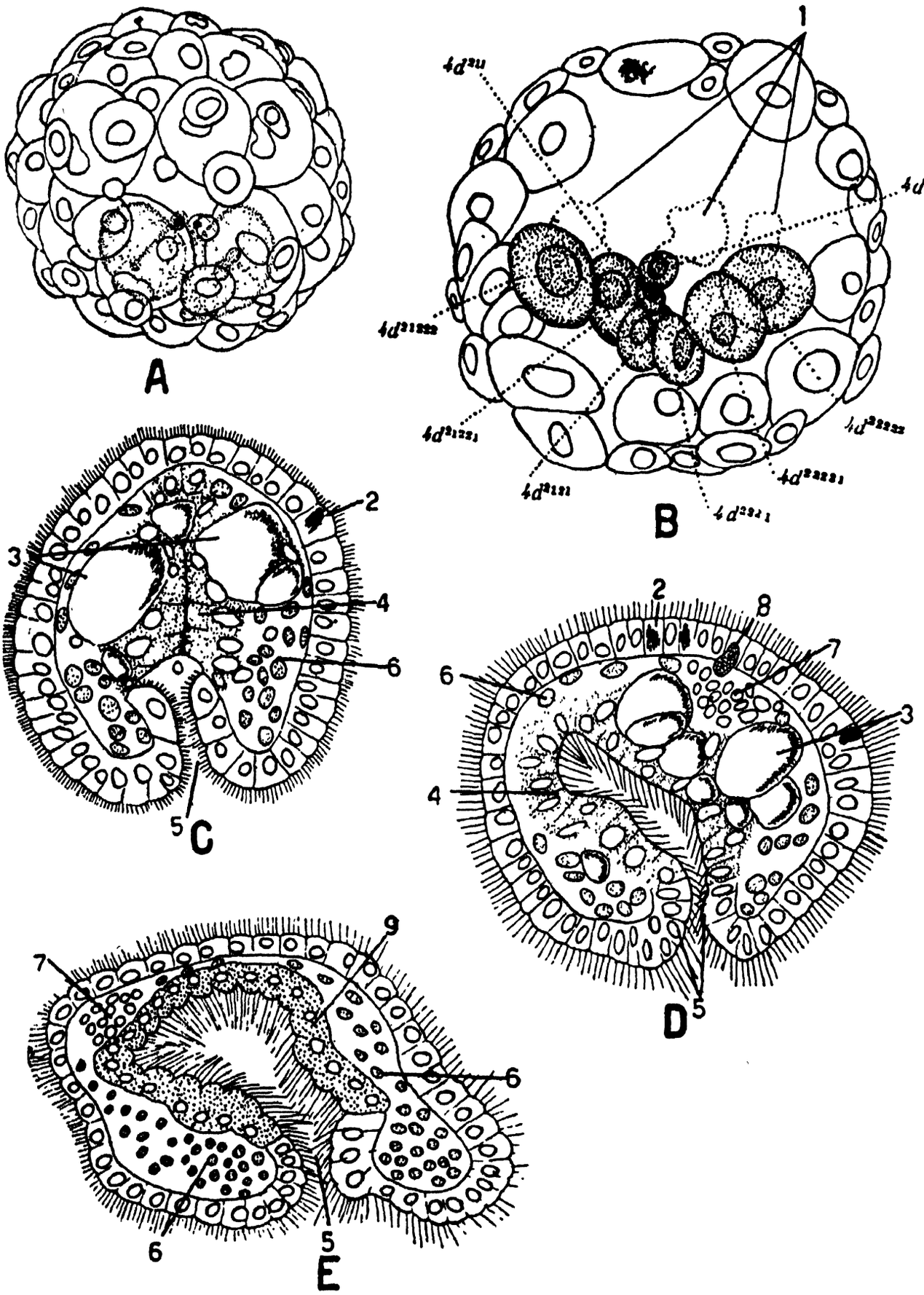

FIG. 66.—Development of polyclads. *A–E*. Later stages of the development of *Hoploplana inquilina* (*after Surface*, 1907); for general type of earlier cleavages see Fig. 3. *A*. Beginning gastrulation, showing offspring of 4*d* (stippled) in the interior. *B*. Section of a slightly later stage, showing offspring of $4d^2$ proliferating in the interior. *C*. Later stage, stomodaeum forming, intestine organizing; yolk has run together to form large droplets. *D*. Later stage, axis shifting forward, intestinal lumen formed, cerebral ganglia and eyes forming. *E*. Larval stage, axial shift completed. 1, degenerating 4*a*, 4*b*, and 4*c*; 2, ectoderm; 3, yolk masses; 4, intestine; 5, stomodaeum; 6, mesenchyme; 7, cerebral ganglia; 8, beginning of eye; 9, completed intestine.

4*a*–4*c*, plus the four macromeres, 4*A*–4*D*, apparently serve only as food material while the single cell 4*d* furnishes the entire entoderm and entomesoderm and hence is the mesentoblast cell. It sinks into the interior and divides (Fig. 66*A*, *B*), and the offspring of $4d^2$ produce the entomesoderm from which originate the mesenchyme, the subepidermal and mesenchymal muscles, the mesenchymal glands, and the reproductive system. The offspring of $4d^1$ give rise to the intestine.

Gastrulation occurs chiefly by epiboly. A stereogastrula is formed, having a ciliated surface ectoderm, an apical frontal gland sometimes bearing a sensory tuft, a blastopore but no archenteron, and an interior mass composed of the cells of the brain, the ectomesoderm, and the offspring of 4*d*. The yolk droplets fuse into large globules (Fig. 66*C*, *D*). Near the original blastopore (which closes and disappears), an ectodermal invagination forms a pharynx simplex (Fig. 66*C*) that connects with the entodermal mass derived from $4d^1$; this mass hollows out to become the intestine (Fig. 66*C*–*E*). The axial relations meantime have shifted; the apical pole bearing the frontal gland moves forward and becomes the anterior end and the mouth region shifts backward (Figs. 66*D*–*E*, 67). The embryo flattens and in the majority of the Acotylea develops directly into a small worm that escapes from the egg capsule. In the Cotylea and some Acotylea (species of *Hoploplana*, *Planocera*), the flattened ciliated embryo puts out eight posteriorly directed lobes or lappets edged with especially long cilia and swims about for a few days in this stage, known from its discoverer as *Müller's larva* (Fig. 67). This may have a caudal sensory tuft opposite the apical one. The finding of a Müller's larva with mature reproductive system was noted above (page 170). In some species of *Stylochus*, the larva has only four lobes, and this is termed Götte's larva. This was regarded by Lang as a developmental stage of Müller's larva but incorrectly so, according to Kato, who finds that Götte's larva does not put out additional lobes. It appears that, in the genus *Stylochus*, some species develop directly and others by way of a Götte's larva. Kato has further found that a modified Müller's larva stage may be passed inside the egg capsule (*Planocera reticulata*). In any of the three cases, the larval lobes are absorbed after a few days, the sensory tufts disappear, additional eyes differentiate, and the larva flattens out as a young polyclad.

The adult plicate pharynx arises from the larval simple pharynx by a secondary ring-shaped ectodermal invagination that becomes the pharyngeal chamber. A circular mesodermal mass that has separated from the rest of the mesoderm provides the muscle and glandular layers of the adult pharynx. The mouth is often closed during embryonic and larval life. There are usually at first only one or two eyes. The protonephridia

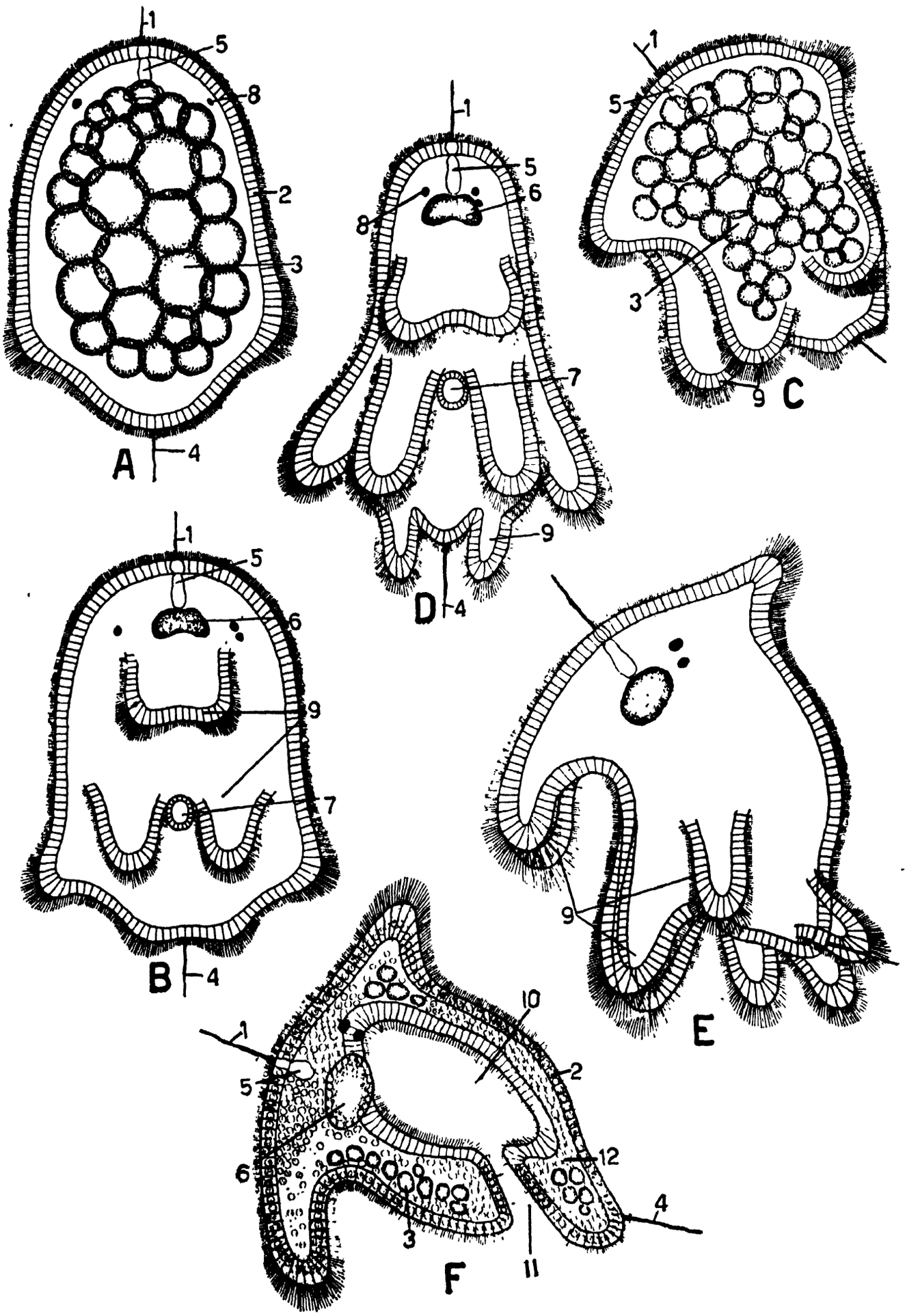

FIG. 67.—Development of Müller's larva. *A*. Beginning formation of lobes. *B*. Later stage of lobes. *C*. Side view of *B*; forward shift of axis has begun. *D*. Completed Müller's larva seen from above. *E*. Same from the side. *F*. Same in sagittal section. (*All after Kato*, 1940.) 1, apical sensory tuft; 2, ectoderm; 3, yolk masses; 4, caudal tuft; 5, frontal gland; 6, brain; 7, mouth; 8, eyes; 9, ciliated lobes; 10, intestine; 11, stomodaeum; 12, mesenchyme.

are believed to originate from paired ectodermal cords that grow into the interior.

b. Entolecithal Development of Acoels.—The development of the Acoela has been studied chiefly in *Polychaerus caudatus* by Gardiner (1895) and for *Convoluta roscoffensis* by Georgievitsch (1899) and Bresslau (1909). The development is of the spiral determinate type and resembles that of polyclads except that the egg undergoes only one meridional cleavage, giving rise to but two blastomeres, *A* and *B* (Fig. 68). The usual four sets of micromeres are given off, but as these consist of only two cells each, they are termed *duets* instead of quartets. In *Convoluta* 3*A* and 3*B* move into the interior before giving off the fourth duet; in *Polychoerus* emboly occurs after this event (Fig. 68*C*). The resulting four cells, 4*A*, 4*B*, 4*a*, 4*b*, are the source of most of the interior mass; the remainder is ectomesoderm derived from the second, possibly also the third, duet. A stereogastrula (Fig. 68*D*) arises in which the interior mass is not definitely separable into entoderm proper and entomesoderm. The blastopore closes and the surface cells separate as epidermis (Fig. 68*E*). The nervous system is derived from the first duet. The mouth (and pharynx when present) originate by ectodermal invagination near the former blastopore. A free larval stage is lacking, and the animal remains permanently in a stereogastrula stage. There is no trace of a digestive cavity, and hence the stereograstrula construction is primary.

c. Ectolecithal Development of Rhabdocoels and Alloeocoels.—Development with yolk cells is highly modified, and although traces of spiral cleavage are seen in some cases there is no possibility of following the fate of the various cells, and germ-layer formation is omitted. The egg surrounded by yolk cells undergoes total cleavage (Fig. 69*A*) into a mass of blastomeres that often become strewn throughout the yolk, later reassembling. The development of several rhabdocoels and alloeocoels has been investigated by Bresslau (1904); that of *Paravortex* by Hallez (1909) and Ball (1916). The following account is based chiefly on Bresslau's work on *Mesostoma*. The blastomere mass moves to one side of the mass of yolk cells which have united into a syncytium (Fig. 69*B*). This side is the future ventral side of the embryo while the other half occupied by yolk is dorsal. The blastomere mass often shows a bilateral arrangement along a plane which is the future median sagittal plane, and becomes divided anteroposteriorly into three masses (Fig. 69*D*). Its peripheral cells arrange into a surface epithelium, which is the ventral epidermis and which gradually spreads dorsally to enclose the dorsal yolk mass. The anterior of the three embryonic masses develops into the paired cerebral ganglia (Figs. 69*E*, *G*) which later become united by commissures and from which the rest of the nervous system grows out. Both pigment and retinal cells of the eyes come from this brain mass. The middle

embryonic mass represents the musculature, glands, and parenchyma of the pharynx. The epithelia of the pharynx, the lining of the pharyngeal cavity, and the epithelium of the esophagus come from a solid epidermal ingrowth that later hollows out (Fig. 69*E–G*). The posterior embryonic mass forms the posterior end of the worm and apparently the reproductive system. The intestine and general parenchyma come from those cells of the embryonic masses that are nearest the yolk (Fig. 70). Some of

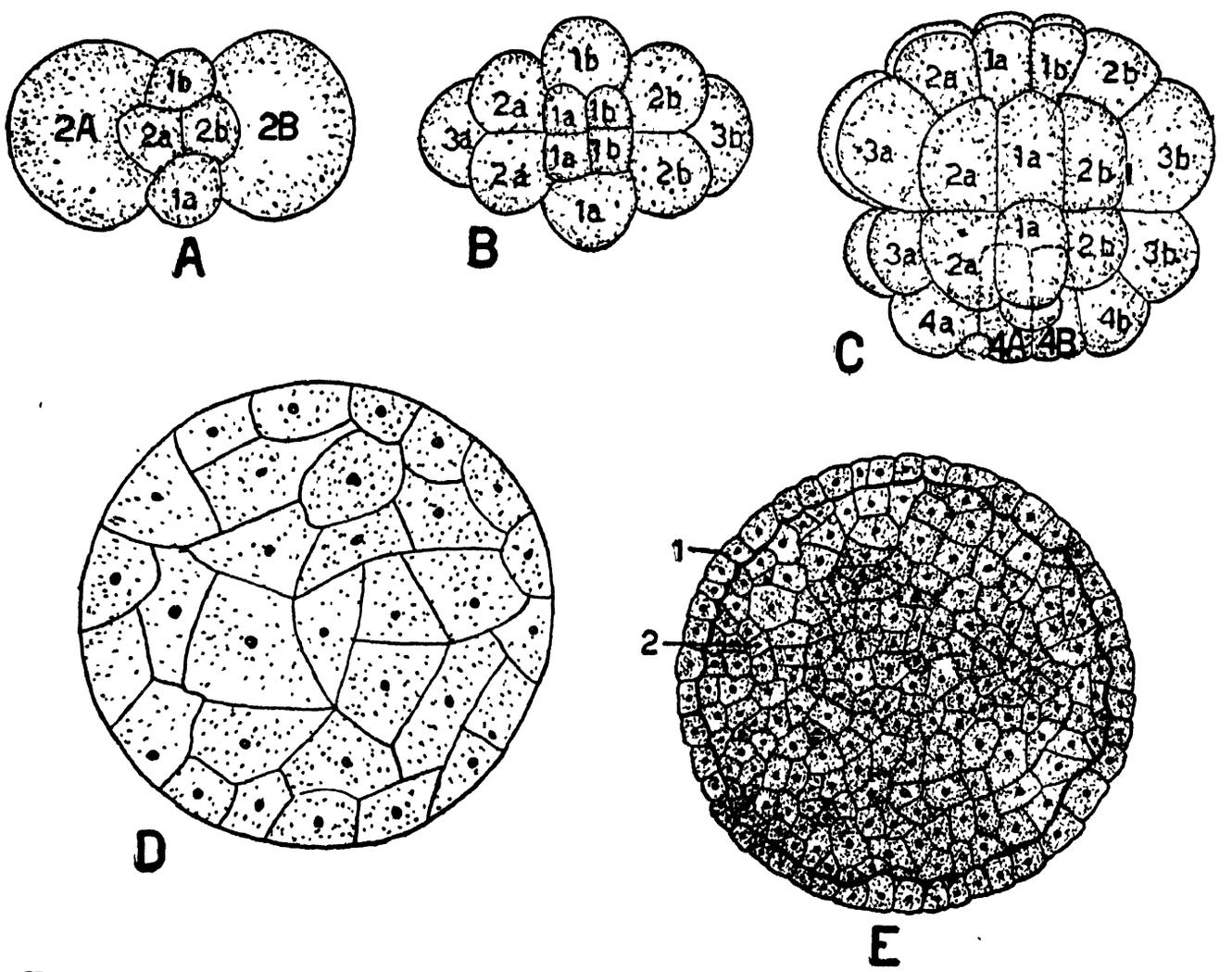

FIG. 68.—Development of Acoela. *A–E*. Development of *Polychoerus caudatus* (*after Gardiner*, 1895). *A*. 6-cell stage seen from above. *B*. 16-cell stage seen from above. *C*. 38-cell stage seen from the side; 4*A* and 4*B* are passing into the interior. *D*. Early stereogastrula stage. *E*. Late sterogastrula stage; surface cells separated as epidermis. 1, epidermis; 2, interior mass.

these work into and absorb the yolk mass and then aggregate to form the intestine, solid at first, later hollowing out. Other indifferent cells of the embryonic masses differentiate into parenchyma and subepidermal and parenchymal musculature.

d. Ectolecithal Development of Triclads.—The development of triclads, known through the work of Metschnikoff (1883), Ijima (1884), Mattiesen (1904), and Fulinski (1914, 1916), is somewhat similar to that of rhabdocoels but is still more modified with relation to the yolk. Certain blastomeres flatten to form an outer membrane that encloses a fluid yolk mass

containing the remaining scattered blastomeres (Fig. 71*A–C*), and such embryonic spheres are surrounded by a yolk syncytium (Fig. 71*E*). Some of the scattered blastomeres aggregate at one point in contact with the outer membrane (Fig. 71*D*) and there form a temporary *embryonic pharynx* (Fig. 71*F–H*) and a small sac, the *temporary intestine* (Figs. 71*F–H*, 72*A*). The embryonic pharynx by sucking movements swallows the whole of the yolk syncytium into the temporary intestine (Fig. 72*B*, *C*). The latter distends until it approaches the outer membrane pushing the remaining blastomeres before it so that a spherical hollow embryo results having a cavity full of yolk cells, an embryonic pharynx, and a wall composed of free blastomeres floating in yolk and bounded externally by the original outer membrane, internally by the distended membrane of the temporary intestine (Fig. 72*C*). This embryonic wall forms the whole of the future worm. The blastomeres in it begin to proliferate rapidly especially on the future ventral side where they aggregate into three masses (Fig. 72*D*) whose fate is substantially the same as in rhabdocoels. The embryo flattens out, and the embryonic pharynx and inner and outer membranes disappear. The innermost cells of the embryonic masses correspond to entoderm, and they invade and devour the yolk cells. Eventually they form the intestine, at first a simple sac, later becoming branched by the invasion of mesenchyme at various points. The rest of the embryonic masses represent the ectoderm and the mesenchyme. The anterior mass, believed from its close association with the epidermis to be largely ectodermal, forms the cerebral ganglia as separate masses that later unite and from which the remainder of the nervous system grows out. The central embryonic mass produces the pharynx by forming cavities that become the pharyngeal chamber and the lumen of the pharynx (Fig. 72*E*). From the different appearance of the cells, the linings of these cavities are taken to be ectodermal while the remaining pharyngeal structure is mesenchymal. A definite stomodaeal invagination is wanting. The remaining indifferent cells of the embryonic masses are mesenchymal and give rise to the subepidermal and parenchymal muscles, the gland cells (probably) and other cells of the general mesenchyme, and eventually to the reproductive system. The mode of origin of the protonephridia of triclads has not been ascertained.

The embryos hatch in two or three weeks as complete minute worms by the rupture of the capsule, often along a predetermined line. In most cases as soon as the young worms have reached a certain size, the reproductive system appears, formed from the free cells of the mesenchyme. Some of these gather into little clusters that differentiate into ovaries and testes. The copulatory complex arises from a mass of mesenchyme that aggregates in the appropriate location, hollows out to form

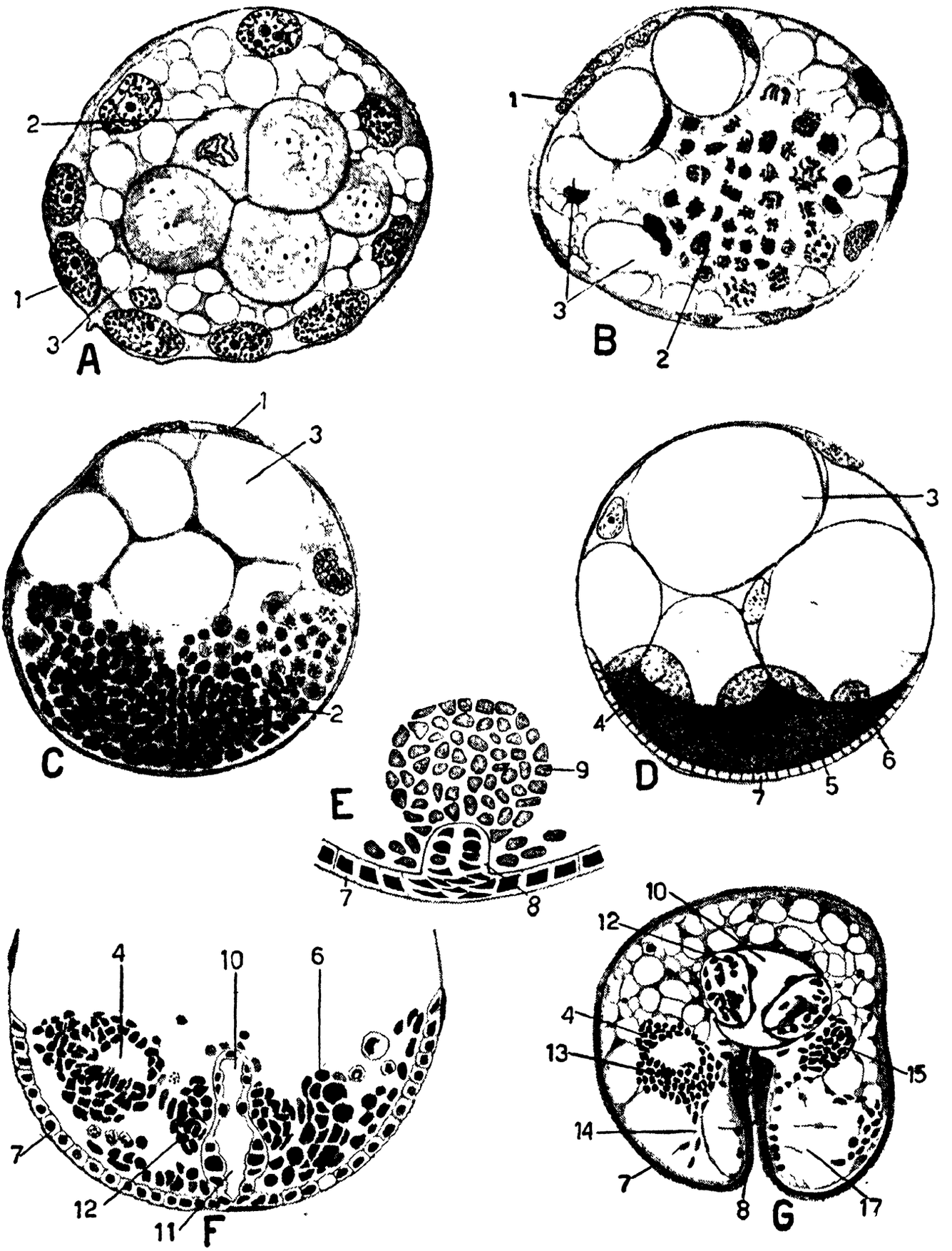

FIG. 69.—Development of rhabdocoels. *A*. Early cleavage. *B*. Later cleavage; mass of blastomeres moving to future ventral side. *C*. Mass of blastomeres at ventral side; epidermis forming. *D*. Three embryonic areas differentiating. *E*. Beginning stage of pharynx formation, showing stomodaeal ingrowth. *F*. Later stage of differentiation; brain and pharynx formed. *G*. Pharynx and stomodaeum completed. (*All after Bresslau*, 1904.) 1, covering membrane; 2, mass of blastomeres; 3, vacuoles; 4, anterior mass to form brain; 5, middle mass to form mesodermal mass of pharynx; 6, posterior mass to form rear parts of worm; 7, epidermis forming; 8, ectodermal invagination to form lining of pharynx and pharyngeal cavity; 9, mesoderm cells to form mesodermal part of pharynx; 10, lumen of pharynx; 11, pharyngeal cavity; 12, wall of pharynx; 13, beginning of eye; 14, ventral nerve cords; 15, primordium of copulatory complex; 17, mesenchyme.

the appropriate cavities, and differentiates into the lining epithelia, muscle layers, and gland cells characteristic of this complex.

Little was known of the embryology of land planarians until the recent study of Carlé (1935) on *Geoplana notocelis*, Brazil, that lays capsules 8 to 9 mm. in diameter, containing five to eight eggs. The development followed through the formation of the provisional pharynx and intestine is similar to that of fresh-water planarians.

There is no trace whatever in the development of any turbellarian of archenteron or coelom. All the evidence indicates that the stereogastrula is the primary embryonic form of the Turbellaria and that entoderm and entomesoderm arise by the mesenchymal method. The development affords no support for the belief that certain embryonic cells persist undifferentiated in the mesenchyme as "formative" cells set aside to function later in the formation of gonads and in regenerative processes. In the triclads and most rhabdocoels and alloeocoels, germ layers are not indicated, and the organ-systems of these animals cannot therefore be assigned to any particular germ layer. In those groups with determinate development it is seen that the mesenchyme and its derivatives are ecto- and entomesodermal; and what may be presumed to be entoderm in the Acoela also participates in the mesenchyme.

20. Asexual Reproduction.—Asexual reproduction occurs in the rhabdocoel families Catenulidae and Microstomidae, in fresh-water triclads of the family Planariidae, and in some land triclads. The rhabdocoels mentioned undergo transverse fission into chains of zooids which become well differentiated before breaking from the chain (Figs. 9, 29). The place where a fission plane is to form is first marked by the appearance of an indentation, soon followed by the differentiation of the ciliated pits. In *Microstomum* (Fig. 50*B*) an internal septum also develops. Pharynx and cerebral ganglia soon form from masses of mesenchyme cells. The order of formation of successive fission planes was already discussed (page 30). In general the time of appearance and locus of a new fission plane are controlled by the degree of development of the nearest fission plane anterior to the site; the more differentiated this plane, the farther away will the new plane appear (Fig. 9). These rhabdocoels multiply extensively by fission until sexual maturity comes on, usually in autumn, whereupon fission ceases and regenerative power is lost, at least in the female phase.

Multiplication by transverse fission is of common occurrence among fresh-water planarians, especially the genera *Dugesia*, *Phagocata*, and *Polycelis*. Fission is not preceded by morphological indications except in two species, "*Planaria*" *fissipara*, Trinidad (Kennel, 1889) and *Dugesia paramensis*, Colombia (Fuhrmann, 1914), in which pharynx and eyes of the new animal appear prior to fission (Fig. 73*C*). The fission process

occurs when the animal has attained a certain size and when other factors are suitable. The rear end suddenly adheres firmly while the anterior region continues to advance so that the fission region is pulled out to an elongated shape and quickly ruptures (Fig. 73*B*). The isolated rear end soon regenerates into a complete small worm. Locomotion and adhesion are essential to the fission process, and fission can be prevented or delayed by interference with these prerequisites as by greasing the container whereupon very long worms can be obtained. On the other hand, rise of temperature and decapitation induce fission (Child, 1910b; Vandel, 1922). Fission usually occurs at a rather definite level shortly behind the pharynx but may take place at other levels, through or anterior to the

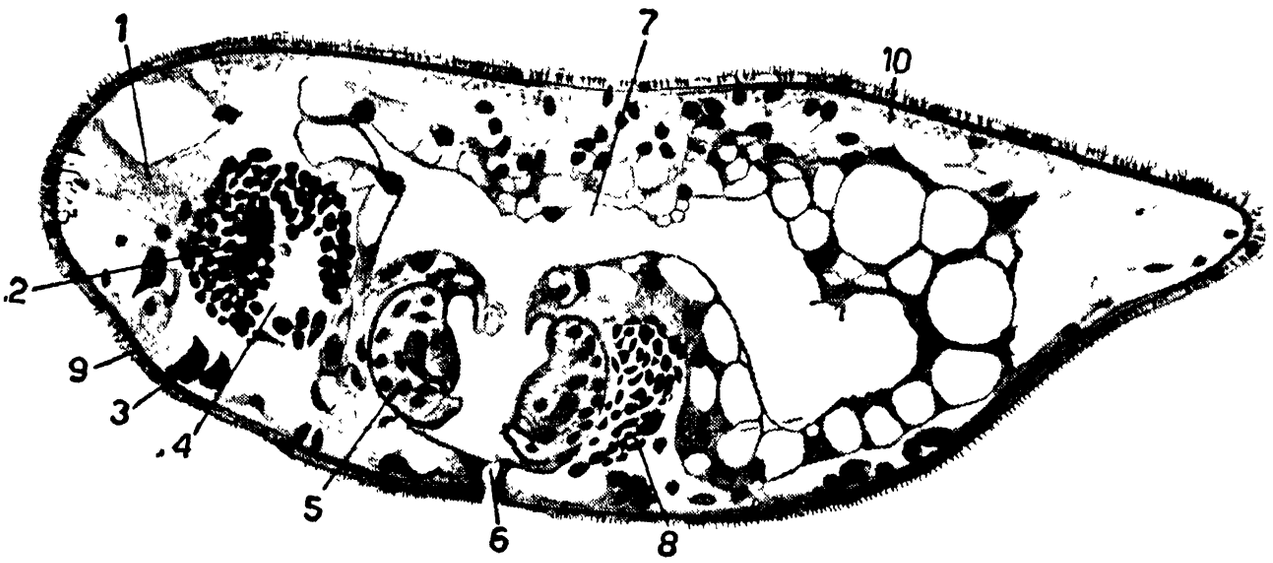

FIG. 70.—Embryology of rhabdocoels; completed embryo of *Mesostoma* (*after Bresslau*, 1904). 1, sensory nerve; 2, retinal cells; 3, rhabdite-forming cells; 4, brain ganglia; 5, muscular mass of pharynx; 6, pharyngeal cavity; 7, intestine; 8, primordium of copulatory complex; 9, epidermis; 10, mesenchyme.

pharynx in some species. The work of Child (1911d) indicates that the fission plane is predetermined physiologically and that the part of the animal behind this plane already has physiological characteristics of a new individual. In nature asexual reproduction of planarians is generally related to the seasonal cycle. Most commonly fissions occur at frequent intervals during the summer and sexual reproduction takes place in winter and spring. Fissions may cease during sexual activity but not necessarily so. As already noted, some species, especially of the genera *Dugesia* and *Phagocata*, exist in sexual and asexual strains (page 157), and also differ as to seasonal cycles in different localities. Some species propagate exclusively by the asexual method and are seldom or never seen in the sexual condition. Certain *Phagocatas* in place of regular fission fragment into a number of pieces (page 159) that encyst; within the cyst reorganization and regeneration of the piece ensue. Some land planarians, especially *Bipalium kewense* and *Dolichoplana striata*, also multiply asexually by fragmentation.

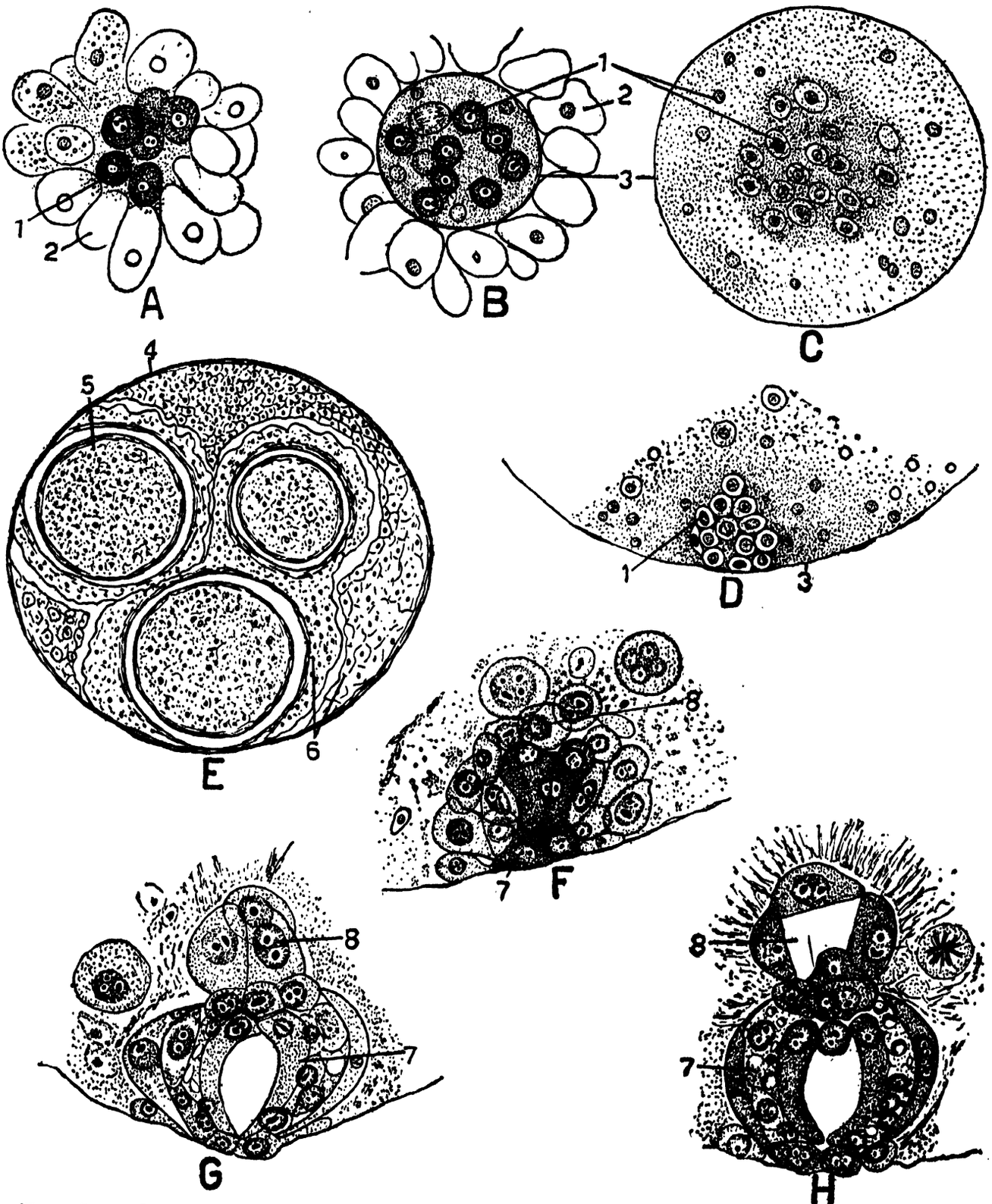

FIG. 71.—Development of triclads. *A–D.* Early cleavage (*after Ijima*, 1884). *A.* Several bastomeres surrounded by yolk cells. *B.* Later cleavage; some blastomeres have formed a surface membrane. *C.* Later; embryo expanding; yolk hereafter omitted. *D.* Mass of blastomeres moved to future ventral surface. *E.* Section through a capsule showing three embryos of about the stage of *C* embedded in the yolk syncytium (*after Metschnikoff*, 1883). *F–G.* Development of the embryonic pharynx (after *Mattiesen*, 1904). 1, blastomeres; 2, yolk cells; 3, bounding membrane; 4, capsule wall; 5, embryo; 6, yolk syncytium; 7, primordium of embryonic pharynx; 8, embryonic intestine.

21. Regeneration and Transplantation.—Those Turbellaria that reproduce asexually also possess high powers of regeneration and consequently have served as material for innumerable studies on regeneration. In other Turbellaria regeneration of a head is limited to pieces from anterior regions or to pieces containing the cerebral ganglia; or else the animals are incapable of regenerative processes beyond wound healing. Many forms can replace posterior regions, including the pharynx and the copulatory apparatus, when the cuts are made posterior to the cerebral ganglia. The region anterior to the ganglia is incapable of regeneration in any case. Polarity is strongly retained in pieces, i.e., the anterior cut surface regenerates a head, the posterior cut surface, a tail; but alterations of polarity occur or may be induced or increased by experimental means. The capacity to regenerate, the rate of the process, the amount of new tissue produced, and often the type of anterior regenerate are markedly related to level, being greatest or most normal anteriorly and declining posteriorly (Fig. 73*D–L*). In short, the flatworm body like the coelenterate (P–C, page 492) is a polarized system; the polarization consists in some sort of physiological gradation along the anteroposterior axis. The characteristics of and evidence for the existence of such an axial gradation have recently been summarized by Child (1941). Regeneration involves two processes: regeneration proper, or *epimorphosis*, in which new tissue grows out from the cut surface in partial replacement of the part removed; and *morphallaxis*, or the working over of the old tissue and organs to fit into the new animal. The relative roles of the two processes vary with different species and with size and level of the piece; but in any event reorganization of the old parts is necessary.

The Acoela have limited powers of regeneration, as illustrated by experiments on *Polychoerus* (Child, 1907; Keil, 1929; Stevens and Boring, 1905) and *Aphanostoma* (Peebles, 1913). Portions removed anterior to the cerebral ganglia or rear portions are replaced perfectly; in pieces cut posterior to the ganglia the amount of anterior tissue formed is less the more posterior the level, but in no case is a normal anterior end regenerated, for ganglia and statocyst are not replaced. Longitudinal halves replace the missing half.

Those rhabdocoels that form chains of zooids naturally regenerate readily, and the regeneration of *Stenostomum* has been much studied (Child, 1902, 1903; Van Cleave, 1929). Pieces from almost any region reorganize into complete new worms. In some species the anterior cut end forms the new head while in others preexisting fission planes or planes formed after cutting absorb the part anterior to them and become the head (Fig. 73*A*); or in cut pieces containing fission planes, these planes may continue to differentiate and fission may ensue, leaving a piece anterior to the fission plane that may or may not be able to regenerate a

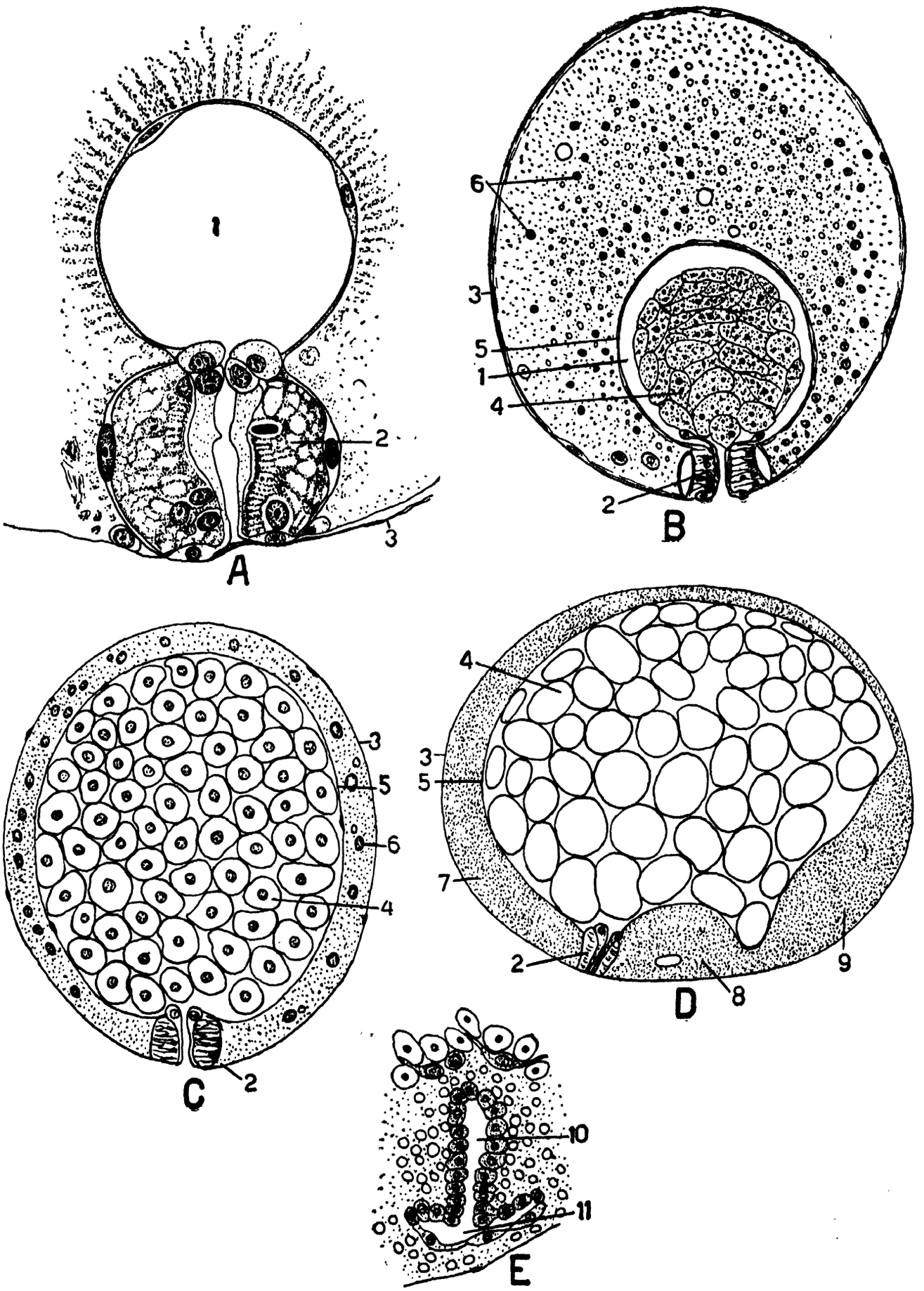

FIG. 72.—Development of triclads (continued). *A*. Embryonic pharynx and intestine completed (*after Mattiesen*, 1904). *B*. Embryo beginning to ingest the yolk (*after Metschnikoff*, 1883). *C*. Ingestion of yolk completed. *D*. Three embryonic masses formed. *E*. Formation of definitive pharynx by appearance of spaces. (*C–E after Fulinski*, 1916.) 1, embryonic intestine; 2, embryonic pharynx; 3, bounding membrane; 4, mass of ingested yolk; 5, inner bounding membrane; 6, blastomeres; 7, anterior mass to form brain; 8, middle mass to form definitive pharynx; 9, posterior mass to form mesenchyme and reproductive system; 10, pharynx lumen; 11, pharyngeal cavity.

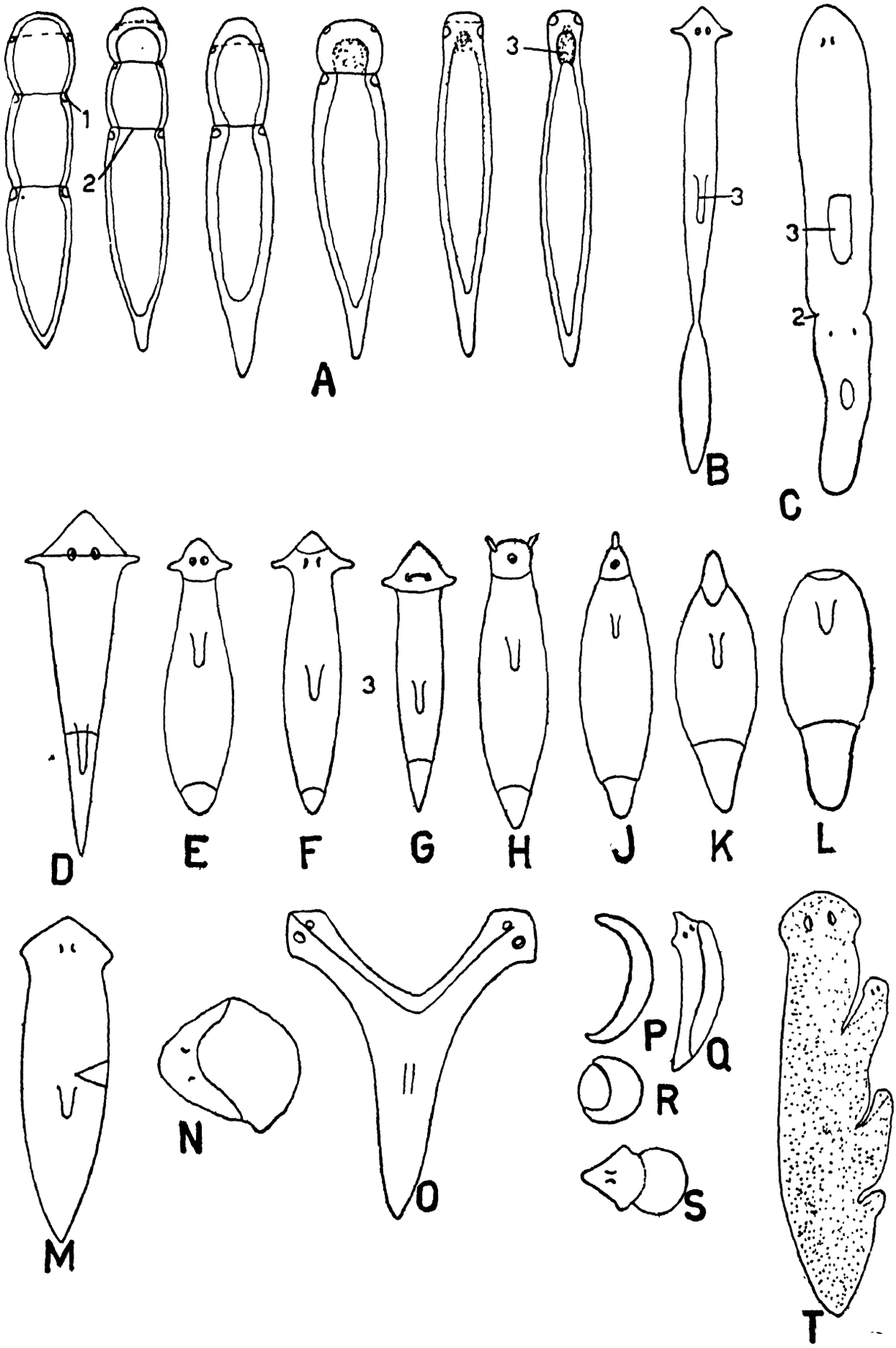

FIG. 73.—Asexual reproduction and regeneration. *A*. Six stages in the regeneration of a piece of *Stenostomum* containing fission planes (*after Child*, 1903); the best developed zooid absorbs parts anterior to it and becomes a new worm. *B*. *Dugesia* in fission, (*after Child*, 1910b.) *C*. *Planaria fissipara*, Trinidad, triclad that forms fission planes prior to fission (*after Kennel*, 1888). *D*, *E*. Effect of level on regeneration (*after Child*, 1911a). *D*. Regenerate from anterior piece; has large head, posteriorly located pharynx. *E*. Regenerate from postpharyngeal piece; has small head, more anterior pharynx. *F–L*. Series to show decline of head regeneration in *Dugesia dorotocephala* with decreasing size and more

head. The regeneration of *Microstomum* is similar to that of *Stenostomum* (Ruhl, 1927). Some other rhabdocoels may regenerate the tail tip (*Macrostomum*, Ruhl, 1927) but in general rhabdocoels that lack asexual reproduction and alloeocoels are incapable of any regeneration (Fulinski, 1922; Hein, 1928; Ruhl, 1927), although wounds are healed by epidermal migration.

Fresh-water planarians of the genera *Dugesia*, *Phagocata*, *Polycelis*, etc., display remarkable powers of regeneration and have been the object of numerous researches. In general, pieces of moderate size from any level form a complete new worm. With reduction in size of piece, complete worms may regenerate from even very short pieces in some species, while in others short pieces tend to regenerate reduced or imperfect heads or may remain headless, and this tendency is greatest the more posterior the level (Fig. 73*F–L*). The size and normality of the regenerated head, the rate of anterior regeneration, and the length of tail produced are generally greater the more anterior the level from which the piece was cut and decline in posterior levels. In *Dugesia dorotocephala* (Fig. 15*B*), extensively studied by Child, a series of anterior regenerates ranging from normal heads through several types of reduced heads to headlessness (Fig. 73*F–L*) occurs in relation to level and shortness of piece (Child, 1911a, b, c). This series shows increasing suppression of the middle region with consequent approximation and fusion of eyes and auricles. These facts constitute some of the evidence for the existence of the axial gradation mentioned above.

Reconstitution also involves the formation of a new pharynx. Pieces that do not regenerate anteriorly may form a pharynx if they were cut from postpharyngeal regions of the original worm; but pieces cut anterior to the pharynx will not regenerate a pharynx unless some sort of head first regenerates. The new pharynx may arise in either the new or old tissue and is nearer the anterior end the more posterior the level from which the piece was cut and the less normal the anterior regenerate (Fig. 73*D*, *E*). If a head has regenerated the old portions of the intestine are worked over so as to reproduce in the regenerated worm the typical three-branched pattern. In general, the ability of a piece to regenerate into a complete worm of typical morphology depends upon the regeneration of a

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posterior location of piece (*after Child*, 1911c). *F*. Normal regenerate. *G*. Teratophthalmic regenerate with fused eyes. *H*. Teratomorphic regenerate with one eye and auricles shifted anteriorly. *J*. Extreme teratomorphic type with fused auricles. *K*. Anophthalmic regenerate without eyes or auricles. *L*. Headless, no anterior regeneration. *M*, *N*. Regeneration of lateral triangular piece at right angles to original polarity (*after Olmsted*, 1918). *O*. Double heads produced by keeping open an anterior split. *P*, *Q*. Regeneration of a narrow side piece, polarity retained. *R*, *S*. Alternative method of regeneration of a narrow side piece, polarity at right angles to original. (*O–S after Morgan*, 1900b.) *T*. Head regenerated on each of three anteriorly directed oblique cuts (*after Li*, 1928). Line in each case separates new from old tissue. 1, ciliated pit; 2, fission plane; 3, pharynx.

head at the anterior cut surface. This means that the head controls the pattern of the morphology, i.e., the spatial arrangement and proportions of parts. This control is an expression of the dominant position of the head in the axial gradation already mentioned.

Some other points in planarian regeneration may be touched on briefly. Very short pieces especially from anterior regions may regenerate biaxial heads, i.e., form a head at each cut surface. Isolated heads cut off just behind the eyes also often regenerate a reversed head at the cut surface (Fig. 74*G*). In some species short posterior pieces produce biaxial tails. After oblique cuts, a head usually forms at the most anterior point, a tail at the most posterior point, of the cut surfaces (Fig. 74*A–C*). Lateral longitudinal pieces usually regenerate with reference to the original polarity (Fig. 73*P*, *Q*); but short lateral strips (Fig. 73*R*, *S*), or those cut lateral to the ventral nerve cords, or small triangular lateral pieces (Fig. 73*M*, *N*) tend to regenerate the new head at the cut surface, i.e., at right angles to the original polarity (Morgan, 1900b; Olmsted, 1918; Beyer and Child, 1930). By means of appropriate splits, double (Fig. 73*O*) or multiple (Fig. 74*E*) heads or tails may be induced at will; heads will grow out from the body sides behind forwardly directed gashes (Fig. 73*T*), tails behind posteriorly directed ones (Li, 1928); one or more "crotch" heads (Fig. 74*D*) may arise in the angle of posterior longitudinal splits if these are carried far enough forward (Beissenhirtz, 1928; Silber and Hamburger, 1939; Hull, 1940); heads will form along the edges of windows through the body (Hull, 1940, Fig. 74*F*); and in fact an endless variety of bizarre forms can be produced by appropriate cuts.[1] Regeneration is also affected by external factors such as temperature, osmotic pressure, and chemical composition of the medium; many experiments have been performed on the effect of various salts, anesthetics, radiations (see below), etc., on regeneration.

If a sexually mature planarian is cut in two between the pharynx and the copulatory apparatus, the latter degenerates and the piece regenerates into an asexual worm. The large anterior piece regenerates a new copulatory apparatus if active testes are present. The presence of ovaries is not pertinent (Vandel, 1920). This result indicates that the formation and maintenance of the copulatory apparatus depend on the presence of testes.

The Dendrocoelidae are incapable of asexual reproduction and have limited powers of regeneration. Anterior pieces retaining the head regenerate the missing posterior parts, but decapitated pieces can reform the head only when taken from anterior levels, in our common dendrocoelid, *Procotyla fluviatilis*, only from the anterior third (Lillie, 1901; Curtis and

[1] As cuts and splits in the planarian body heal rapidly, they must be kept open by repeated cutting if regenerates are wanted.

Schulze, 1934). Similar conditions obtain in marine triclads (*Procerodes, Cercyra*), some of which cannot regenerate a head when the cut lies behind the cerebral ganglia whereas in others prepharyngeal pieces may regenerate a head (Lloyd, 1914a; Lus, 1926; Steinmann, 1908). Pieces from pharyngeal and postpharyngeal regions are incapable of head regeneration but may regenerate a tail at the anterior cut surface. In marine triclads slight dilution of the sea water accelerates regeneration; other osmotic changes retard (Lloyd, 1914b). Some land planarians, as *Bipalium kewense*, regenerate very well (Morgan, 1900a); others, as *Geoplana* (Goetsch, 1933), regenerate perfectly when the pieces are large, less so in short pieces.

The polyclads in general have poor powers of regneration (Child. 1904a, b, c, 1905a, b, c, d, 1910a; Levetzow, 1939; Olmsted, 1922b). Pieces containing the cerebral ganglia regenerate perfectly. Pieces cut behind the cerebral ganglia are incapable of anterior regeneration but can regenerate parts behind their level of section.

Grafting experiments may also be performed with suitable fresh-water planarians; species of *Dugesia* are generally used. When crosspieces are fused in normal or reversed orientation, the result is similar to that found with hydroids (P–C, page 491), i.e., regeneration occurs according to the original polarity of each piece except that the polarity of very short pieces fused to larger pieces may be altered. Triangular or rectangular pieces may be excised and grafted into windows made into other parts of worms (Miller, 1938; Okado and Sugino, 1937; Santos, 1931) in normal or altered orientation. Such grafts from the cephalic region containing much nervous tissue are more effective in inducing a head-like outgrowth and causing reorganization of adjacent parts of the host with production of one or more pharynges, the more posteriorly they are grafted into the host (Fig. 75*A–C*). Similar grafts from tail regions implanted anteriorly are influenced by the host to develop into a tail regardless of their original polarity (Fig. 75*D*).

Heads regenerated from grafts or at a cut influence adjacent regions for a certain distance, reorganizing them to a greater or less degree into postcephalic regions (with pharynx and intestinal branches), and prevent the formation of another head at a cut surface or otherwise within a certain distance.

The histology of the regenerative process has been repeatedly studied in planarians with not entirely concordant results; the differences are probably real, depending on the species employed. The wound is considerably closed by muscle contraction (this contraction is omitted if the cutting occurs in an isotonic medium) and the adjacent epidermal cells flatten, become syncytial, and creep over the cut surface. If the exposed surface is sufficiently large, regeneration cells may participate in the

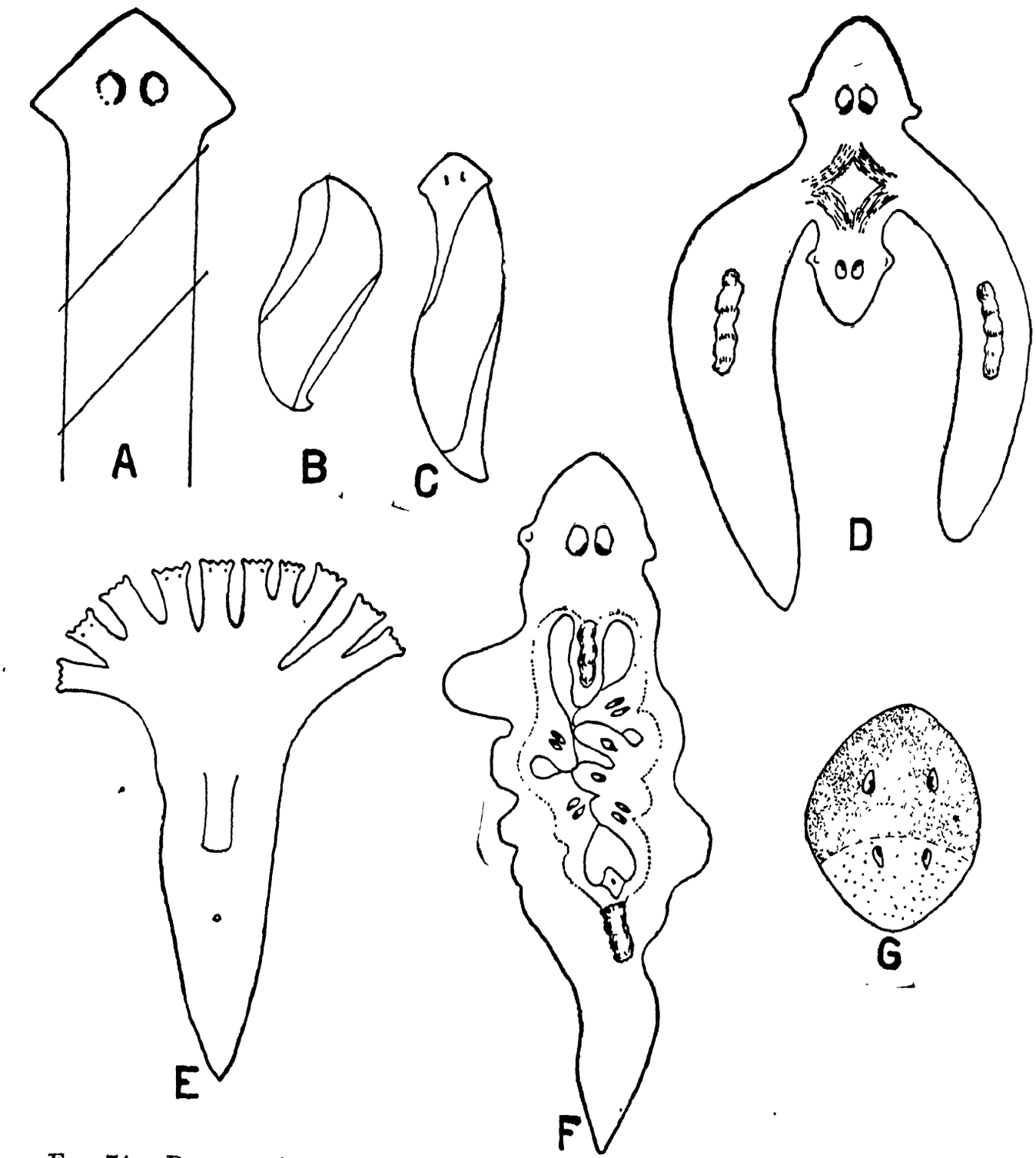

FIG. 74.—Regeneration of planarians (continued). *A–C.* Regeneration of an oblique piece (*after Morgan*, 1900b). *D.* Crotch head, produced at anterior end of posterior split that extends far forward (*after Hull*, 1940). *E.* Numerous heads produced on *Dendrocoelum lacteum* by repeated splits (*after Lus*, 1924). *F.* Many heads regenerated along the sides of a central long window (*after Hull*, 1940). *G.* Head regenerated at posterior cut surface of head piece of *Curtisia foremanii* (*after Morgan*, 1900b).

formation of this covering membrane, which later differentiates into the typical epidermis. A mass of cells, variously known as regeneration cells, formative cells, etc., accumulates beneath the covering membrane and differentiates into the various missing parts (Bartsch, 1923; Lang, 1912; Bandier, 1936; Steinmann, 1926). In the case of anterior regeneration strands of these cells attach to the cut nerve cords and differentiate into brain and eyes. They also adhere to the cut intestinal branches and build on appropriate terminations, and differentiate into muscle cells and

gland cells in appropriate locations. It appears, however, that in some species or with regard to some systems, the new parts may be formed by proliferation of the adjacent cells of the old parts, i.e., Bandier (1936) states that in the regeneration of land planarians both cut nerve ends and intestinal branches grow from their own cells. The source of these regeneration cells is still under dispute. There is little doubt that they comprise preexisting cells that migrate to the cut surface either with or without multiplying by mitosis. According to some authors, they consist entirely of the free cells of the mesenchyme; others state that, after cutting, various body cells, such as gastrodermis, yolk glands, gland cells, etc., undergo dedifferentiation into amoeboid cells and join the free mesenchymal cells to form the mass of regeneration cells (Lang, 1912; Steinmann, 1926). An extreme view is to the effect that the regeneration cells are persistent embryonic cells held as a reserve to function in regeneration and formation of the reproductive system (Curtis, 1936; Curtis and Schulze, 1934). It appears to the author that there is no evidence in support of such a view and that some of the evidence cited above opposes it. Curtis and Schulze have found that there are conspicuously fewer free mesenchymal cells in planarians with poor powers of regeneration, as *Procotyla fluviatilis*, than in those with high powers, as species of *Dugesia;* but their tabulation fails to show any marked decline in number of free mesenchymal cells in those regions of *Procotyla* that cannot regenerate a head as compared with regions that can. Further regions unable to regenerate a head can regenerate a tail and also can produce (from free mesenchymal cells) the entire complicated copulatory apparatus.

Attempts to shed some light on these problems have been made by studying the effect of X rays and radium on regeneration (Bardeen and Baetjer, 1904; Gianferrari, 1929; Meserve and Kenney, 1934; Schaper, 1904; Strandskov, 1937; Weigand, 1930). The subject has been reviewed by Curtis (1936) who has researched extensively on the matter. In general, exposure to sufficient dosage of X rays and radium inhibits regeneration altogether in most species, although *Dugesia dorotocephala* will regenerate after any exposures that do not kill.[1] The failure to regenerate is caused, according to some of the above workers, by the killing off of the free mesenchyme cells, according to others by the inability of these cells after radiation to migrate or to differentiate. The result therefore only proves what was already known, namely, that cells of the type of free mesenchymal cells are responsible for regeneration. It does

[1] It is very difficult to reconcile the results of Curtis using *D. agilis*, which he says does not regenerate after X-ray treatment, with those of Strandskov and Meserve and Kenney using *D. dorotocephala*, since, in the author's opinion, *D. agilis* is only a geographic variant of *D. dorotocephala* and cannot with certainty be distinguished from it by morphological criteria.

not settle the questions whether these cells are in fact embryonic rests and whether they get contributions from dedifferentiated tissues. The difference in susceptibility to radiation between the mesenchyme cells and other body cells evidently varies with different species.

22. Ecology, Physiology, and Behavior. *a. General Ecology.*—The Turbellaria are in general marine animals; only the Catenulida and

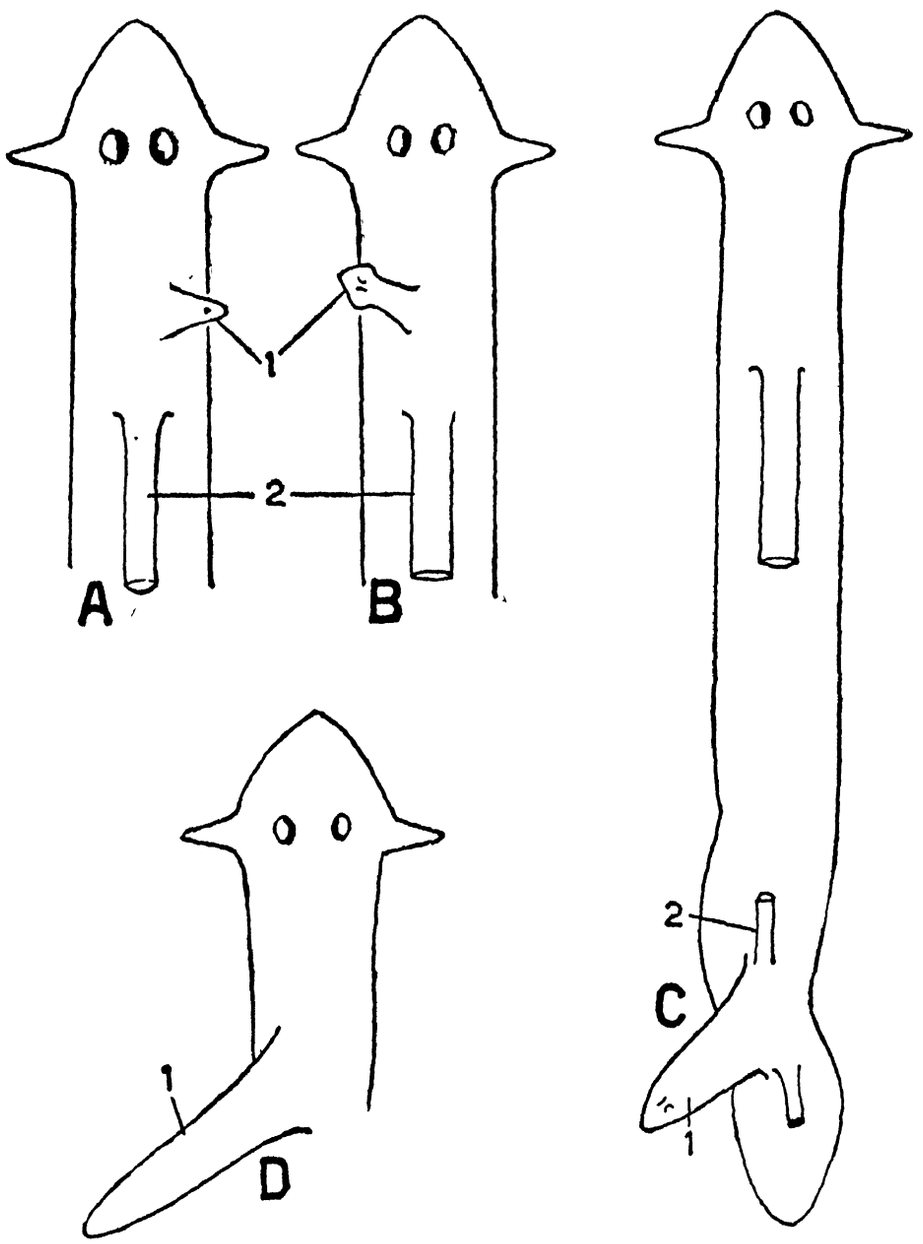

FIG. 75.—Grafts of planarians. *A*, *B*. Types of outgrowth produced by grafts of small pieces from the brain region into the prepharyngeal region of *Dugesia*. *C*. Same kind of graft grafted into the postpharyngeal region; produces larger head that has induced two pharynges in relation to itself. *D*. Postpharyngeal piece grafted into the prepharyngeal region of *Dugesia;* becomes a tail. (*All after Santos*, 1931.) 1, regenerate induced by graft; 2, pharynx.

Temnocephalida are typically fresh-water groups without evident marine relatives or forebears. The Turbellaria have obviously spread from marine into fresh-water habitats and from thence into humid terrestrial regions. There has also been a considerable amount of return invasion of brackish and even salt water by fresh-water turbellarians, notably among the Catenulida, Macrostomida, triclads, and such rhabdocoel genera as *Dalyellia, Castrada,* and *Phaenocora.* The Turbellaria are

characteristic and constant members of a variety of habitats. They are typically bottom dwellers. The larger forms, as the triclads and polyclads, are generally found on hard bottom, under rocks and among shells and gravel, etc.; the small and microscopic members are more apt to occur on sandy and mucky bottoms. A characteristic assemblage of sand-dwelling rhabdocoels and acoels has been found on north European coasts (page 144). These have certain adaptive characteristics in common: long, slender muscular body, long sensory hairs, tail appendages, eyelessness, loss of rhabdites, especial development of food-catching devices, overdevelopment of adhesive organs including girdles of adhesive papillae in a number of species, some reduction of the reproductive system, posterior displacement of the gonopores (Fig. 76). The species of such sand communities appear to have a very limited distribution, i.e., those of the north German Coast are different from those of the west French Coast, although ecologically similar. Whether such sand-dwelling turbellarian communities occur along American coasts has not been ascertained but is highly probable. The benthonic Turbellaria are mostly limited to the littoral zone of the ocean, although some occur at considerable depths; however, there are no abyssal species. Some acoels (Fig. 49*A*) and polyclads have pelagic habits and show some adaptation to pelagic life by transparency and broadly oval form; many polyclads also have pelagic larvae or juvenile stages. Acoels and polyclads are regular components of the animal association of the floating Sargassum and may have the adaptive brown-and-white color pattern characteristic of Sargassum animals. Nearly all pelagic Turbellaria are limited to tropical or subtropical waters; the chief exception is the rhabdocoel *Alaurina composita* in the North Atlantic (Fig. 32*B*) of which large numbers may be found in late summer in the Zuider Zee and adjacent waters (Hofker, 1930). Although the ocean is in general a very constant habitat, turbellarians that live along shores in the tidal zone are subject to wide changes of

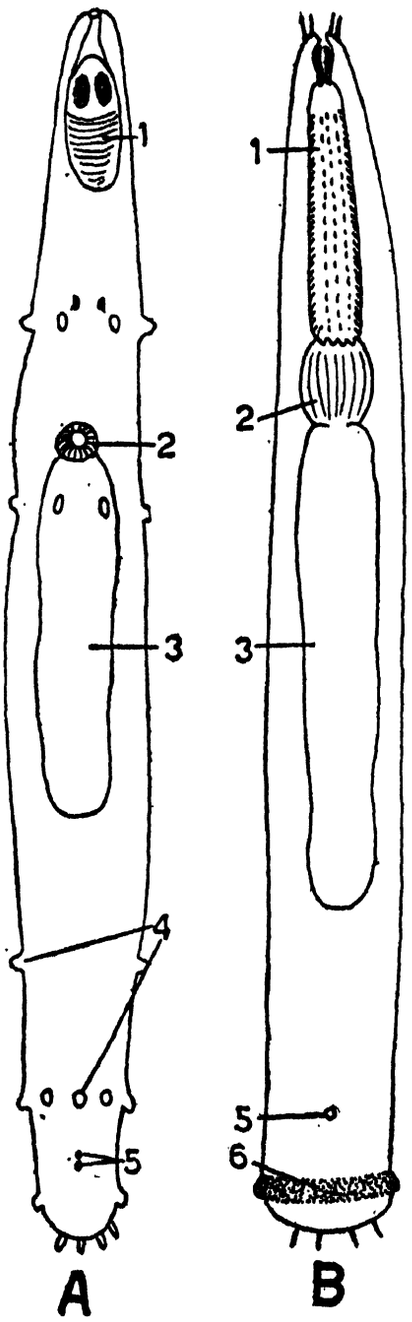

FIG. 76.—Sand-dwelling types: two kalyptorhynchid rhabdocoels from the Bay of Kiel (*after Meixner*, 1928). *A. Acerina remanei*, with five bands of adhesive papillae. *B. Rhinepera remanei*, with a caudal adhesive girdle. 1, proboscis; 2, pharynx; 3, intestine; 4, adhesive papillae; 5, gonopores; 6, adhesive girdle.

temperature and salinity. The alloeocoel *Monocelis fusca* lives in tide pools on the Welsh Coast where the natural temperature range is −1 to 28°C. and can recover from exposure to 44.5°C. (Rees, 1941). This species and the marine triclad *Procerodes ulvae* also endure great changes in salinity (see further below).

The fresh-water Turbellaria are chiefly inhabitants of lentic waters and often have seasonal cycles related to such habitats, especially in the case of planarians and rhabdocoels that inhabit vernal pools (pages 135). Some turbellarians are *rheophilous*, i.e., limited to flowing water, such as springs and hill and mountain streams. Outstanding examples of stream planarians are the European *Dugesia gonocephala*, *Polycelis felina* (= *cornuta*), and *Crenobia alpina* (Fig. 61*C*) which occur along streams with increasing altitude and decreasing temperature in the order named. *Crenobia alpina* requires cold temperature and running water. No alpine planarians are known for North America, but the species *Phagocata morgani*, Appalachians, and *Polycelis coronata* (Fig. 32*D*), western mountains, seem limited to flowing waters. Our common *Dugesia dorotocephala* (Fig. 15*B*) appears to live only in springs or spring-fed waters, probably because of the high calcium content of such habitats. Although some turbellarians are *stenothermous* (enduring only a limited temperature range) as *Crenobia alpina*, most fresh-water forms are *eurythermous*, i.e., indifferent to wide changes of temperature. An extreme case is *Microstomum lineare* found in a variety of habitats ranging from alpine lakes to hot springs at 40 to 47°C. Rhabdocoels are characteristic parts of the fauna of alpine lakes, but most of these are common species with a wide distribution in fresh waters. More specific are the rhabdocoels, chiefly of the genera *Phaenocora* and *Mesostoma*, found in *shallow* waters in high altitudes and latitudes, and having in common a very dark coloration. Several *Mesostomas* occur in such pools in the mountains of Tibet at elevations of over 15,000 feet (Ruebush, 1939), and the author described *Mesostoma arctica* from a pool on the Canadian tundra near the arctic circle and from swamps in the Wyoming Mountains at 10,500-foot altitude (Hyman, 1938). A considerable number of fresh-water planarians occur only in cave or subterranean waters; they are generally white, eyeless, and provided with adhesive organs. The most notable cave planarians are the North American ones, of the family Kenkiidae (page 159). The turbellarian fauna of tropical fresh waters appears to be very scanty, consisting chiefly of a few widely distributed or cosmopolitan species (Reisinger, 1933) that tolerate a broad range of conditions.

The terrestrial Turbellaria, comprising the land triclads, and a few rhabdocoels and alloeocoels, being devoid of protective armor, require high humidity and most seem unable to mature their sex organs except in warm temperatures. Hence they are mostly limited to tropical and sub-

tropical jungles with high rainfall where they live by day surrounded by mucus under stones, fallen logs, and leaf accumulations, in earth burrows, or between the leaf bases of tropical plants, coming forth at night to hunt food. *Bipalium*, subjected to desiccation, lost water according to the simple laws of evaporation and could recover if the water loss did not exceed 45 per cent of its weight (Kawaguti, 1932). However, mucous secretion plus aggregation into the most humid spot should furnish some protection against drying.

b. Relations with Other Organisms: Symbiosis, Commensalism, Parasitism, Parasitic Infections, Enemies.—Most acoels and some rhabdocoels and alloeocoels harbor symbiotic chlorellae and xanthellae; these occur in the mesenchyme chiefly just inside the subepidermal musculature and appear to be of the same nature and function as in other animals. They are absent in the eggs and newly hatched young, and it is known that they are acquired during juvenile stages by ingestion with food. They pass into the gastrodermis whence they are ingested by free mesenchymal cells that convey them into the mesenchyme (von Haffner, 1925). Much study has been devoted to the chlorellae of the acoel genus *Convoluta*, especially *Convoluta roscoffensis*, which occurs on the channel coast of France in such vast numbers as to color large areas green. Keeble and Gamble (1907) have shown that the green cells in this worm are flagellates of the chlamydomonad group and that they occur abundantly in the habitat and on the egg masses of *Convoluta*. These authors state that this acoel feeds while young but after attaining sexual maturity subsists entirely by digesting its chlorellae. A number of fresh-water rhabdocoels of the families Dalyelliidae and Typhloplanidae (Fig. 36*A*) contain green cells that can be cultivated apart from the worms and appear to be green algae of the genus *Chlorella* or close to this genus (von Haffner, 1925). It is notable that the *Dalyellia* species harboring these symbionts are much larger (2 to 5 mm.) than other *Dalyellias*. Sojourn in darkness almost but not entirely eliminates the green cells of *Dalyellia*. *Dalyellia* digests senile and degenerating green cells but does not damage healthy ones. The green and brown symbionts of Turbellaria contain starch, fats, and other lipoids and undoubtedly possess some nutritive value for their hosts. Their chief advantages are, however, that they utilize in their metabolism waste products of their hosts (it will be recalled that the Acoela have no excretory system) and that they give off oxygen enabling the host to endure stagnant conditions. Thus the acoel *Amphiscolops langerhansi* will survive enclosure in small airtight bottles of sea water for 2 weeks or more in the light but succumbs in the dark under otherwise similar conditions (Welsh, 1936); in the light, oxygen is added to the water by the photosynthetic activity of the brown cells of the worm.

As already noted, all groups of Turbellaria, except the fresh-water and

terrestrial triclads, contain members that inhabit other animals in a relation that appears to be commensal rather than parasitic. Here may be recalled the acoels that live in the interior of echinoderms (page 131); the rhabdocoel families Graffillidae and Umagillidae, entocommensals of mollusks, echinoderms, and some other invertebrates (page 140); the wholly ectocommensal group Temnocephalida (page 145); the marine triclad ectocommensals of *Limulus* (page 155) and of skates (page 156); and the polyclad habit of dwelling in shells of live snails or in dead snail shells occupied by hermit crabs (page 166). The epizoic or ectocommensal forms are characterized by loss of pigment, cilia (especially dorsally), rhabdites, and often eyes, and especially by the strong development of adhesive areas and organs. The entocommensals, on the other hand, usually lack adhesive organs and are generally completely ciliated although they also tend to lose rhabdites and eyes; their most outstanding feature is the enlarged female system, exemplified by the branching yolk glands, elongated ovaries, etc. Such adaptation for increased egg production is a common feature of genuine parasites and no doubt indicates a tendency toward true parasitism among the entocommensal Turbellaria. However, probably the only genuine entoparasites among the Turbellaria are the Fecampiidae (page 140) and *Oekiocolax* (page 140).

The Turbellaria are themselves hosts to commensals and parasites. Euglenoid flagellates of the genera *Astasia* and *Euglena* occur in catenulids (de Beauchamp, 1911; Hall, 1931). A trypanosome-like flagellate, *Cryptobia* (= *Trypanoplasma*) *dendrocoeli*, inhabits the digestive tract and copulatory bursa of *Dendrocoelum lacteum* (Gelei, 1913). Holotrichous ciliates of the mostly free-living genera *Holophyra* and *Ophyroglena* may occur in *Stenostomum* (Kepner and Carroll, 1923) and planarians. Members of the parasitic ciliate group Astomata (P–C, page 189) are also represented, as *Hoplitophyra uncinata* with an anterior hook in the intestinal branches of marine triclads and *Sieboldiellina* (= *Haptophrya*) *planariarum* with an adhesive disk in fresh-water planarians (Bishop, 1926). *Coleps* (P–C, page 50) and *Trichodina* (P–C, page 199) species are often epizoic on fresh-water planarians. The most common endoparasites of planarians are gregarines, chiefly of the genus *Lankesteria* (P–C, page 149; Vandel, 1921). Encysted stages of larval trematodes are sometimes found in Turbellaria but probably represent accidental penetrations of wrong hosts. Land triclads seem much subject to nematode infestations.

The Turbellaria are seldom eaten by other animals as their surface secretions appear to be distasteful if not actually toxic (see below). Planarians, if taken into the mouth by fish and salamanders, are usually quickly ejected with signs of distaste. Bolen (1938) saw dragonfly and damsel fly nymphs eat planarians. The worst enemies are other turbel-

larians for the group is highly cannibalistic, promptly attacking weak or injured members or new fission products; the larger species may also eat the smaller ones.

c. Duration of Life, Cycles, Senescence, Rejuvenescence.—The length of life of turbellarians is known chiefly from laboratory cultures. The smaller forms, except those capable of fission, probably live but a short time, a few weeks or months, usually dying in summer or autumn after laying dormant eggs. Some, however, may survive a year or more by encysting during unfavorable seasons (Sekera, 1926). Species capable of fission can presumably under favorable conditions propagate indefinitely by the asexual method. Thus Nuttycombe and Waters (1938) cultivated *Stenostomum tenuicauda* for 11 years during which there were over 1000 asexual generations without the appearance of sexuality. They also had male specimens of *S. grande* that reproduced continuously by fission for 4 years. Sekera (1926) kept a *Microstomum* colony going for 3 years. Similar facts are known for asexually reproducing species of fresh-water planarians. Child (1914) maintained *Phagocata velata* in asexual culture for nearly 3 years during which there were 13 cycles of fragmentation, encystment, and hatching of small worms from the cysts (page 159). Individuals of the larger turbellarians survive in laboratory cultures 2 or 3 years (de Beauchamp, 1935; Vandel, 1922) and may have several periods of sexual propagation alternating with periods of fission or lack of any reproduction.

Something has been said in the preceding pages concerning sexual reproduction in relation to season. This matter has been studied in fresh-water planarians by several workers (de Beauchamp, 1931, 1935a, 1935b; Curtis, 1902; Kenk, 1937, 1940; Vandel, 1922). In general sexual reproduction is intermittent, alternating with periods of fission or of lack of any reproduction; the periods of capsule laying correspond in nature with external factors, chiefly temperature. In laboratory cultures, sexual reproduction is also intermittent but does not recur with the regularity noted in nature. Kenk, Vandel, and others believe there is an inherent cyclic reproductive rhythm in these planarians, but the author found that the same species used by Kenk (*Dugesia tigrina*) can, when fully grown, be caused at will to develop a copulatory apparatus and lay viable capsules by exposure to low temperature followed by rise of temperature. In some individuals even 2 or 3 days of exposure to lowered temperature is sufficient to bring on sexuality. Some time must elapse before another sexual period can be induced in the same individual by temperature manipulation. This time is much less than a year, mostly a few months, so that the alleged inherent rhythm is probably only an expression of such a "refractory" period following a period of reproductive activity.

After continued laboratory culture or after sexual reproduction in

nature, turbellarians often evince signs of senescence such as loss of pigment, sluggish behavior, unwillingness to feed, and disintegrative processes in the eyes, head, or pharynx. Death by general disintegration frequently follows such changes. In species with high regenerative powers, however, rejuvenescence may be brought about experimentally or occurs naturally. Thus fission products or animals emerging from cysts are physiologically like young animals. Through starvation, adult worms may be reduced to the size of very young worms and so far as can be tested have actually become young again. Adult worms may be cut into small pieces, and these after regeneration are also indistinguishable from young worms. The already much mentioned *Phagocata velata* has in temporary pools a natural cycle of senescence and rejuvenescence; the worms grow to mature size, show the above symptoms of senescence, then fragment into small bits, each of which inside a cyst regenerates to a tiny worm that in all respects is identical with young worms hatched from capsules. Apparently this cycle is repeated in nature indefinitely with no loss of vitality. By underfeeding this species so that it does not grow, senescence and fragmentation are prevented, and the worms remain in a state of perpetual youth (Child, 1913a, 1914).

d. Osmotic Relations.—As already noted, both fresh- and salt-water turbellarians may invade brackish habitats. In a fresh-salt-water gradient as the entrance of a river into the sea, there is generally a barren zone, poor in animals, lying between the limits of increasing salinity endurable by the fresh-water animals and of decreasing salinity endurable by the marine forms. To endure changes of salinity animals must have some mechanism for regulating loss or entrance of water and salts. Generally fresh-water forms invading brackish water show reduction in size and greater tissue density as a result of water loss, and the reverse changes occur in marine forms adapting to lowered salt content. The best-studied case is that of the marine triclad *Procerodes ulvae* living on the English Coast at the mouth of streams (Pantin, 1931; Beadle, 1934). This animal is subject in nature to changes lasting several hours from the fresh stream water (salt content, 0.03 g. per liter) to sea water (salt content, 35 g. per liter). It can live indefinitely in all dilutions of sea water to 5 per cent; it swells and loses salts in the greater dilutions but not at all in proportion to the decreased osmotic pressure. In pure fresh water (i.e., without salts), it swells to nearly twice its volume, loses salts, and survives only 1 to 3 days. The worm can recover after loss of 85 to 90 per cent of its salts. In the natural stream water, swelling and salt loss are much less and survival better than in pure water. Osmotic pressure appeared not to be an important factor in the effect of the various media tried. It was found that calcium, in which the stream where *Procerodes* lives is rich, is the most effective factor in reducing swelling and salt loss

in diluted media. Hence it appears that the presence of calcium in fresh waters enables marine animals to invade such waters. The cause of the protective action of calcium is not clear, although probably calcium makes the epidermis resistant to the passage of water and salts. Beadle (1934) studied sections of *Procerodes ulvae* that had been exposed for varying periods to diluted sea water and found that water, passing through the epidermis, at first accumulates in the mesenchyme but later is transferred to the gastrodermis where it accumulates in numerous vacuoles. Through this vacuole formation swelling is reduced, the mesenchyme is restored to normal, and the animal regains more normal appearance and behavior. In time the epidermis develops resistance to further water intake, although the gastrodermal vacuoles remain as long as the worms are kept in diluted media; i.e., there is no discharge of excess water through the mouth.

A number of other littoral turbellarians live under conditions in which they are exposed daily to large changes in environmental salinity. Thus *Monocelis fusca* inhabits tidal pools subject to evaporation and hence concentration of the sea water. The salinity of these pools was found to vary from 26 to 64 parts per thousand; the alloeocoel endured in tests a range from 5.6 to 76.8 parts per thousand but began to show sluggish behavior at 80 parts per thousand. It can, however, form a mucous cyst within which it can survive exposure to salinities of 298 parts per thousand, or over eight times the salinity of sea water (Rees, 1941).

Fresh-water planarians when exposed to solutions hypertonic to natural waters lose water and weight but not in proportion to the increased osmotic pressure, and they show some ability to resist water loss (Adolph, 1925; Gresens, 1928). *Dendrocoelum lacteum* was studied by Gresens (1928) in a stream opening into the Danish Wiek where it lives in a salt gradient from pure stream water (salt content, 0.01 to 0.04 per cent) to the Wiek water (0.5 per cent salt). Individuals from the more brackish water proved more resistant to high salinities than stream individuals. Worms could be acclimated by gradual changes so as to live normally and reproduce in 1.5 per cent salinity. Low temperature is an important factor in enabling planarians to resist increased salinity.

Some data are available on the salt content of the turbellarian body. According to the work of Pantin (1931), the salt content of *Procerodes ulvae* is about half that of sea water, or about 1.7 per cent. In *Stylochus frontalis*, the salt content is a little over 2 per cent (Pearse and Wharton, 1938). Hence the osmotic pressure of the body fluids of marine turbellarians is considerably less than that of sea water and the epidermis must be able to resist water loss or salt intake or some other regulating mechanism must be present. Dilution of the sea water causes increased oxygen consumption in marine invertebrates (Beadle, 1931), and this

represents energy consumed in resisting water intake. The osmotic pressure of fresh-water turbellarians is greater than that of fresh water, and they require some mechanism to resist water intake and salt loss or to eliminate excess water. Murray (1927), seeking a medium suitable for growing planarian cells in tissue culture, found that the balanced salt solutions (e.g., Locke's, salt content, 0.9 per cent) in use for vertebrate tissues are far too concentrated for fresh-water planarians and require one-tenth to one-twelfth or more dilution. This indicates that the osmotic pressure of the species used (*Dugesia dorotocephala*) is equal to about a 0.08 per cent solution of sodium chloride. This species also requires a higher ratio of calcium to potassium than is customary in salt solutions made up for vertebrate tissues (Murray, 1928).

The water content of the polyclad *Stylochus frontalis* is 76.2 per cent (Pearse and Wharton, 1938); that of the land triclad *Bipalium* averages 81.5 per cent, grading from 80.7 per cent in the anterior third to 82.9 per cent in the posterior third (Kawaguti, 1932); and that of a fresh-water planarian, *Dugesia dorotocephala,* is 78 per cent (Buchanan, 1931).

e. Hydrogen-ion Concentration.—Turbellarians are in general indifferent to the pH of their environment, enduring without evident effect wide changes in this factor. *Dendrocoelum lacteum* will live indefinitely in a range from pH 4.2 to 9.5 (Gresens, 1928); greater acidities or alkalinities are fatal. The toxicity of acids for *Dugesia dorotocephala* depends on the acid used, being less for mineral acids such as hydrochloric and nitric, which kill in 2 to 3 hours at pH 3.0 to 3.4, than for organic acids, especially butyric, which is fatal in the same time at pH 5.0 (Hyman, 1925a). Similarly alkalinity caused by ammonium hydroxide is more toxic (lethal at pH 9.0) than that caused by sodium hydroxide (lethal at 9.2) (Anderson, 1927). In alkalinities and acidities less than those mentioned, *D. dorotocephala* survives indefinitely, although it is to be noted that planarians are able to reduce the alkalinity and acidity of the medium and it is very difficult to maintain a constant pH in solutions in which they are immersed. In general, alkalies accelerate (Anderson, 1927) and acids depress (Hyman, 1925a) the rate of oxygen consumption of planarians, but the acid effect results, not from the pH as such, but from the carbon dioxide set free when natural water is acidified.

f. Locomotion.—The smaller Turbellaria, including juvenile stages of the larger forms, probably move entirely by ciliary action. Although they probably can swim, few of them habitually do so, but for the most part they glide along the substratum or the underside of the surface film. The ciliary waves pass from anterior to posterior, thus driving the animal forward, and appear to be independent of the nervous system. Forms exceeding 2 to 3 mm. in length mostly crawl along a substratum with a characteristic gliding movement. Although the ventral cilia probably

play some role in this gliding, if the worm is not too large, this type of locomotion is caused largely or wholly by muscular waves that pass from the anterior end backward either across the whole width (monotaxic) or alternately along the two sides (ditaxic). Triclads have mostly monotaxic, polyclads ditaxic waves (Stringer, 1917; Crozier, 1918; Olmsted, 1922a). The waves are mostly invisible to the naked eye in planarians, more noticeable in polyclads. The relative roles played by cilia and by muscular waves in locomotion can be determined by treating worms with lithium chloride which paralyzes ciliary action and with magnesium chloride which paralyzes the muscles. The first chemical does not stop locomotion in triclads and polyclads, whereas the second does. A number of polyclads swim by means of body undulations; these also may be monotaxic or ditaxic depending on the body shape.

Most turbellarians are capable of a more hasty type of locomotion which they employ when stimulated. This consists of large evident muscular contractions and expansions accompanied in those forms with adhesive organs or areas by alternate attachments of these, so that a leech-like form of progress results. Usually such an effort lasts but a short time and the usual gliding is soon resumed.

Mucous secretion probably plays an important role in gliding, even in aquatic turbellarians, and is obviously indispensable to terrestrial forms. The slime trail lubricates and smooths out the substratum on which progression occurs. The land triclads and some other Turbellaria also use slime threads in dropping from one level to another or in bridging gaps in a substratum (Kew, 1900).

The role of the nervous system in locomotion has been investigated by several workers (Bardeen, 1901a; Levetzow, 1936; Moore, 1923; Olmsted, 1922a). In general, turbellarians from which the cerebral ganglia have been removed tend to cease locomotion and to remain quiescent. They can, however, be stimulated to locomotion by mechanical or chemical means and are able to execute the usual creeping. Levetzow (1936) found that even quite small postcerebral pieces of *Thysanozoon* and *Eurylepta* are able to crawl. Such experiments indicate that the more simple muscular waves are independent of the brain and are mediated by the general nerve plexi. Most polyclads, however, are unable to swim following decerebration, and some cannot even execute the regular ditaxic crawling (Olmsted, 1922a). Therefore, the more complicated types of locomotion depend on initiation from the brain, also on transmission along the main nerve cords, since cuts through these inhibit swimming waves posterior to the cuts.

g. Food and Feeding Behavior.—The Turbellaria are as a class carnivorous. A few acoels and rhabdocoels are said to eat diatoms and other algae, but the vast majority of turbellarians eat other animals of suitable

size or ingest bits of flesh of intact, damaged, or dead larger animals as fish and mollusks. Favorite items of food of the smaller species are rotifiers, copepods, cladocerans, nematodes, annelid worms, etc., and the larger species feed on earthworms, snails, insect larvae, isopods, amphipods, other crustaceans, fish, oysters, and so on. Although the Acoela lack a digestive cavity, they are on the whole strictly carnivorous, ingesting copepods and similar small animals whole and digesting them in their interior cells. Aquatic and land triclads can attack and subdue intact animals of considerable size such as snails, earthworms, and insect larvae, and polyclads often devour bit by bit live sessile, helpless animals such as oysters, barnacles, ascidians, and the like. Turbellarians often gather, often in numbers, on animal corpses if these are not too decayed. Insects falling into the water constitute a regular food supply for pond turbellarians. Although most turbellarians will eat almost any kind of animal flesh, some appear limited to particular items. Thus *Stylochus frontalis* (= *inimicus*) of the southern Atlantic Coast of the United States seems to eat nothing but oysters, slipping between the shell valves and devouring the oyster bit by bit despite shell partitions erected against it (Pearse and Wharton, 1938), and *Pseudoceros crozieri* apparently feeds exclusively on ascidians (Crozier, 1917). In laboratory cultures, turbellarians can be fed on chopped or crushed earthworms or other annelids, mealworms and other insects, clams, snails, isopods, amphipods, clotted blood, or, most conveniently, bits of beef liver, although some species will not eat the last. Some species require live prey such as *Daphnia*. In general, turbellarians from lentic waters are most easily kept in the laboratory. Polyclads are usually difficult to maintain under laboratory conditions. Turbellarians may often be captured in numbers by baiting suitable habitats with pieces of beef or dead fish; at short intervals the bait is examined and any worms present shaken off into jars.

The presence of intact prey (not emitting juices) is detected either by direct contact with chemoreceptors or by the disturbance created in the water by the prey. The turbellarian then quickly grips the prey with the anterior end, especially the anterior adhesive organ when this is present, and wraps its body about the prey, holding the latter firmly against the substratum. Adhesive margins, disks, etc., are used by the worm to maintain a firm hold on the substratum while subduing the prey. Mucous and adhesive secretions assist in entangling the prey and rendering it helpless. Crustaceans and baby fish living in the same habitat with planarians may become coated with the slime left by planarians so as to be unable to move and are then attacked. Some turbellarians use the penis stylet to damage prey.

Food emitting juices is sensed in still water at a distance varying with species from 1 or 2 to 10 to 15 cm. or more. A turbellarian, previously

gliding aimlessly about, when coming within the radius of diffusing juices exhibits a characteristic behavior (Pearl, 1903; Koehler, 1932; Müller, 1936). The worm pauses, swings the raised head about, then turns toward the food and goes to it in a direct line. Planarians living in running water detect food juices coming downstream at considerable distances, and if such places are baited with meat or fish the worms can be seen emerging in hordes from under stones and leaves and traveling in processions upstream to the bait. The European stream planarian *Crenobia alpina* is in fact more or less incapable of directing itself toward the food in the absence of a current (Doflein, 1925; Koehler, 1932) and even if it finds the food may often fail to feed in still water. Having reached the food, planarians test it with the anterior margin, then grip it with the head and move the body along until the pharynx can be brought into play. The protruded pharynx is inserted into the food, and ingestion begins. During feeding the worm keeps some part of its body firmly attached to the substratum.

The extirpation experiments of Koehler (1932) and Müller (1936) have shown that the lateral sensory organs of the head—the ciliated pits of *Stenostomum*, the ciliated grooves of *Phaenocora* and *Bothromesostoma*, the auricles including the auricular sense organs of planarians, or the corresponding lateral angles of the head in planarians that lack definite auricles—are the chief or only sensory areas involved in chemical perception of dissolved juices. *Stenostomum* after extirpation of the ciliated pits cannot detect the presence of food or find it, and planarians deprived of their auricles or corresponding regions show great loss in their food reactions. However, fresh-water planarians appear to have some chemoreceptors over the entire body and after such operations may in time find food. The testing of the suitability of food after finding it is vested chiefly in the anterior margin, which also functions to release the feeding reaction of the pharynx. After extirpation of this margin, planarians find the food as readily as before but fail to test it or grip it and often glide away without ingestion. The tip of the pharynx is, however, sensitive to food, and the pharynx may protrude on contact with food in the absence of anterior sensory regions. The pharynx tip can discriminate between normal food and the same food mixed with deleterious chemicals; but, after removal of both the anterior margin and the pharynx tip, the pharynx loses this discriminatory ability and may protrude into such treated food. The presence of fluid nutrients such as bouillon or blood in the water may induce repeated pharynx protrusions of intact planarians. According to some workers, headless pieces containing the pharynx or isolated pharynges will not feed when placed in contact with food, but according to others such reactions do occur in some species (page 101).

According to the available experiments, then, the ciliated pits,

auricles, auricular sense organs, and corresponding head areas have sensory functions similar to smell in higher animals, and the anterior margin and pharynx tip function like taste.

After the prey has been subdued and firmly gripped, ingestion ensues. Turbellaria with simple and doliiform types of pharynx generally swallow their prey whole by means of muscular waves in the distended but not very protrusible pharynx. The rosulate pharynx is not distensible, and hence the contents of the food are sucked in. The triclads also do not swallow their food whole, but the highly protrusible plicate pharynx is inserted into the food or into the prey and the contents sucked in bit by bit through the peristaltic action of the pharynx. In polyclads the food is usually taken whole into the interior of the voluminous ruffled pharynx. Even those polyclads that have a cylindrical pharynx like that of triclads appear to swallow their prey whole, apparently limiting themselves to small animals. Whether the secretions of the pharyngeal glands have a softening and digestive action on the food cannot be answered categorically. These secretions possibly have such action in some species, but in general they function only to lubricate the food and facilitate its ingestion. Even in those cases where food is held in the pharynx and seen to undergo digestion, it does not necessarily follow that the enzymes involved are of pharyngeal origin.

Extirpation of the brain (without disturbance of the main chemoreceptors of the head) may greatly retard or altogether abolish the food-finding and food-ingesting reactions. The result, however, varies with species. The most marked effects of brain removal appear in *Crenobia alpina* which will not ingest food after this operation (Koehler, 1932), but other species may show little alteration of food reactions after decerebration.

Whether the surface and pharyngeal secretions of turbellarians have a toxic and paralyzing as well as an entangling effect on prey is a question often raised but never satisfactorily answered. In reviewing this question, Arndt and Manteufel (1925) note that large land planarians may produce an unpleasant astringent effect on the human tongue and that a South American land planarian, *Polycladus gayi*, is believed by the natives to be fatal when eaten by horses and cattle. These authors found that water extracts of ground fresh-water planarians were toxic or even fatal when injected into the coelom of small mammals. Later Arndt (1925) located this toxin in the surface secretions of planarians and found that it exercised its effect by stopping the heart. Mattes (1932) observed that the cercariae of flukes are damaged and killed by the surface slime of planarians. However, students of planarians, including the author, in general fail to see any toxic or paralyzing action of planarian slime on the usual prey, such as crustaceans and insect larvae.

The nutritional requirements of planarians are not definitely known, although attempts in this direction have been made by Wulzen, Bahrs, and others (Wulzen, 1923, 1926, 1929; Bahrs, 1929, 1931; Wulzen and Bahrs, 1931, 1935; Bahrs and Wulzen, 1936; Pettibone and Wulzen, 1934; Greenberg and Schmidt, 1936). Vertebrate liver, kidney, thymus, adrenal, and gray matter of the brain support excellent growth, whereas little or no growth is obtained with egg white, egg yolk, lean beef and other muscle, thyroid, pancreas, gelatin, beef fat, and the white matter of the brain. Tissues from animals fed on deficient diets also have an adverse effect on planarian growth and may cause a pathological condition in which the worms shrivel and turn black. Raw egg white alone or in high proportions in the food is very deleterious, causing disintegrating protrusions on the worms. Refrigeration at 0°C. or heating decreases the growth-promoting power of vertebrate tissues. Greenberg and Schmidt failed to find any favorable effect on planarian growth of adding vitamins and auxins to inadequate foods, although yeast addition was effective. Of all vertebrate tissues, liver has about the best growth-promoting power for planarians, and it contains an ether-soluble heat-labile growth factor of unknown nature.

h. Digestion, Assimilation, and Food Storage.—It was discovered by Metschnikoff in 1866 for *Convoluta* and later verified for rhabdocoels and triclads (Metschnikoff, 1878) that digestion in the Turbellaria is largely intracellular. As already indicated, it is improbable that the pharyngeal secretions have any digestive action, at least in planarians. Westblad (1922) failed to find any digestive action on protein or fat of extracts of 50 pharynges of *Dendrocoelum lacteum* and 100 pharynges of *Polycelis nigra.* It is also improbable that any digestion occurs in the lumen of the intestine in planarians (Westblad, 1922; Willier, Hyman, and Rifenburgh, 1925). The granular clubs (page 104), usually regarded as enzymatic cells emitting enzymes into the intestinal lumen, are in the author's opinion protein reserve cells (see below).

The details of intracellular digestion are best known for fresh-water triclads where the most complete studies are those of Westblad (1922) and Willier, Hyman, and Rifenburgh (1925). The latter fed planarians, starved 2 weeks, on beef liver and studied sections of worms fixed at varying intervals after the beginning of feeding. The liver torn into minute bits by the suctorial action of the pharynx fills first the anterior, then the posterior rami of the intestine. Some 45 to 60 minutes were required for complete filling of the intestine in the species used (*Dugesia dorotocephala*), but the phagocytic cells of the gastrodermis begin to engulf the food as soon as this comes in contact with them. These cells swell through intake of water, bulge into the lumen, often fuse into syncytia, and take in food particles in amoeboid manner by putting out pseudo-

podial processes. The food particles together with fluid are formed into typical food vacuoles like those of Protozoa. About 8 hours were required for all the food in the lumen to be phagocytized by the phagocytic cells which at this time are found packed with food vacuoles in various stages of digestion (Fig. 77). The food in the vacuoles, at first loose and faintly stainable, gradually condenses to a strongly staining (eosinophilous)

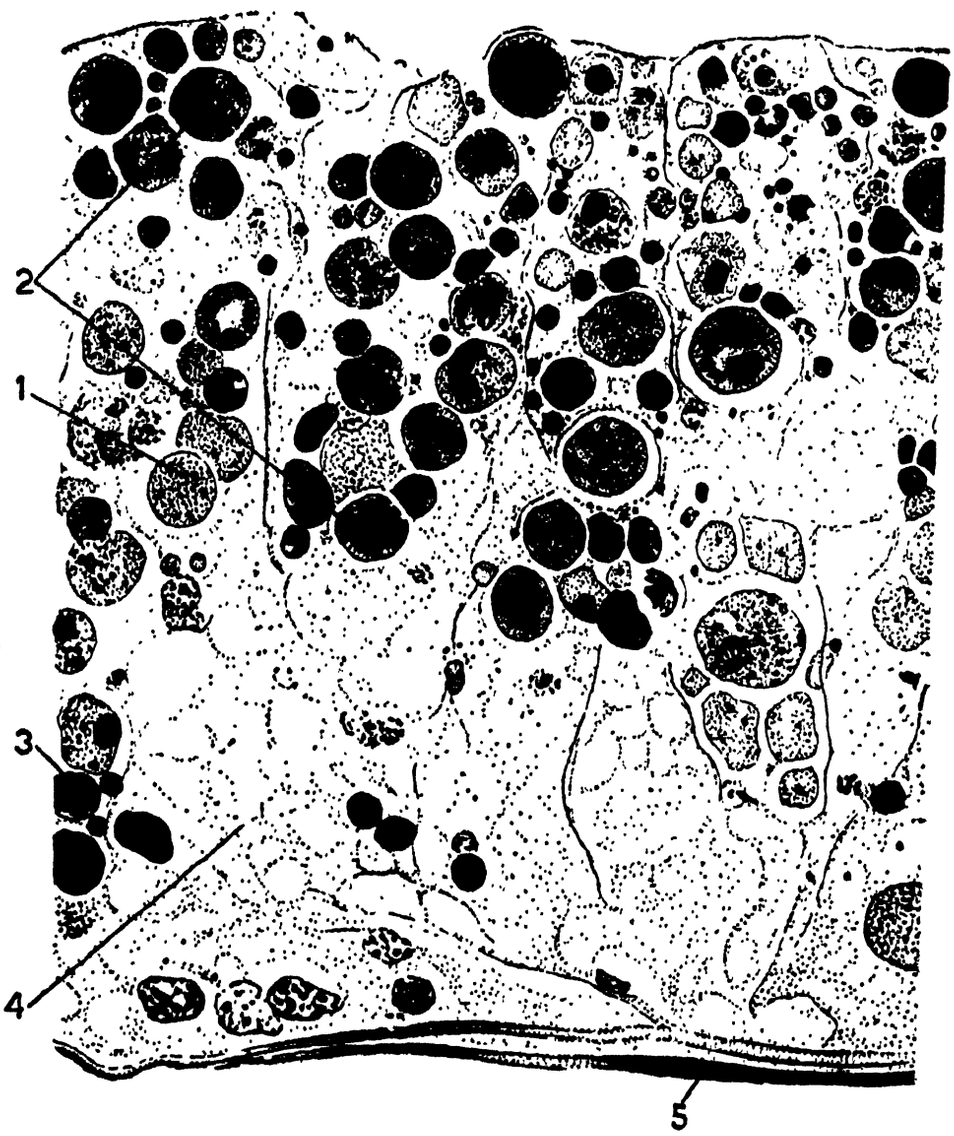

FIG. 77.—Intracellular digestion. Gastrodermis of *Dugesia dorotocephala* 6 hours after feeding beef liver showing various stages of food vacuoles (*after Willier, Hyman, and Rifenburgh*, 1925). 1, early stage of digestion; 2, later stage with homogeneous areas forming; 3, final stage, vacuole becomes a homogeneous eosinophilous ball; 4, fat vacuoles; 5, muscle fibers.

homogeneous ball (Fig. 78) shown by chemical tests to be of protein nature. About 8 hours are required for food vacuoles to reach the homogeneous ball stage. These balls then gradually disappear, presumably as a result of the breakdown of their protein into soluble substances; about 5 days are required for the complete disappearance of the food balls from the phagocytic cells. In a few phagocytic cells, the food balls do not disappear but subdivide into small spherules, and such cells then become granular clubs. Westblad, using indicator dyes with the food, was unable to detect any change of hydrogen-ion concentration in the food

vacuoles so that digestion appears to take place in a neutral medium. He found evidence of proteolytic and lipolytic enzymes but not of diastatic ones; in fact it appears that planarians are unable to digest carbohydrates.

In *D. dorotocephala*, the basal halves of the phagocytic cells are normally packed with fat, which largely disappears during the early stages of intracellular ingestion and digestion. It is also known that, during this period, the oxygen intake is doubled or tripled (Hyman, Willier, and Rifenburgh, 1924). It thus appears that the phagocytic activities of the gastrodermis consume extra energy and that this energy is supplied by the oxidation of the fat reserves. During the later stages of digestion fat reappears in the phagocytic cells and increases to its former amount. The indications are that the protein of the food is transformed into fat, without the intervention of carbohydrate stages, and that this fat is stored in the gastrodermis as a reserve. Fat droplets also occur sparingly in the mesenchyme of planarians. As already noted, planarians cannot digest carbohydrates and no carbohydrate reserve (glycogen) has been detected in most species studied, although von Brand (1936) found 3 per cent by weight in *Planaria torva* in autumn, less in winter.

The available researches indicate, then, that in fresh-water planarians practically the entire processes of digestion, assimilation, and storage of food occur within the phagocytic cells of the intestine. Nothing is known of the manner in which the food reserves are transported to and utilized by other body tissues.

In those Turbellaria that swallow their food whole one infers that considerable digestion must take place in the lumen before phagocytosis can occur. Metschnikoff (1878) and Westblad (1922) claim that digestion is wholly extracellular in those rhabdocoels having a ciliated gastrodermis (Catenulida, Macrostomida). Westblad saw protein and fat particles undergo digestion in the intestinal lumen of *Stenostomum* while starch grains remained unaltered. However, Jacek (1916), also using *Stenostomum*, found that digestion is wholly intracellular and that protein particles (egg white) and oil droplets are digested in vacuoles in the gastrodermis; during protein digestion the vacuolar fluid changed from an acid to an alkaline reaction and protein was converted into and stored as fat. Starch grains were ejected unaltered. Some observations of the author confirm the occurrence of intracellular digestion in *Macrostomum*. It may be assumed that in rhabdocoels small enough particles are ingested at once by the gastrodermis whereas larger ones must first undergo some extracellular digestion. Extensive storage of glycogen in temnocephalids was reported by Fernando (1945). Nothing is known of digestive processes in polyclads, which, it may be recalled, also have a ciliated gastrodermis.

Defecation has been witnessed by several observers. The worm first takes in water through the pharynx, then by vigorous muscular contractions expels indigestible remnants. Those polyclads that possess them use the anal pores as well as the mouth for defecation.

i. Starvation.—The fresh-water planarians can endure prolonged starvation, from 6 to 14 months, depending on species (Schultz, 1904; Stoppenbrink, 1905; Berninger, 1911). During this time they may reduce to $\frac{1}{10}$ to $\frac{1}{13}$ the original length and $\frac{1}{300}$ of the original volume. This

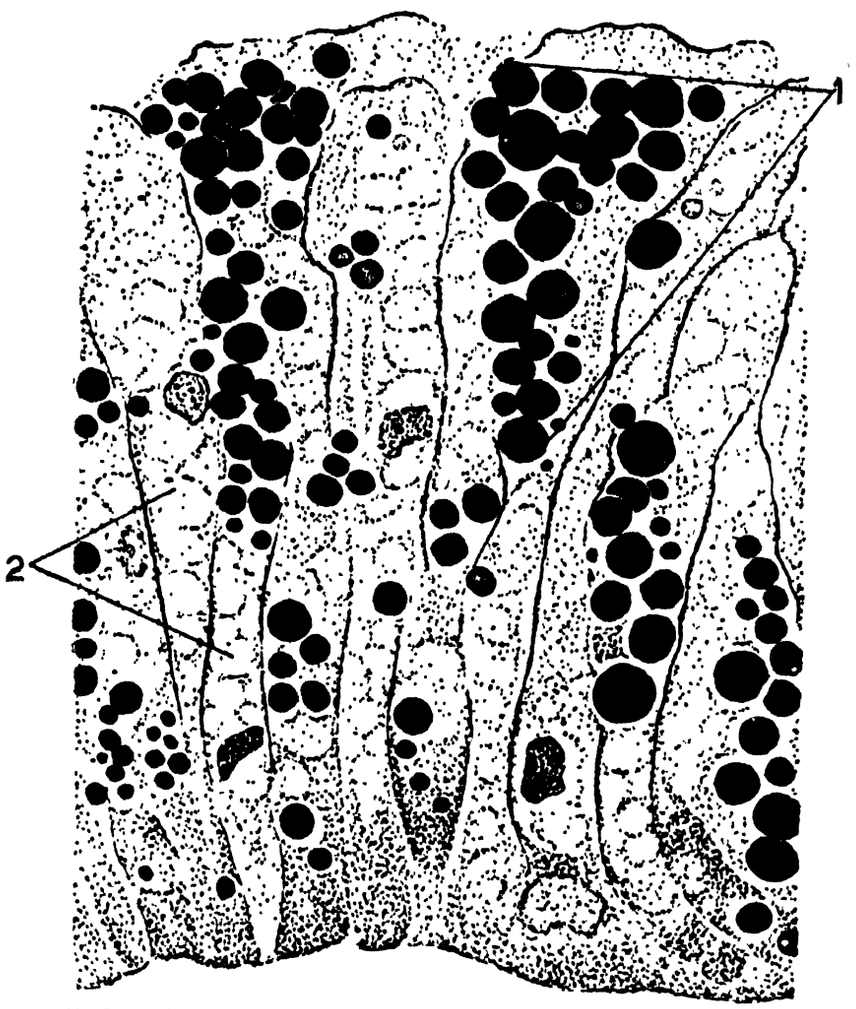

FIG. 78.—Intracellular digestion (continued). Gastrodermis of *Dugesia dorotocephala* 3 days after feeding beef liver; all food vacuoles have reached the stage of homogeneous eosinophilous balls (*after Willier, Hyman, and Rifenburgh*, 1925). 1, food ball; 2, fat vacuoles.

reduction results from tissue degeneration and does not involve any alteration of cell size. The nervous system undergoes no alteration so that greatly starved animals have disproportionately large heads. Epidermis and musculature are also practically unaltered, but the mesenchyme degenerates and disappears for the most part. The digestive system retains its form, and there appears to be no reduction in the number of diverticula, but the volume of the intestine is greatly diminished through degeneration of large numbers of the phagocytic cells. The gastrodermis loses food inclusions and reduces to a flattened syncytial state. In the later stages of starvation the fat stored in the phagocytic cells begins to be utilized but Willier, Hyman, and Rifenburgh

(1925) found that the surviving gastrodermis still contained considerable fat after 3 months' starvation in *D. dorotocephala*. However, the complete breakdown of most of the gastrodermis must furnish a large amount of fat and protein to the planarian. The greatest degeneration in starving worms is seen in the reproductive system. The copulatory apparatus, sex ducts, and yolk glands entirely disappear, and the gonads reduce to small clusters of cells. The oxygen consumption of planarians per unit weight declines during early starvation but rises continuously later, an indication that starvation in these worms acts as a rejuvenating factor (Hyman, 1919a, 1920).

The ability of other Turbellaria to endure prolonged starvation is not well known, but the smaller forms are probably able to survive for only short periods in the absence of food.

j. Respiration.—The Turbellaria are devoid of any special respiratory structures; the exchange of respiratory gases takes place by simple diffusion through the body surface. So far as known, respiration is of the ordinary aerobic type, comprising the intake of free oxygen and the emission of carbon dioxide. Exact measurements of respiratory rate have been made chiefly on fresh-water planarians. The rate of oxygen consumption of *Dugesia dorotocephala* is about 0.2 to 0.3 cc. per gram per hour in adult worms; the rate per unit weight is higher the smaller (younger) the worms, and is also increased by regeneration, during the early stages of intracellular digestion (see above), and during later stages of starvation (Hyman, 1919a, b, c, 1920; Hyman, Willier, and Rifenburgh, 1924). The oxygen consumed is also affected by the osmotic pressure of the medium as well as by the kind of salts in the medium (page 197; Buchanan, 1931; Hess, 1930). The rate of oxygen consumption of *Dugesia* species is constant at different oxygen concentrations in the water until this concentration falls below about one-third saturation (Hyman, 1929; Lund, 1921). The cutting of planarians into pieces accelerates the rate of oxygen consumption, and this increase is greater the smaller the pieces, i.e., if planarians are cut into six or eight pieces the rate of oxygen intake of the combined pieces is greater than that of intact worms (Hyman, 1923). This stimulatory effect of cutting declines with time and disappears within 24 hours. After allowance has been made for this effect, an axial series of pieces of *D. dorotocephala* shows an anteroposterior decline in rate of oxygen intake (Hyman, 1923), another expression of the axial gradation already mentioned several times.[1] Some

[1] The existence of such an axial gradient in respiratory rate in planarians has been disputed by others (e.g., Parker, 1929) for other species, but the author feels that in their experiments insufficient account was taken of the stimulating effect of section and of the sexual condition of the animals. Only nonsexual animals should be employed.

experiments on the carbon dioxide production of the polyclad *Stylochus ijimai* are also available (Watanabe and Child, 1933). Here, too, the rate of carbon dioxide production was found to decline with increasing size and to show an axial gradation in the form of a U, i.e., a decrease from the anterior end toward the middle and an increase again toward the posterior end. Unfortunately sexual worms were used, and as the reproductive system is not evenly distributed throughout the worm, a factor incapable of evaluation was present.

The oxygen consumption of planarians is depressed in the presence of potassium cyanide (Hyman, 1919d). It can be depressed as much as 90 per cent without injury to the worms. This indicates that the oxidative mechanism of planarians is chiefly of the cyanide-sensitive type, that it belongs to the "Warburg-Keilin" system, involving an iron-containing oxidase, a cytochrome complex, and a dehydrogenase. The dehydrogenase enzyme attacks the substance furnishing the energy, oxidizing it, and reducing the cytochrome complex which in turn becomes reoxidized by reducing the oxidase enzyme. The latter is restored by means of the free oxygen in the air or water, and so the system continues indefinitely as long as free oxygen is available (Commoner, 1940). Cyanide acts by preventing the oxidase from taking up free oxygen. The cyanide-stable respiration, which constitutes only a small part of the respiration of planarians, operates by way of enzymes other than oxidases.

k. Excretion.—Nothing whatever is known of the form in which turbellarians eliminate their nitrogenous wastes. From the fact cited above (page 205) that protein food is stored chiefly as fat in planarians, it seems evident that a process of deaminization must occur and hence that ammonia or some related substance must be given off. Several attempts have been made by use of vital dyes to determine what tissue is involved in elimination. Such experiments rest on analogy with conditions in vertebrates where it is known that vital dyes introduced into the body are treated like waste products and ejected by way of the kidneys.

When the Acoela (which have no protonephridial system) are exposed to vital dyes, the dyes collect in the central or digesting mesenchyme and are ejected through the mouth (Löhner, 1911). In triclads, also, the gastrodermis serves as the chief means of elimination of vital dyes (Westblad, 1922); the dye granules collect in mesenchymal vacuoles which are then passed to the intestine. In a number of kalyptorhynchid and typhloplanid rhabdocoels, also in *Stenostomum*, the dye collects in certain portions of the protonephridia, mostly the more proximal portions, and in the paranephrocytes (page 111) which also pass it into the protonephridia (Westblad, 1922; Reisinger, 1922, 1923), so that in these forms some evidence is available of an excretory function of the proto-

nephridia, aided by paranephrocytes. No evidence has been seen of any passage of substances through the flame bulbs in any turbellarian. It seems probable that in Turbellaria the necessity of eliminating nitrogenous wastes is avoided by converting them into insoluble granules ("concrements") that are held permanently in the mesenchyme and in pigment cells.

Regulation of water content is in all probability one of the chief functions of the protonephridial system and the only function of the flame bulbs. This view is supported by the fact that the protonephridia are much better developed in fresh-water than in marine Turbellaria. Atrophy of the protonephridium of *Stenostomum* is followed by edema and general degeneration (Hess, 1937). New flame bulbs were formed by the evagination of capillaries in response to the accumulation of water in the worm. In a comparison of specimens of *Gyratrix hermaphroditus* from fresh, brackish, and salt water, Kromhout (1943) noted a gradual reduction in the protonephridial system with increasing salinity of the medium. Probably influx of water into the turbellarian body evokes activity of the flame bulbs, resulting in a current of water along the protonephridial tubule.

l. Chemotaxis.—This was already discussed in connection with finding of food, which is in effect a chemotactic reaction. Experiments have also been performed on the behavior of planarians to chemical substances in capillary tubes placed in the same dish with them. Pearl (1903) tested in this manner various concentrations of several acids, alkalies, and salts, and found that in general a positive response is given to weak concentrations of all the substances tried, and a negative one to stronger concentrations. A positive reaction is the same as that toward food, i.e., the planarian on perceiving the diffusing chemical turns toward and then proceeds directly to the capillary. In the negative response, the animal turns away from the capillary. Weak acids proved especially attractive, and planarians would often grip the capillary and extend the pharynx into its orifice. Koehler (1932) also employed the capillary method, using snail blood or crushed planarians, and found highly positive responses in some species, which can be caused to follow such a capillary around. Reactive species will also take a median course between double capillaries. Planarians with one auricle removed may show "circus movement" in a dish of diluted snail blood, circling toward the intact side. By adding india ink to snail blood diffusing from a capillary, it can be seen that response occurs when the carbon particles have passed along the auricular sense groove.

m. Reactions to Contact; Thigmotaxis.—The reactions of fresh-water planarians to mechanical stimuli have been investigated in detail by Pearl (1903). To a light touch on the side of the head, the worm may

give a positive response, pausing, turning the raised head toward the stimulus, and moving to it. A similar stimulus along the body sides causes usually a small local contraction and may evoke the positive turning if not too far posterior. A positive reaction is never exhibited by postpharyngeal regions. Stronger tactile stimulation of the anterior end evokes the typical negative response, a turning of the head away from the stimulus and a gliding off in the new direction. Very strong or repeated prodding of the head causes jerking back by means of longitudinal contraction and turning through a larger angle. Moderate to strong mechanical stimulation of the sides of the body or the posterior region evokes local contraction and the hurried type of locomotion (page 199) for a short time, followed by the usual gliding.

If a planarian is cut in two, the anterior piece reacts as to strong posterior stimulation, i.e., moves by the hurried method for a short time, then returns to the usual gliding. The posterior piece generally crawls backward immediately after the cut and continues for some time to give this response to mechanical stimulation of the cut surface. To such stimulus elsewhere it gives either the negative turning away or the hurried crawling. A positive reaction to contact is not obtained in the absence of a brain.

The Turbellaria are markedly thigmotactic; the dorsal surface is negatively, the ventral surface positively thigmotactic. This is another way of saying that flatworms strive to keep their ventral surface in contact with a substratum, regardless of gravity, and their dorsal surface freely exposed to the medium. Pearl (1903) notes that if a light object is gently placed on the dorsal surface of a resting or moving planarian, the worm will promptly move away from under the object. Planarians will not come to rest in a situation where both surfaces are in contact. When placed on their backs, planarians, polyclads, and probably all flattened Turbellaria give a characteristic *righting reaction*. The worm twists into a spiral in such a way that the ventral surface of the head finally comes in contact with a substratum. The head then glides away and the spiral unwinds as the rest of the body follows. Planarians dropped through water (planarians cannot swim) give the righting reaction, usually several times, as they fall. Pieces of planarians also give the righting reaction although more slowly than when the head is present. Brainless pieces of polyclads also right themselves, but the reaction differs from the normal in that any part of the piece, not always the anterior end as in the case of intact worms, may attach first (Levetzow, 1936). However, this may also occur in pieces of planarians.

The entire body of planarians is sensitive to contact, but in general tangoreceptivity is highest on the auricles or sides of the head and decreases in an anteroposterior direction. In the absence of the brain,

the auricles are no longer more sensitive than other parts of the body margin (Koehler, 1932).

n. Phototaxis.—Although some Turbellaria are positive to light, especially pelagic types, larval and juvenile stages of polyclads, acoels, and rhabdocoels that contain holophytic symbionts, and the rhabdocoels of Lake Baikal (Nasonov, 1935), the members of the class as a whole avoid light and unless other factors are operative seek the darkest areas of their environment. Many studies have been made on the response of turbellarians, chiefly fresh-water planarians, to light (Parker and Burnett, 1900; Walter, 1907; Taliaferro, 1920; Erhardt, 1932; Lemke, 1935; Ullyott, 1936). Exposure to light increases the activity of planarians and causes resting individuals to start locomotion; the rate of locomotion may also be more rapid in the light (Pearl, 1903; Werner, 1926). This stimulating action of nondirective light has been termed *photokinesis*. After a time the effect decreases, and the worms slow down and finally come to rest in the least illuminated region of the container, if such exists. The avoidance of light by planarians is an example of a phobotactic or phobic response (P–C, page 67), that is, the darkened area is found by random movements, a negative reaction when passing into more lighted areas and a lack of reaction when passing into more darkened regions. The most careful test of the phobic nature of light avoidance in planarians is that of Ullyott (1936). In a light gradient in which all possibility of directed rays from reflections, etc., was avoided, the planarians eventually came to rest in the darker part of the gradient. This phobic response to light is given equally well by specimens from which the eyes have been removed; these also show no change in rate of locomotion. Decapitated specimens also avoid light, although they move more slowly. In most species light is perceived by the entire surface, although in some the posterior region shows no reaction to light (*Procotyla fluviatilis*, Lillie, 1901; *Bdelloura candida*, Walter, 1907; *Bipalium*, Kawaguti, 1932). Both dorsal and ventral surfaces are sensitive to light (Walter, 1907), although planarians tend to keep their dorsal surfaces toward the light (Bock, 1936).

Planarians perceive changes in light intensity and may give evidence of such perception by hesitation, head swingings, and change of path when encountering a new intensity. Various experiments that have been performed on the possibility of color perception by planarians are really tests of intensity discrimination according to the more critical papers (Erhardt, 1932; Lemke, 1935). On contrasting backgrounds of black and white or dark and light colors, planarians come to rest on the darker ground and in general on colors of longer wave lengths. Such reactions are probably merely avoidance of light of higher intensity. A very exact phobic reaction was reported by Lemke (1935) for *Dugesia*

lugubris on a background of alternate black and white circles; the planarian follows the black circles, turning back at the boundary with the white circles (Fig. 79). Eyeless specimens lose the reaction. Other species may not give such exact response to intensity boundaries and may in fact exhibit no change of behavior to considerable changes of intensity.

To directed light, planarians give a fairly precise negative response, turning away from the light and proceeding in a direction approximately opposite to the incidence of the light rays. The path of a planarian can therefore be directed by means of light rays. This phototopic reaction is mediated primarily by the eyes, for in worms from which the eyes have been removed (without injury to the brain) the response is much less definite and precise (Taliaferro, 1920), although still elicitable. If a spot of light is shone upon the eyes or head the negative turning away results, but if it is shone on middle or posterior regions there is no such response. Hence the topic reaction is mediated by the anterior end only, whereas the phobic response to light is mediated by the entire body in most species, with sensitivity decreasing in an anteroposterior direction. The sense organs responsible for the phobic reaction have not been identified, but the eyes are evidently the chief receptors for the topic response.

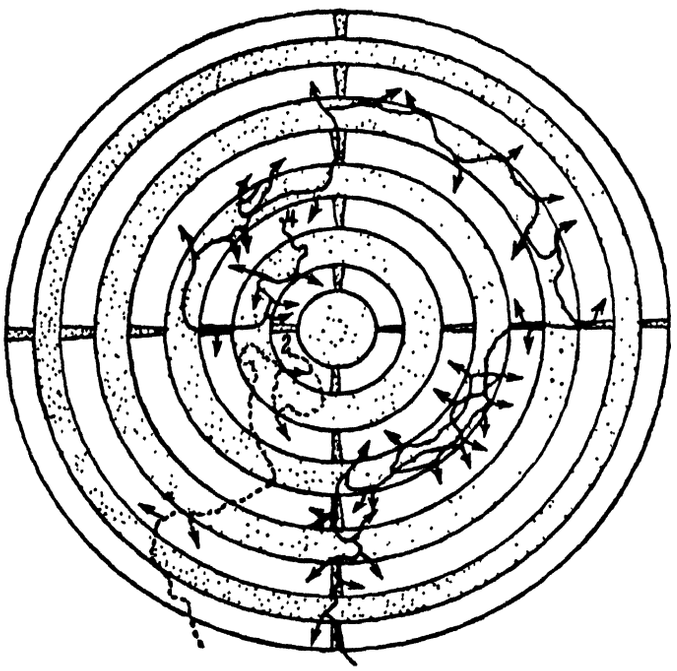

FIG. 79.—Reaction to light. Continuous line gives path of normal *Dugesia lugubris* on background of alternate white and black circles; worm gives avoiding reaction to white circles. Broken line gives path of individual of which the eyes have been extirpated. (*After Lemke*, 1935.)

According to the generally accepted analysis of Taliaferro (1920), directed light affects only those retinal cells whose long axes are parallel to the light rays. Because of the curvature of the planarian eye, only a few such cells would be affected in any given position of the planarian. The pigment cup also acts to shade retinal cells except those parallel to the light rays. This mechanism accounts for the highly directive effect of light on planarians, i.e., their ability to perceive rather exactly the direction of light, and it also makes it rather probable that planarians can see movement, although not objects. The decrease in intensity of light as a moving object interrupts light rays would affect a succession of retinal cells. Probably perception of movement is the function of

the numerous eyes of land planarians and polyclads since a moving decrease of intensity would affect successive eyes rather than successive retinal cells of the same eye. According to Kawaguti (1932) the rear part of *Bipalium* is insensitive to light because it lacks eyespots.

Planarians can perceive ultraviolet radiations; they react negatively to them but move more slowly than in visible light (Werner, 1926). The behavior is the same in normal and eyeless specimens. Short exposures to ultraviolet and to direct sunlight are fatal to planarians (Merker and Gilbert, 1932). White species appear to be more sensitive to sunlight than colored ones.

Some data are available on the behavior to light of cave planarians that live in perpetual darknesss. *Sphalloplana percoeca* from Kentucky caves showed no avoidance of light or seeking of dark areas but would writhe on exposure to direct sunlight and might be killed by less than 2 minutes of such exposure (Buchanan, 1936). *Phagocata subterrannea* from an Indiana cave, however, was negative to light but less exact and more given to wandering than epigean species (Walter, 1907). Whether this different behavior is correlated with the fact that the first species is eyeless and the second has eyes cannot be stated.

o. Rheotaxis.—In general fresh-water turbellarians inhabiting still waters fail to react to water currents. Strong currents usually elicit only a "clamping" reaction, contraction and increased adhesion to the substratum. Weak currents may, however, call forth a positive rheotactic response, a turning of the anterior end toward the current and placing of the body in line with it. This has been reported for planarians (Pearl, 1903) and the rhabdocoel *Bothromestoma* (Müller, 1936). In the latter animal, extirpation experiments indicated that the eight groups of sensory bristles along the lateral body grooves are rheoceptors (page 93). The reaction of still-water species to *weak* currents is probably part of the food-catching mechanism, since turbellarians are able to detect the presence of intact prey by water disturbances created by them. Pond planarians may develop a rheotactic response after being kept for some time in a rather strong water current (Koehler, 1932). Planarians that habitually live in flowing water usually exhibit a positive rheotaxis, for obviously without such a reaction they could not maintain themselves in their habitat. Thus, *Dugesia dorotocephala,* a spring-dwelling species, was found to show positive rheotaxis (traveling upstream) in nature and in the laboratory (Allen, 1915); but the positive reaction could be altered to a negative one (traveling downstream) by change of water or lowering the temperature. The outstanding example of a positively rheotactic planarian is *Crenobia alpina,* inhabitant of rapid alpine streams. As already noted, this animal is more or less incapable of finding food in the absence of a water current. It is highly positive to currents and will

follow a tube from which a water current is issuing. In case of two currents of equal velocity opposite or at right angles to each other, it will take a resultant path between them, and of two currents of unequal velocity it will select the faster one (Koehler, 1932). The rheotactic reaction is given by all parts of the body, although most readily and to weaker currents by the head. Loss of the entire body margin does not eliminate the reaction so that rheoreceptors must be distributed over the entire body surface being, however, most numerous on the head. After being kept for long periods (6 months to a year) in still water this species retains its rheotactic response undiminished (Koehler, 1932). Beauchamp (1933) worked with a British stream planarian[1] in which the rheotactic response showed a definite seasonal cycle. In winter when temperatures were low and the reproductive system developing, the animal was positively rheotactic and accumulated at the head of hill streams; after the breeding season, negative rheotaxis ensued and the worms traveled downstream and even into the lake into which the streams flow.

p. Thermotaxis and Temperature Relations.—The majority of the Turbellaria are undoubtedly eurythermous, enduring wide ranges of temperature, but some species appear to be somewhat stenothermous. The behavior to temperature changes is considerably dependent on the temperature at which the worms had been living prior to the tests. Available data are limited to fresh-water planarians (Mast, 1903; Koehler, 1932). For local application of temperature change, a narrow hairpin-shaped tube is used through which water of the desired temperature is circulated. Planarians react to temperature change of 2 to 3°C. from that at which they have been living. To moderate increase applied to the anterior end a positive reaction may be given at first; the worm turns toward the tube and may test it with the anterior end, before turning away. Usually a negative reaction is eventually given. If the tube is very hot, a negative reaction may occur at once. Reactions to lowered temperatures are similar but less definite, and often no reaction is given. Localized heat applied to posterior regions results in local contraction, more rapid gliding away, or the hurried type of crawling. The lower limit of reaction to increased temperature was found by Koehler to be 24°C. for the anterior end of *Crenobia alpina*, 32 for its posterior part, 28 to 30 and 40, respectively, for *Dugesia lugubris*. The ventral surface of planarians is also sensitive to temperature, so that thermal perception is evidently distributed over the whole body. When placed in a temperature gradient, *D. dorotocephala* which had been living at 22°C. aggregated in a zone ranging from 17 to 26 (Mast, 1903); *Phagocata gracilis* aggregated at 0 to 10°C., whether taken directly from its natural

[1] Said to be *Crenobia alpina* but this seems improbable.

habitat at 9.5°C. or kept for a month in the laboratory at 20 to 22°C. (Eddy and Gleim, 1932). The thermal death point of the former species is about 42°C., of the latter 30°C.

The most interesting behavior to temperature is that of *Crenobia alpina*. This animal when presented with two streams of different temperature selects the cooler one and follows this about, being able to distinguish a difference of 3°C.

Planarians possess a high capacity for acclimation to temperature, being able when kept at high temperature (27 to 30°C.) to lower their rate of metabolic activity below and when kept at low temperature (8 to 10°C.) to raise it above that expected for such temperatures (Behre, 1918).

q. Geotaxis.—The Turbellaria in general show perception of gravity for when the oxygen supply of the medium decreases below requirements they come to the surface, i.e., exhibit negative geotaxis. This is not a response to an oxygen or other gradient for it is given by worms in a closed vessel completely filled with water of uniform constitution and turned upside down. Unfed planarians in water of good oxygen content in the dark tend to seek the bottom of the vessel, but after feeding they tend to come to the surface (Olmsted, 1917) probably because of the increased oxygen demand during intracellular digestion. The outstanding example of geotactic response among Turbellaria is seen in the acoel *Convoluta roscoffensis* (Bohn and Drzewina, 1928; Fraenkel, 1929). This animal is negatively geotactic when undisturbed, positively so when disturbed. On the sandy tidal zone on the channel coast of France, where it lives in countless numbers, it comes to the surface of the sand at low tide, and disappears into the sand when the tide returns or on any other disturbance. This rhythmic geotactic behavior with reference to the tides is retained for about a week by *Convoluta* when kept in the laboratory in vessels of still water (Martin, 1907; Bohn and Drzewina, 1928). It is independent of day and night. That the tidal response is really a geotactic one was proved by Fraenkel (1929) who showed that when *Convoluta* is simultaneously exposed to centrifugal force and gravitation it takes a resultant path between the two forces.

Although Turbellaria without statocysts react to gravity, it appears that the statocyst is of some importance in the geotactic reactions of the Acoela. The anterior tip of *Convoluta*, which contains the statocyst, reacts normally to gravity, but the rest of the body has lost the geotactic response. In regeneration experiments on Acoela it has been noticed that pieces without the statocyst have difficulty in righting themselves and in general react poorly to stimuli (Peebles, 1913; Keil, 1929).

r. Galvanotaxis.—The reaction of turbellarians to the direct constant electric current has been ascertained by a number of workers. All

forms tested are cathodic, i.e., they turn their anterior ends toward the cathode and may swim or crawl toward this pole. *Stenostomum* (Pearl, 1903) in an electric current behaves exactly like ciliate Protozoa and its cilia also beat with reference to anode and cathode as in ciliates (P–C, page 68). *Convoluta* is highly cathodic (Bohn and Drzewina, 1928). Fresh-water planarians turn the anterior toward the cathode and may place the body in line with the current and proceed toward the cathode (Pearl, 1903; Alverdes, 1922; Hyman, 1932), or the body may curve into a C-, U-, or W-shape with ends and often ventral surface facing the cathode (Hyman and Bellamy, 1922; Robertson, 1927; Hyman, 1932). This cathodic orientation of posterior as well as anterior end may be attributed to the presence in such species of a fission region or some region of especial activity, such as an adhesive area, in the posterior part of the animal. Decapitated planarians show the same response as entire ones, and middle pieces move anterior end first to the cathode or backward to the anode. The land planarian *Bipalium* is likewise cathodic, moving by loops to the cathode, and pieces obtained by cutting the body in thirds also loop to the cathode. The one polyclad tested (Hyman and Bellamy, 1922) behaved like planarians, turning toward the cathode and usually also curving its body into a U-shape toward this pole.

The various explanations of galvanotaxis that have been advanced are based chiefly on the idea of a compulsory effect of the current directly on the ciliary or neuromuscular mechanism. This type of explanation appears unsatisfactory to the author, for it fails to explain reversals that occur under different physiological conditions. It can hardly be supposed that the neuromuscular mechanism also undergoes reversal during temporary changes of conditions. The fact that individuals facing the anode at the time the current is made also turn and proceed to the cathode is further difficult to explain on any such theory. According to the author's theory of galvanotaxis (Hyman, 1918, 1932; Hyman and Bellamy, 1922) also expressed independently by Robertson (1927), the flatworm takes that position with reference to the electric current which best corresponds with its own electrical currents. For at least the lower animals, as has been shown by numerous experiments (for flatworms, see Hyman and Bellamy, 1922), have inherent electrical currents related to their anteroposterior axiation. These currents presumably originate from different rates of chemical activity along this axis. In general, the anterior or head end is electropositive to lower levels, and hence it orients so as to face the cathode. The rear end of flatworms through the presence of a fission plane or other active region may also be electropositive with reference to the middle; hence the C or U attitude taken by such species in the current.

s. Desiccation.—The Turbellaria have no surface protection against evaporation and hence require an aquatic or humid environment. Some species secrete a mucous cyst or covering when exposed to desiccation and some land planarians can endure relatively dry environments as the South American pampas by habitually dwelling under cattle dung. In general, however, exposure to desiccation results in death. Freshwater planarians when subjected to drying curl up so as to expose as little surface as possible (Pearl, 1903) and from time to time attempt to escape by extending the head in seeking movements or giving backward crawling waves but are unable to progress on a dry surface. When placed on a wet spot in a dry environment they give a phobic reaction whenever the head extends outside the wet spot. The land planarian *Bipalium* was found by Kawaguti (1932) to lose water according to the simple laws of evaporation in relation to the humidity and temperature of the environment. Water was lost even in an atmosphere of 100 per cent humidity. Recovery occurred if the water loss did not exceed 45 per cent of the fresh weight.

t. Mass Protection.—Following the discovery by Bohn and Drzewina (1920) that a number of *Convoluta* are more resistant to fresh water or much diluted sea water than single specimens in the same (limited) volume of fluid, much work was done by these authors and also by Allee and his students (reviews in Bohn and Drzewina, 1928, and Allee, 1931) on such mass protection in various turbellarians (and other animals) against adverse conditions and agents, such as toxic chemicals, ultraviolet radiation, salinity changes. In general, resistance to such agents and conditions is much greater when there are a number of individuals as contrasted with single or a few individuals in the same quantity of medium. The protection is not caused primarily by the fact that, in the case of a toxic chemical, for instance, there is less of the chemical per worm in the mass experiment, but it does result from the greater quantity of animal in a limited amount of medium. The French authors postulate the secretion under these conditions of a special protective substance of which of course more would be emitted by the larger number of animals, but the experiments of Allee indicate rather that the normal secretions and exudates of the animals furnish the protective materials. Protective action is furnished by disintegrated animals or the water in which the same or other animals had lived. In the case of turbellarians the mucous and other glandular secretions emitted from the surface are probably the chief means of protection. Such secretions, exudates, or disintegrated remains neutralize toxic chemicals and, in some unknown way, probably not by adding salts to the medium, also protect marine turbellarians against fresh water.

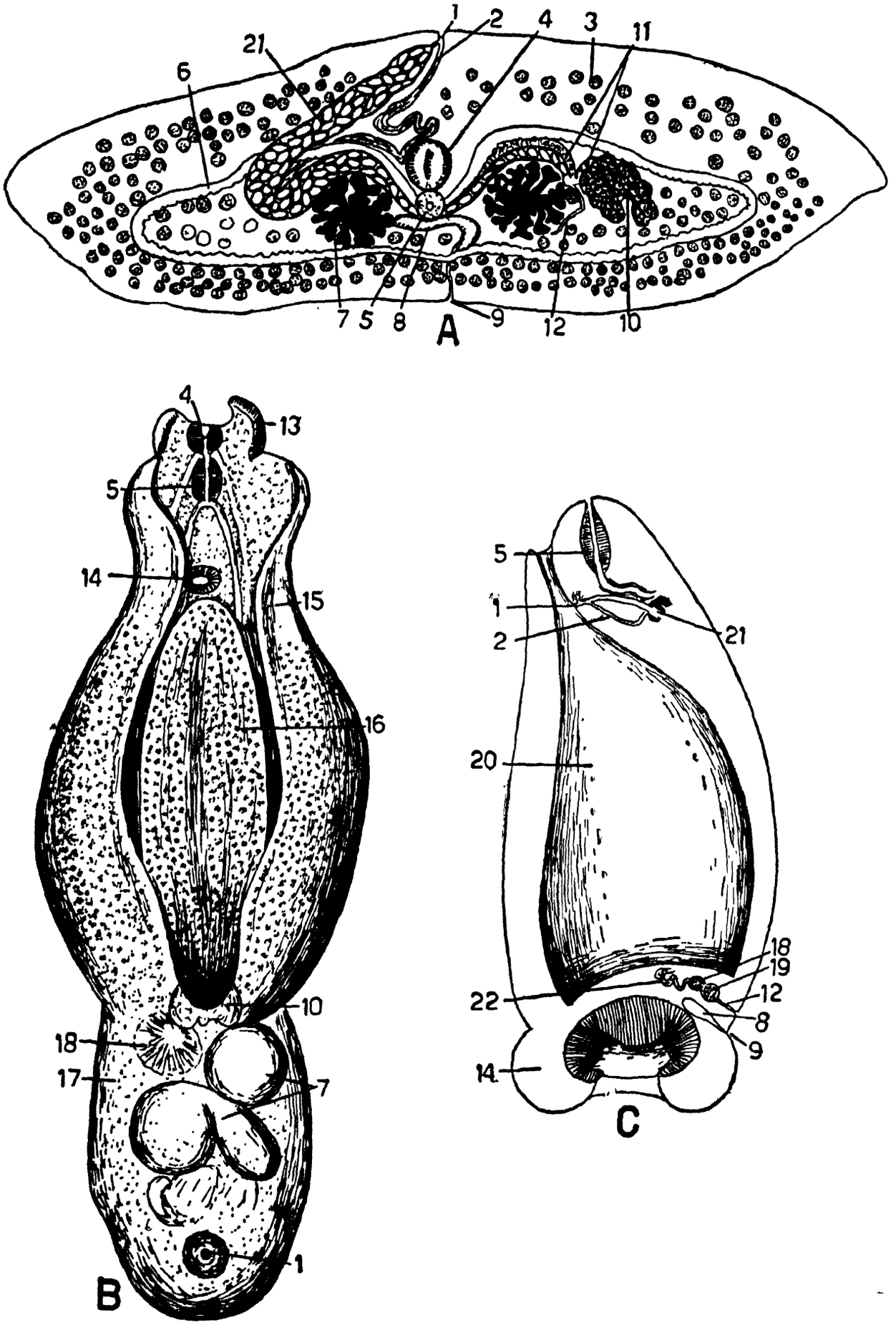

FIG. 80.—Variants of trematode shape. *A. Transversotrema* (*after Witenberg*, 1944), fish trematode from the Red Sea. *B.* Strigeid fluke *Alaria alata* (*after Krause*, 1915). *C.* Longitudinal section of the amphistome fluke *Gastrothylax* (*after Fischoeder*, 1903), showing deep ventral pit. 1, gonopore; 2, sperm duct; 3, yolk glands; 4, oral sucker; 5, pharynx; 6, intestine; 7, testis; 8, excretory bladder; 9, nephridiopore; 10, ovary, 11; yolk ducts; 12, Laurer's canal; 13, lateral suckers; 14, acetabulum; 15, forebody; 16, holdfast; 17, hindbody; 18, ootype; 19, seminal receptacle; 20, ventral pit; 21, uterus; 22, beginning of uterus.

u. Learning.—The Turbellaria are capable of associative memory. *Stenostomum* can be trained to turn back into the dark at a light-dark boundary if punished by an electric shock when entering the light area (Soest, 1937). As *Stenostomum* is negative to light only a very weak light to which it does not react can be employed. The reverse experiment, training it to avoid the dark and remain in the light, requires longer training and gives a less definite result. Retention is poor. Similar experiments have been performed with the fresh-water planarian *Dugesia gonocephala* (Dilk, 1937), using shaking and electric shock as punishments, and rough versus smooth substratum, weak light versus darkness, and vertical versus horizontal surfaces as contrasting conditions. In general, the planarian could be taught by repeated punishment to avoid that condition to which it normally gives a negative response, as light and rough substratum, i.e., to turn back at the boundary in the absence of punishment, but the reverse attempt, to teach it to turn back into conditions that it normally avoids, gave poor or no results. The experiments of Soest and Dilk came from the same laboratory as the experiments with the formation of associations in Protozoa reported in P–C (page 181). Much more convincing is the work of Hovey (1929) on the formation of an association in a leptoplanid polyclad. These worms were subjected for hours to alternating periods of light lasting 5 minutes and darkness lasting 30 minutes. Light induces movement, darkness a quiescent state as is general in Turbellaria. Whenever a worm started to move on exposure to light it was stopped by being touched on the anterior margin. The number of touches required to cause the worms to cease movement in the light decreased notably with repeated trials although no worm learned to remain entirely motionless when exposed to light. Possibility of motor fatigue, injury to the anterior margin, or adaptation to light was ruled out. Following extirpation of the cerebral ganglia, worms did not learn to move less in the light, and repeated hindrance to such movement had no effect. Evidently the brain is involved in associative learning in polyclads.

V. CLASS TREMATODA

1. Definition.—The Trematoda are ecto- or entoparasitic Platyhelminthes with a digestive system but without an epidermis, being covered externally by a cuticle devoid of cilia and resting directly on the mesenchyme.

The class name refers to the cavity of the suckers (Greek, *trema*, a hole) with which most members are provided as adhesive organs. The trematodes are commonly known as *flukes*, apparently from the Anglo-Saxon *flok*, referring to the flat shape. The class is divided into three orders (considered subclasses by some) to which it is constantly neces-

sary to refer: the Monogenea or Heterocotylea, the monogenetic trematodes, chiefly ectoparasitic and with simple life histories; the Aspidobothria or Aspidocotylea, mostly entoparasitic and with simple cycles; and the Digenea or Malacocotylea, the digenetic trematodes, entoparasitic and with complicated life cycles, involving two to four hosts.

2. External Characters.—The trematodes are commonly of short to elongated oval form (Fig. 82*A*), but a few are rounded or disk-like, one or

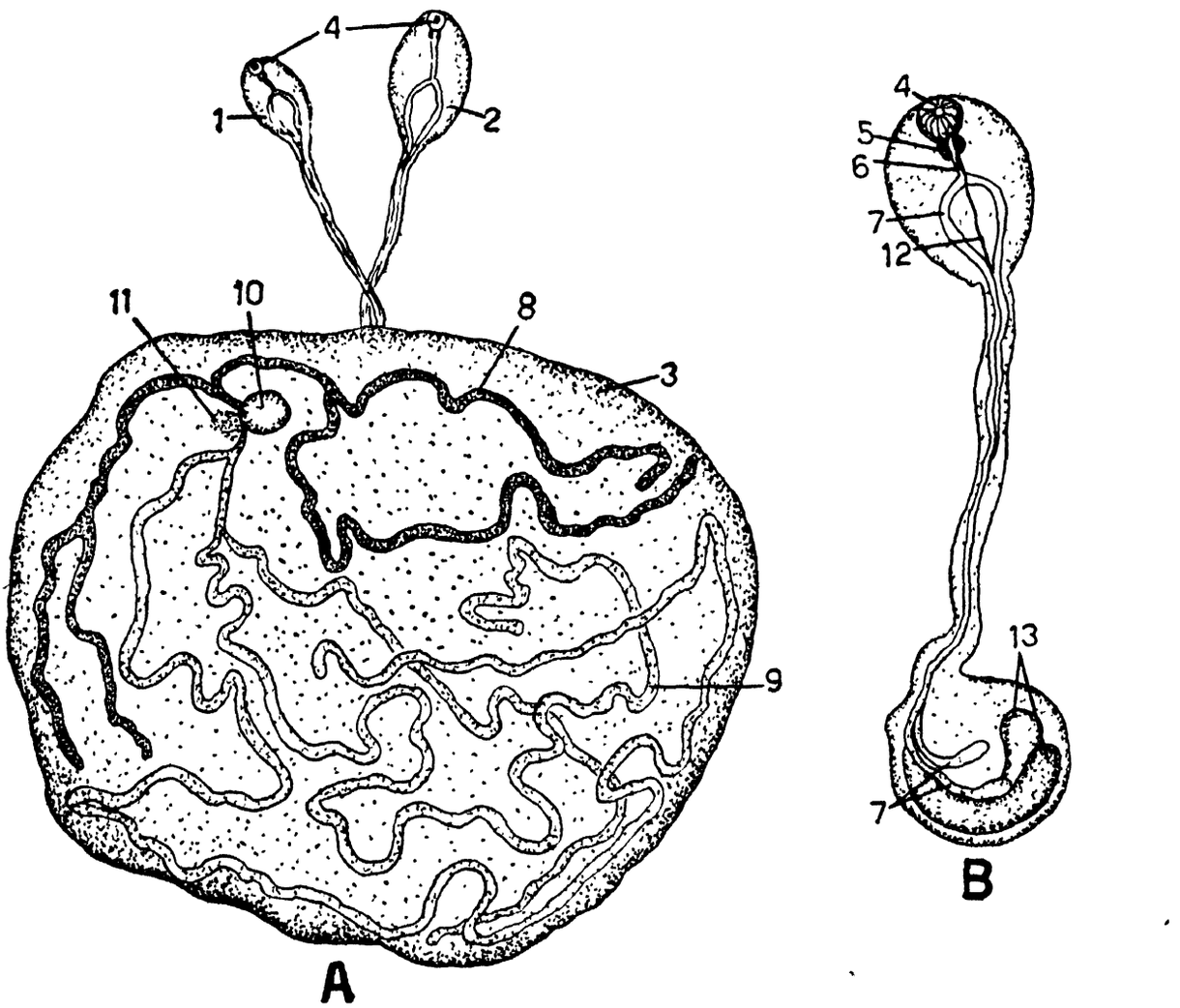

FIG. 81.—Peculiar trematodes (continued). *A*. Didymozoonid fluke *Wedlia* (*after Ishii*, 1935), showing female body with male and female forebodies protruding from the female hindbody. *B*. Male removed from depression in female hindbody. 1, male forebody; 2, female forebody; 3, female hindbody; 4, oral sucker; 5, pharynx; 6, esophagus; 7, intestine; 8, ovary; 9, yolk gland; 10, seminal receptacle; 11, ootype; 12, sperm duct; 13, testes.

two are broader than long (Fig. 80*A*), and the blood-inhabiting flukes tend to be slender (Fig. 123). The body usually tapers to the anterior end, which is not marked off as a head. The flukes are mostly much flattened dorsoventrally with flat ventral and convex dorsal surfaces, but some are rounded in cross section. Peculiar shapes obtain in the digenetic families Strigeidae in which the body is divided into the flattened, concave, or cup-like *forebody*, bearing the adhesive organs, and the narrower, cylindroid *hindbody* (Fig. 80*B*); and the Didymozoonidae, some members of which have a slender forebody and a rounded sac-like

hindbody (Fig. 81*A*). A few Digenea are dioecious, and in these the males and females differ in size, shape, and general appearance (Fig. 123*D*). The trematodes are mostly of small, even minute, size, ranging usually between 0.5 and 10 mm. in length, but some Digenea are larger, 1 or 2 to several cm. long. The body is usually colorless or slightly tinted, although parts of the reproductive system may be dark or the intestine may be colored by food.

The adhesive organs furnish the most striking external feature and as in the Turbellaria vary from glandulo-muscular disks, projections and pits to true suckers. The true sucker or *acetabulum*, highly characteristic of the trematodes, is a bowl-shaped depression set off or not by a constriction and separated internally from body tissues by a muscular stratum paralleling the concavity of the bowl (Fig. 82*C*). The sucker is highly muscular (Fig. 82*C*) and although usually provided with adhesive glands works primarily on the vacuum principle. The adhesive organs reach their highest and most varied development in the Monogenea which are usually also provided with claws and hooks for attachment. In the Monogenea, adhesive structures occur at both body ends and for them Dawes (1946) has suggested the useful terms *prohaptor* and *opisthaptor*. The mouth of the Monogenea is seldom encircled by a sucker, but instead the prohaptor consists of a pair of adhesive areas, disks, pits, or suckers. The principal clinging structure is the opisthaptor at the posterior end, consisting in its original form as seen in the Gyrodactylidae of an adhesive disk bearing two or four large hooks or claws (anchors), usually accompanied by smaller hooks (Fig. 83*A*). Next the disk alters more or less into a large circular sucker often divided by radial ridges into several sucking depressions (*Monocotyle*, *Tristoma*, Figs. 83*B*, 93*A*). This condition leads to the complete division of the originally single disk into a number of separate suckers, often six in a circle as in *Polystoma* (Fig. 94*A*) or eight bilaterally arranged (*Octocotyle*, *Diplozoon*, Fig. 93*C*) or six larger ones and two small ones on a terminal appendage (*Rajonchocotyle*, Fig. 83*C*) or two lateral suckers (*Sphyranura*, Fig. 93*B*). Another line of development is seen in *Microcotyle* (Fig. 84*B*) and *Axine* where the margin of the expanded rear is provided with a row of numerous (to 240) minute suckers resembling clamps. The suckers of the Monogenea are usually accompanied by hooks and are often supported by a complicated cuticularized framework (Fig. 83*C*).

The Aspidobothria have a characteristic adhesive organ in the form of a large oval to circular sucker divided by cross and longitudinal ridges into three or four longitudinal rows of depressions (Fig. 84*A*). An oral sucker is usually absent.

The adhesive apparatus of the Digenea is less developed than in the preceding orders, lacks hooks and spines, and commonly consists of two

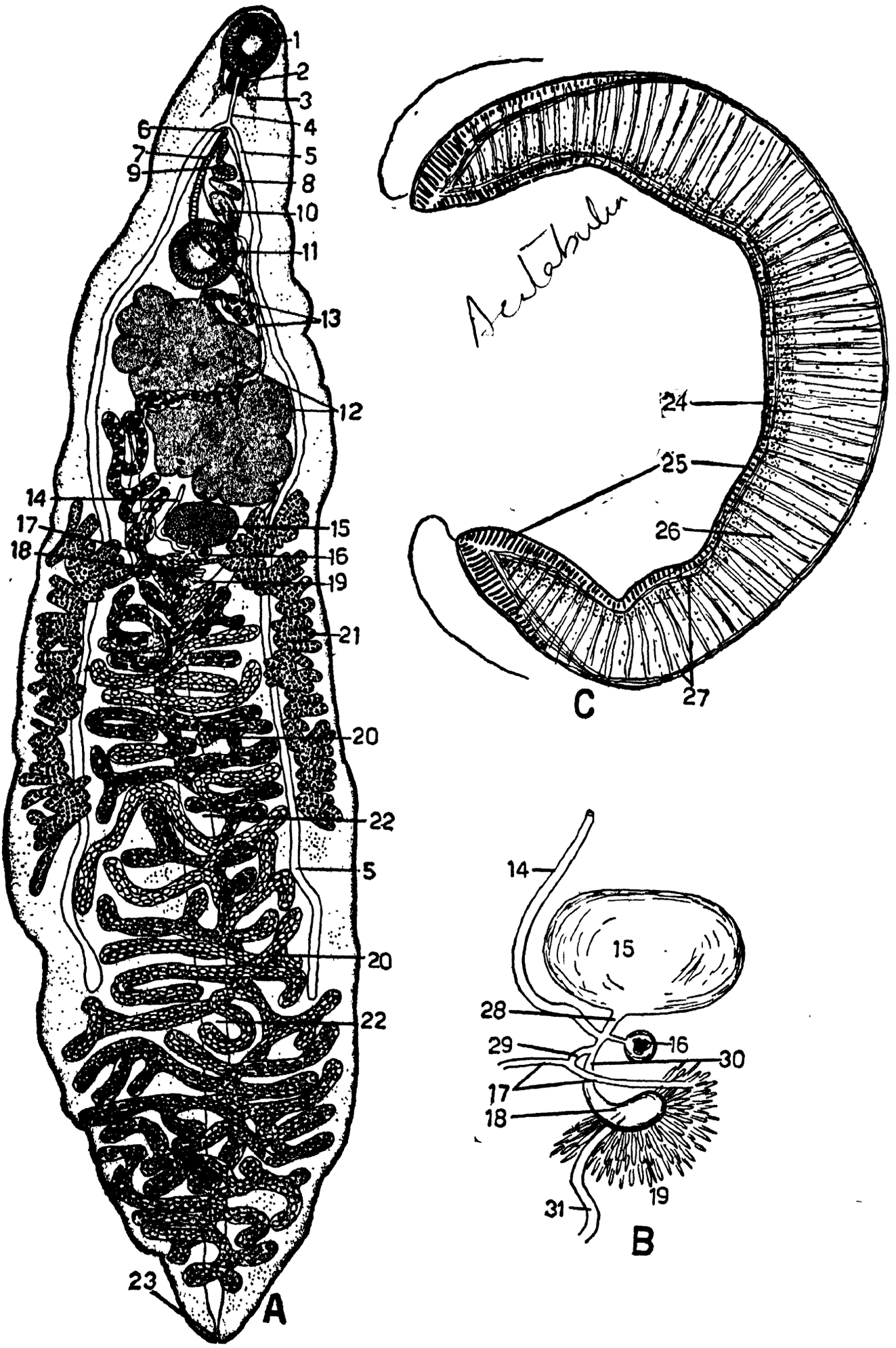

FIG. 82.—Trematode structure. *A*. A typical distome fluke, *Dicrocoelium dendriticum* showing general structure of the Digenea (*after Neuhaus*, 1938). *B*. Details of the female apparatus of the same. *C*. Structure of an acetabulum (*after Näsmark*, 1937). 1, oral

suckers (either or both of which may be absent), an anterior or *oral* sucker encircling the mouth, and a ventral or posterior sucker, usually called the *acetabulum*, on the ventral surface (Fig. 82*A*). In the family Bucephalidae (= Gasterostomidae), the mouth occurs in the middle of the ventral surface (Fig. 84*C*) and lacks a sucker, as the anterior sucker retains its position at the anterior end. The acetabulum is a typical bowl-like sucker and may attain a very large size. The position and presence and absence of the acetabulum formerly served as a family character and still furnish convenient descriptive terms. Thus digenetic flukes with the acetabulum at or near the posterior end, probably the original location, are termed *amphistomes* and constitute the family Paramphistomidae (Fig. 107). Those in which the acetabulum has the usual position near or anterior to the middle of the ventral surface, often quite close to the oral sucker, are called *distomes* (Fig. 82*A*) and constituted the old family Distomidae, now scattered among many families. In a number of cases, the acetabulum has been secondarily lost; and such flukes, having only an oral sucker, are referred to as *monostomes*, although this character does not indicate relationship (Fig. 87*C*). Flukes that occupy very sheltered positions as blood flukes tend to have weak suckers or none at all (*Sanguinicola*, Fig. 123*A*). In the distome family Echinostomidae, the *echinostomes*, the anterior end bears a collar-like ridge edged with a single or double row of thorns (Fig. 119*A*). The family Rhopalidae can protrude two spiny processes at the anterior end. In the curious family Strigeidae, also called *holostomes*, the modified forebody already mentioned bears besides the usual two suckers a large adhesive organ of varied shape, the *holdfast*, situated behind the acetabulum (Figs. 119, 120).

The mouth of the trematodes is usually situated at or near the anterior end except in the Bucephalidae as noted above. The common gonopore, although often not far behind the mouth, may have almost any other location on the ventral surface or may be located laterally or even dorsally.

3. Cuticle.—The trematodes lack an epidermis and are clothed instead with a resistant cuticle (Fig. 85). The homology and origin of this cuticle have been long disputed, and several theories have been advanced: (1) that the cuticle is an altered and degenerated epidermis; (2) that it is the basement membrane of the former epidermis; (3) that it is the outer layer of an insunk epidermis, the cells and nuclei of which have sunk beneath the subcuticular musculature; (4) that the cells in

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sucker; 2, pharynx; 3, brain; 4, esophagus; 5, intestinal crura; 6, gonopore; 7, uterus; 8, cirrus sac; 9, cirrus; 10, seminal vesicle; 11, acetabulum; 12, testes; 13, sperm ducts; 14, Laurer's canal; 15, ovary; 16, seminal receptacle; 17, yolk ducts; 18, ootype; 19, Mehlis's glands; 20, coils of uterus; 21, yolk glands; 22, bladder; 23, nephridiopore; 24, cuticle; 25, circular muscles; 26, radial muscles; 27, longitudinal muscles; 28, oviduct; 29, common yolk duct; 30, ovovitelline duct; 31, beginning of uterus.

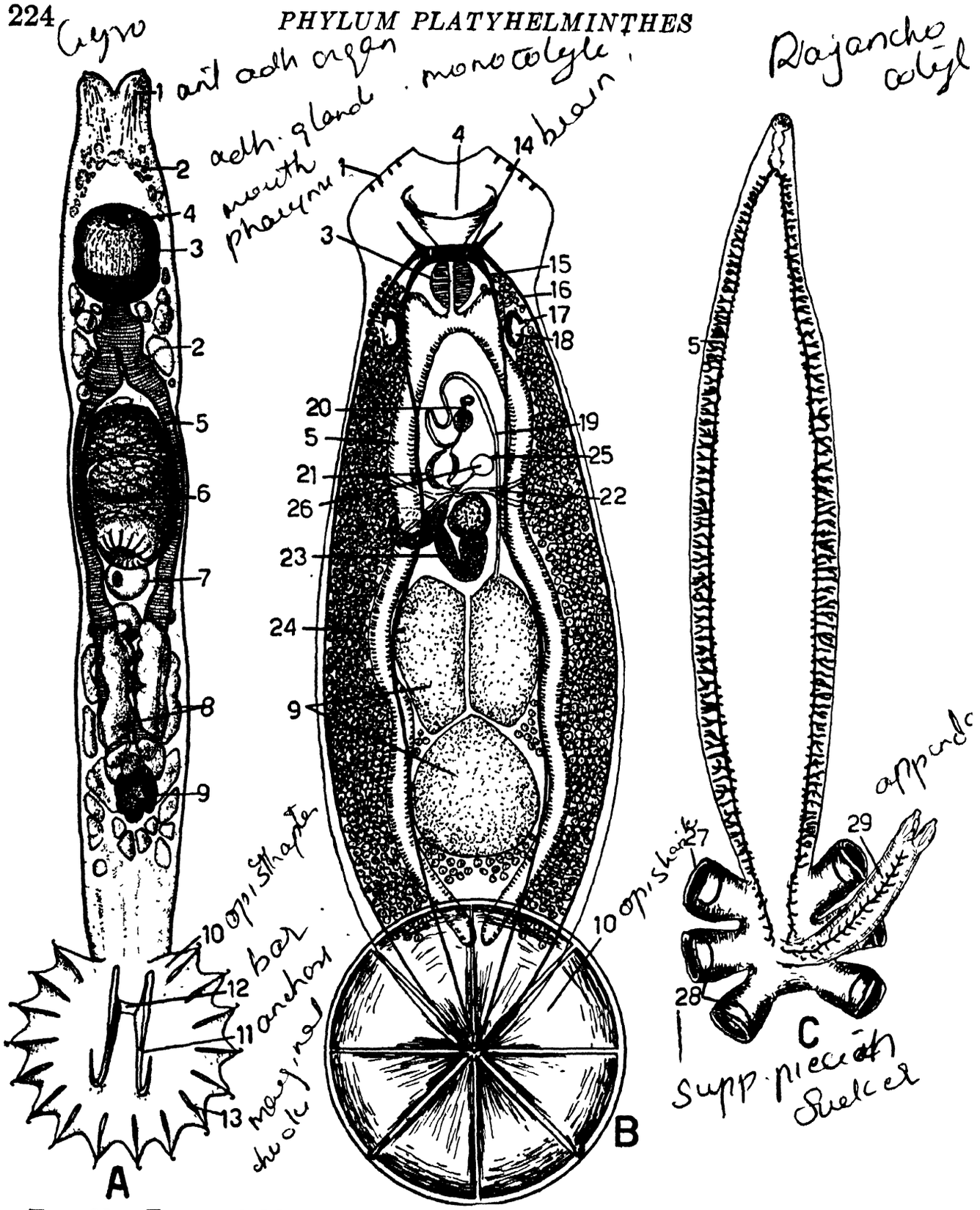

FIG. 83.—Types of Monogenea, showing especially various kinds of haptors. *A. Gyrodactylus* (*after Mueller and Van Cleave*, 1932). *B. Monocotyle* (*after Goto*, 1894). *C. Rajonchocotyle*, from a skate, from life, Pudget Sound. 1, anterior adhesive organ; 2, adhesive glands; 3, pharynx; 4, mouth; 5, intestine; 6, embryo; 7, uncleaved egg; 8, ovary; 9, testis; 10, opisthaptor; 11, anchors; 12, bar; 13, marginal hooks; 14, brain; 15, ventral nerve cords; 16, lateral nerve cords; 17, nephridiopore; 18, bladder; 19, sperm duct; 20, penis; 21, uterus; 22, yolk ducts; 23, ovary; 24, yolk glands; 25, copulation canal; 26, seminal receptacle; 27, suckers; 28, supporting piece in suckers; 29, appendage.

question are not epidermal but are mesenchymal (parenchymal) cells that secrete the cuticle; and (5) that the cuticle is secreted by the ordinary mesenchyme, not by special cells. Theories 1 and 2 have been discarded and seem to be definitely erroneous. Theory 3 has received much acceptance since the work of Hein (1904), who confirmed previous investigators

that in many adult Digenea there exist beneath the musculature clusters of gland-like cells that send processes to the cuticle and seem to be secreting it (Fig. 85). However, the question obviously cannot be settled by study of adult flukes, and therefore Roewer (1906) undertook to shed light on the matter by a study of cercarial development. He found that in early stages the cercaria forms an epidermis by the same process as does the miracidium, i.e., by the separation of surface cells from the general mass, but that this epidermis later degenerates and is absorbed and the definitive cuticle is secreted by cells that differentiate in the general interior mass of the embryo. Further, cells supposed to be insunk epidermal cells are wanting in some flukes, especially Monogenea. Therefore theories 4 and 5 are the most acceptable, i.e., that the cuticle is a mesenchymal secretion, either of special cells or of the general mesenchyme. The chemical nature of the cuticle appears not to have been investigated, but doubtless the cuticle is a scleroprotein; it is definitely not chitinous.

The cuticle is thin and usually smooth in the Monogenea except for the hooks, spines, and supports of the adhesive apparatus which are of the same composition as the cuticle. In the Digenea, the cuticle is thicker and often bears minute spines, scales, or bristles that clothe the body in whole or part.

4. Musculature.—Beneath the cuticle occurs a typical muscle sheath like that of the Turbellaria, which may be termed the subcuticular musculature. It consists usually of an outer circular, middle longitudinal, and inner diagonal layer (Fig. 85); or the diagonal layer may lie between the other two, as in most Monogenea. The musculature is very weak in some forms, well-developed and even strengthened by additional layers, in others. The parenchymal musculature is usually poorly developed except for dorsoventral strands in lateral regions. Special muscle bands operate the hooks of the Monogenea. The musculature of the suckers derived from the subcuticular musculature consists chiefly of powerful bundles of radial fibers that give the sucker a striated appearance; in addition circular and longitudinal layers occur next to both inner and outer walls (Fig. 82*C*). The muscles are elongated fibrils with a persistent myoblast which may be connected to several fibrils by strands.

5. Mesenchyme and Gland Cells.—The mesenchyme or parenchyma consists in the Monogenea of discrete cells closely packed together; or sometimes the central mesenchyme has this structure while the peripheral mesenchyme is a fibrous syncytium. In the Digenea, the mesenchyme is mostly a syncytial meshwork with fluid-filled spaces containing free cells that give rise to lymphocytes and gonads (Fig. 85). Gland cells are scanty as compared with the Turbellaria. They are practically always of an adhesive nature. They are present in both ends of Mono-

genea in connection with adhesive structures and in relation to the oral sucker of Digenea. Some Digenea have clusters of gland cells on the ventral surface opening onto ridges or into pockets that are protrusible (families Paramphistomidae, Notocotylidae, Fig. 118*D*).

6. Nervous System and Sense Organs.—The nervous system entirely resembles that of the Turbellaria and consists of a pair of cerebral ganglia and a submuscular plexus concentrated into longitudinal cords and transverse connectives (Fig. 87*A*). The principal articles on the nervous system and sense organs are those of Looss (1894), Bettendorf (1897), and Zailer (1914). The two cerebral ganglia connected by a broad commissure lie dorsally, above or behind the pharynx in the Monogenea, between the oral sucker and the pharynx in the Digenea. From them several nerves, usually three pairs, proceed anteriorly, and three pairs of cords—dorsal, lateral, and ventral—proceed posteriorly (Fig. 87*A*). The ventral cords are the best developed; the dorsal cords are lacking in most Monogenea (Fig. 92*D*), and the lateral cords may be absent in elongated types. The adhesive organs and the pharynx receive a rich nerve supply (Fig. 86).

The trematodes like most parasitic animals are not well provided with sense organs. Eyes occur in most Monogena and in larval stages of some Digenea. They are closely related to the brain and consist in the cases investigated of a pigment cup containing a single rounded retinal cell with a rod border (André, 1910; Faust, 1918a; Hesse, 1897); sometimes the pigment cell is wanting. Bulb-shaped nerve endings, that may send a bristle to the surface have been found in abundance in trematodes, especially in the suckers, and are regarded as tangoreceptors (Fig. 86). The edge of the large sucker of the Aspidobothria bears sense organs in the form of little bulbs that apparently can be protruded (Fig. 97*D*).

7. Digestive System.—The digestive system closely resembles that of the dalyellioid rhabdocoels. The mouth, situated at or ventral to the anterior tip (except in the gasterostomes, as already noted) and encircled by the oral sucker in most Digenea, leads into a funnel-like mouth cavity which in many Monogenea connects with the pits of the adjacent lateral suckers. The mouth cavity is followed directly or after the intervention of a short buccal tube ("prepharynx") by a rounded or elongated doliiform pharynx whose strong radial musculature gives its wall a cross-striated appearance. In Monogenea, the distal end of the pharynx often projects free into the buccal tube. The pharynx has lateral pockets in some cases (Fig. 108*A*). Both internal and external pharyngeal glands may be present. The pharynx is reduced or absent in some Digenea, as some blood flukes (Fig. 123). Following the pharynx either with or without the intervention of an esophagus, usually short,

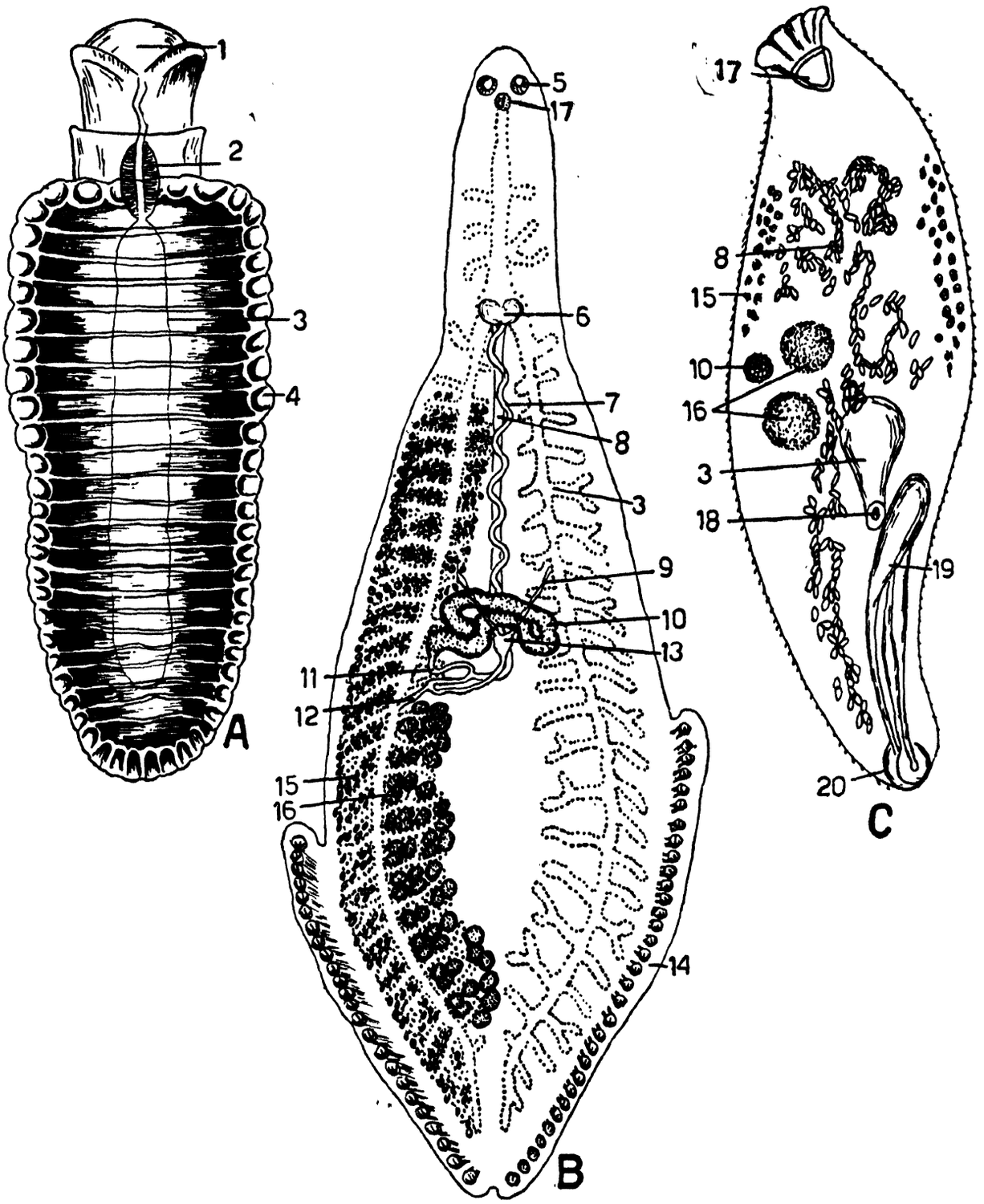

FIG. 84.—Types of trematodes. *A. Cotylogaster*, order Aspidobothria. *B. Microcotyle*, from life, Puget Sound, order Monogenea. *C.* Gasterostome fluke *Rhipidocotyle* (*after Nicoll*, 1914), order Digenea. 1, mouth funnel; 2, pharynx; 3, intestine, 4, sucker with three rows of alveoli; 5, lateral suckers; 6, gonopore; 7, sperm duct; 8, uterus; 9, yolk ducts; 10, ovary; 11, oviduct; 12, genitointestinal canal; 13, yolk reservoir; 14, opisthaptor with small suckers; 15, yolk glands; 16, testes; 17, anterior sucker; 18, mouth; 19, cirrus sac; 20, genital antrum.

sometimes long, comes the intestine, a simple rhabdocoel-like sac in some Monogenea, in the Aspidobothria, and in the digenetic family Bucephalidae (Fig. 84*C*). In the great majority of trematodes, however, the intestine forks at once into two branches, called *crura* or *caeca*, that extend posteriorly as blind tubes (Fig. 82*A*), usually to the rear end of the animal. These are usually simple in the Digenea; but in most Monogenea (Fig. 84*B*) and some Digenea, i.e., liver flukes, they give off a few

to many lateral branches (Fig. 116*A*) that may anastomose to a network. The two crura may be confluent at their posterior ends (Fig. 87*C*) or may be very short (Fig. 88*A*), or sometimes one is lacking. In several Digenea, the posterior ends of the crura open into the excretory bladder, and in a few species of fish trematodes, they open directly to the exterior either separately or after union, so that one or two anal pores are present (La Rue, 1926; Ozaki, 1928a; Odhner, 1928; Stunkard, 1931; Fig. 87*B*).

The digestive system up to the intestine is lined by cuticle. The intestinal wall is composed of a cuboidal to columnar epithelium which in

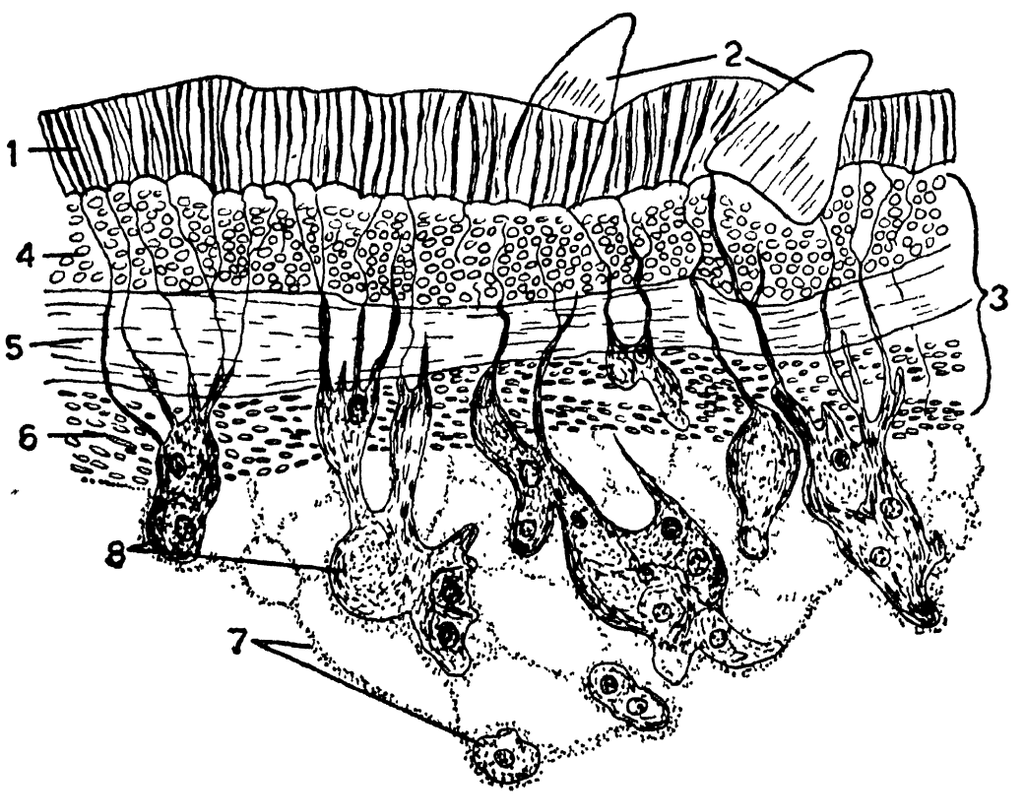

FIG. 85.—Histological structure. Longitudinal section through the surface of *Fasciola hepatica* (*after Hein*, 1904). 1, cuticle; 2, cuticular scales; 3, subcuticular musculature; 4, circular layer; 5, longitudinal layer; 6, diagonal layer; 7, mesenchyme; 8, mesenchymal cells secreting the cuticle.

the Digenea is usually underlain by a delicate muscle layer of circular and longitudinal fibers. In some Monogenea, the intestinal epithelium consists of scattered separated cells (Goto, 1894).

8. Excretory System.—This system likewise resembles that of rhabdocoels, consisting of a protonephridial tubule on each side that commonly recurves on itself. In the Monogenea, the two tubules are completely separate; each begins anteriorly, runs backward to the posterior end, and there bends upon itself, running forward again to terminate near the mouth on the dorsal side by a nephridiopore usually preceded by a small contractile bladder. The Aspidobothria are similar except that the nephridiopores are near the posterior end, and fusion to a single pore may occur. In the Digenea the two tubules unite to a median oval or elongated or Y-shaped bladder (Fig. 88*A*) opening by a single pore at the

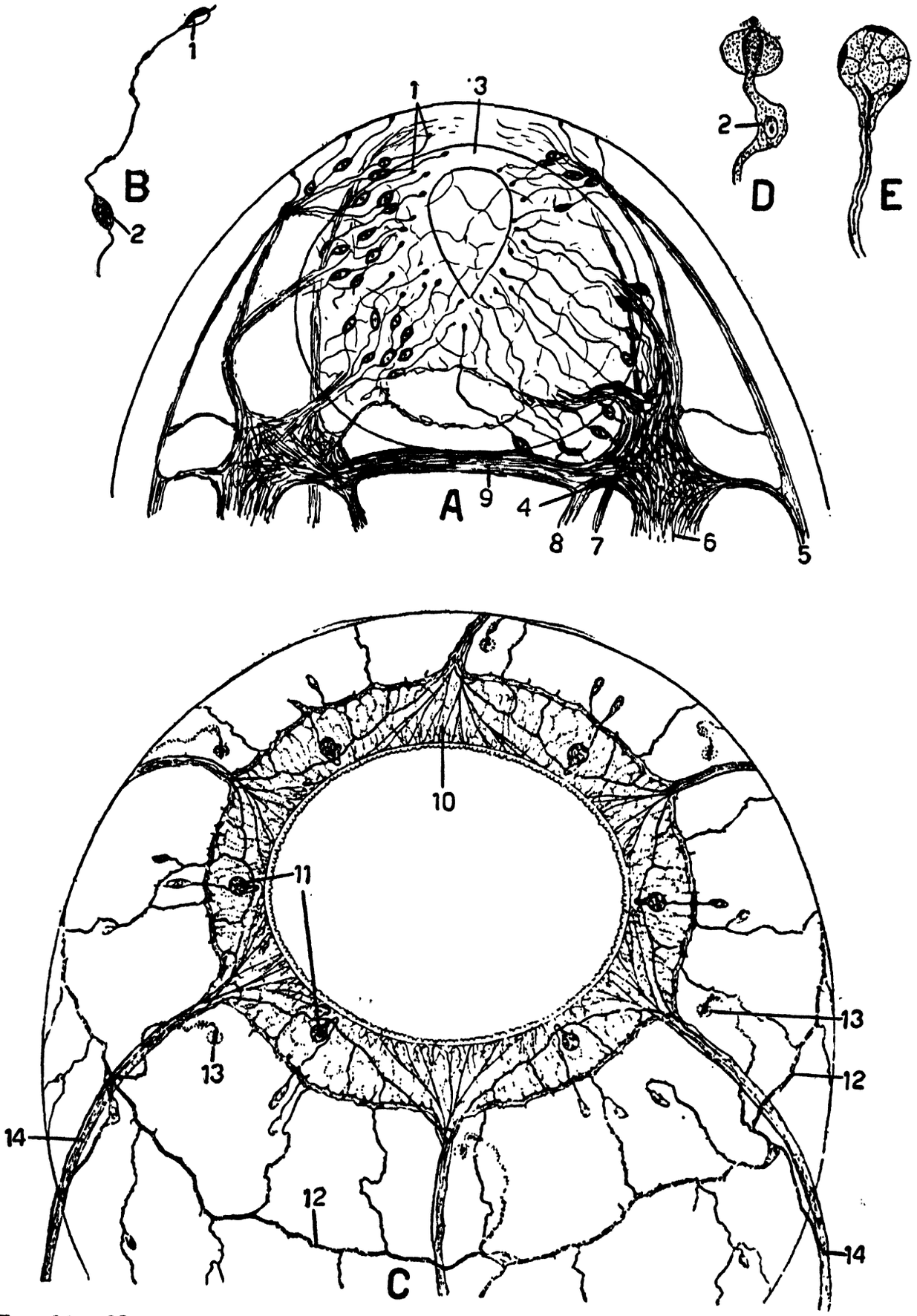

FIG. 86.—Nervous system and sense organs. *A*. Innervation of the oral sucker of a digenetic fluke (*after Bettendorf*, 1897), ventral view; right side of animal shows dorsal sensory cells, left side ventral ones. *B*. Tactile bulb of the same, enlarged. *C*. Innervation of the acetabulum of a digenetic fluke (*after Zailer*, 1914); three nerves from each ventral cord form a strong ring plexus at the margin of the sucker and a less developed deeper ring; each ring has six special sensory bulbs. *D*. Sensory bulb of deeper ring. *E*. Sensory bulb of outer ring. 1, tactile bulb; 2, sensory nerve cell; 3, oral sucker; 4, brain ganglion; 5, lateral nerve cord; 6, ventral nerve cord; 7, dorsal nerve cord; 8, nerve cord to pharynx; 9, connective between two brain ganglia; 10, marginal nerve ring of acetabulum; 11, sensory bulbs of same; 12, deeper nerve ring of acetabulum; 13, sensory bulbs of same; 14, nerves to sucker from ventral cords.

middle of the posterior end or near this location, usually dorsal, but sometimes ventral. Study of the development of the Digenea shows that the two protonephridial tubules are separate at first and later fuse terminally (Fig. 105D). From the anterior end of the bladder, the two tubules run forward and either extend to the anterior end, there recurving on themselves, or very often they fork near the body middle into an anterior and a posterior branch (Fig. 88*A*). In some Digenea there are several main tubules instead of the usual two, and these anastomose to a network. The family Heronimidae differs from all other Digenea in that the nephridiopore is near the anterior end (Fig. 125*B*).

The terminal flame bulbs are attached to the recurved portions of the tubules or to the branches, not to the main trunks. In the trematodes, each flame bulb is always a nucleated cell. It usually sends off delicate processes into the mesenchyme. Extra flames, apparently originating by division of the original flame, may be present, and lateral flames also occur. In the Digenea, the terminal flame bulbs and capillaries occur in clusters of two to four attached to a single collecting tubule (Figs. 88*A*, 102*E*) and the arrangement of the flame bulbs is held by many helminthologists to constitute an important taxonomic character (Faust, 1932). The arrangement begins in the cercaria and can be traced through to the adult so that it may constitute an important means of linking larval with adult flukes. The flame-bulb pattern is also employed to determine familial placing of adult flukes as related forms usually show the same pattern. However, members of the same family may have different flame-bulb arrangements (Stunkard, 1929), and in general caution is necessary in basing taxonomic relationships on flame-bulb patterns. These patterns are recorded by a formula devised by Faust (1919) which expresses the number of flame bulbs in each group and the number of groups on each main branch of the tubule. Thus the flame-bulb formula for Fig. 88*A* would be $2[(2 + 2) + (2 + 2)]$ and that for Fig. 102*E* would be $2[(3 + 3 + 3) + (3 + 3 + 3)]$.

9. Lymphatic System.—In a number of Digenea, particularly in the Paramphistomidae, but also in the Angiodictyidae, Cyclocoelidae, and Heronimidae, there is a system of mesenchymal vessels that seems to represent a primitive circulatory system. It consists on each side of one to four blind longitudinal tubes, unconnected with each other, that give off blind branches to the intestinal crura and reproductive organs and into the suckers (Fig. 88*B*). These lymph channels are lined by flattened mesenchyme and contain a fluid in which float free cells closely resembling primitive vertebrate blood cells (haemocytoblasts, Jordan and Reynolds, 1933). These free cells are mesenchymal cells that have wandered into the lymph channels where they eventually disintegrate. A center of formation of the lymph cells also exists at the forking of the

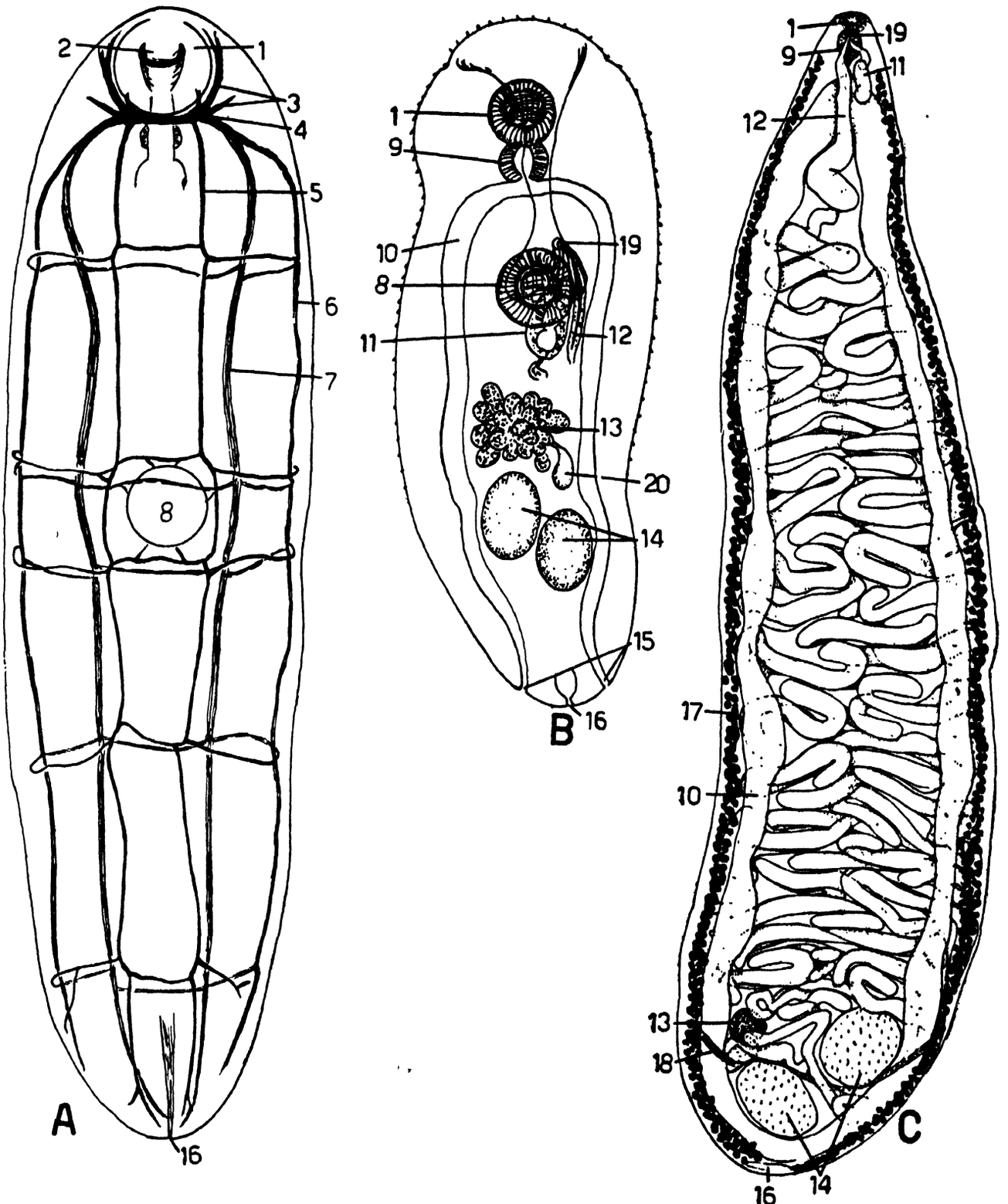

FIG. 87.—Nervous system (continued). Digestive system. *A*. Nervous system of a distome (*after Looss*, 1894). *B. Diploporus*, distome with two anal pores (*after Ozaki*, 1928). *C. Cyclocoelum*, monostome with confluent intestinal crura (*after Harrah*, 1922). 1, oral sucker; 2, mouth; 3, anterior nerves; 4, brain ganglia; 5, ventral cords; 6, lateral cords; 7, dorsal cords; 8, acetabulum; 9, pharynx; 10, intestinal crura; 11, cirrus sac; 12, uterus; 13, ovary; 14, testes; 15, anal pores; 16, nephridiopore; 17, yolk glands; 18, yolk ducts; 19, gonopore.

intestinal crura. In the mesenchyme the haemocytoblasts may also differentiate into cells resembling the eosinophils of vertebrate blood. The lymph channels seem to function in the distribution of food, respiratory gases, and excretory products.

10. Reproductive System.—This is built along the same lines as in the Turbellaria and similarly exhibits multitudinous variations, taxo-

nomically important, of a few fundamental parts. The trematodes are hermaphroditic except for the digenetic families Didymozoonidae and Schistosomatidae. Some of the former are functionally dioecious in that one or the other system fails to mature (Fig. 81*A*), and the latter occur only as easily distinguishable males and females (Fig. 123*D*). The trematode reproductive system differs from that of turbellarians mainly in the utilization of the common ovovitelline duct as a uterus in which the capsules are stored before laying. Whereas in the Turbellaria, a uterus is infrequently present as a blind sac from the genital antrum, in the Trematoda the uterus is the main female canal and constantly present, being usually greatly elongated and coiled. Nearly all trematodes have yolk glands distinct from the ovary. Many trematodes possess as part of the female system a single or paired copulation canal, variously named, with its own external pore or pores. The male copulatory organ is generally a cirrus.

a. Monogenea.—The reproductive system of the Monogenea strikingly resembles that of rhabdocoels. There are usually several to many testes (Figs. 83*B*, 84*B*) posteriorly located but sometimes only one or two (Figs. 89*B*, *C*, 92*D*, 94*A*). The sperm duct runs forward to the copulatory organ before which it may widen to a spermiducal vesicle. The copulatory organ, essentially a penis bulb, is of varied construction. The muscular bulb may receive single prostatic glands or a single or paired prostatic vesicle (Fig. 89*C*). From the bulb projects the penis, consisting of a muscular or fibrous papilla (Fig. 89*B*) often armed with hooks or of a hard tube or stylet or a complex cuticularized apparatus (Fig. 89*C*) similar to that of the Dalyelliidae. Where the penis is unarmed the genital antrum may bear copulatory hooks.

There is a single ovary, usually of elongated form (Figs. 83*B*, 84*B*) and even often extensively coiled, and a pair of follicular yolk glands lying in lateral body regions. Yolk glands are said to be absent from *Gyrodactylus* (Fig. 83*A*), which seems to have a germovitellarium, and in some forms yolk glands occur on one side only. From the main yolk duct of each side a transverse duct arises and meets its fellow of the opposite side to form a *yolk reservoir* from which the short common yolk duct extends to the oviduct. The oviduct shortly after leaving the ovary receives the common yolk duct, may receive a long-stalked seminal receptacle, often connects with the right intestinal crus by a genitointestinal canal (Fig. 84*B*), and then presents a small widening commonly known as the *ootype* which is encircled by numerous gland cells, the so-called shell glands, also termed Mehlis's glands. Beyond the ootype, the common ovovitelline duct continues as a widened but relatively short tube, the uterus, that extends to the common genital antrum. In the majority of the Monogenea there occur single or paired copulation canals (usually

called vaginae[1]) whose outer ends open independent of the gonopore on dorsal, lateral, or ventral surfaces. The inner end of these canals may open into the oviduct before the latter receives the common yolk duct or into the latter or into the yolk reservoir or into the transverse yolk ducts (Fig. 89*B*, *C*). When paired, the copulation canals may be united for

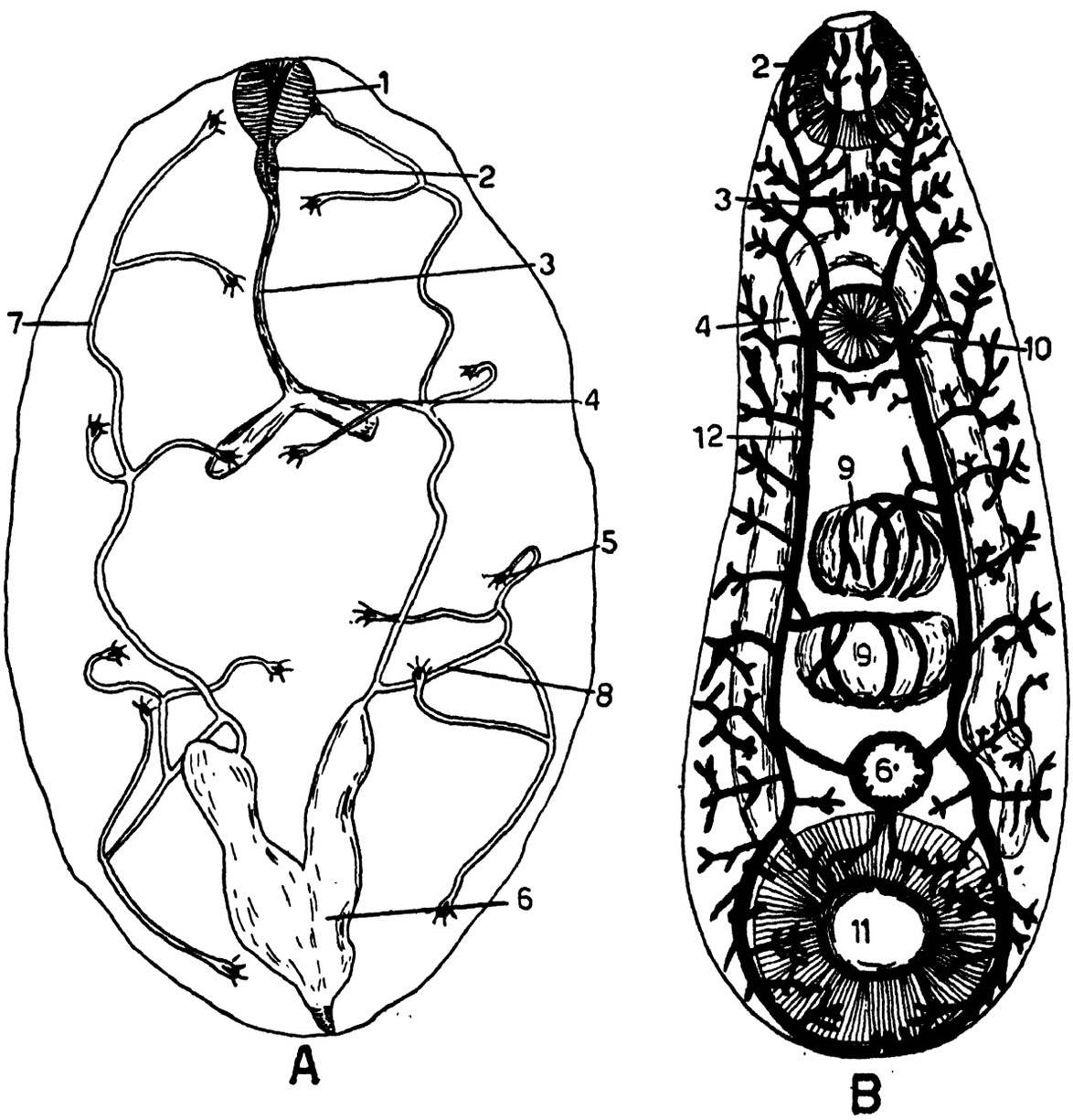

FIG. 88.—Excretory system; lymphatic system. *A*. Excretory system of *Microphallus* (*after Wright*, 1912); the flame-bulb pattern on each side is (2 + 2) + (2 + 2). *B*. Lymphatic system of the amphistome *Cotylophoron cotylophorum* (*after Willey*, 1930). 1, oral sucker; 2, pharynx; 3, esophagus; 4, intestinal crura; 5, flame bulbs; 6, bladder; 7, anterior branch; 8, posterior branch, excretory system; 9, testes; 10, gonopore; 11, acetabulum; 12, lymphatic system.

part of their course. They receive the penis in copulation and may have a widened portion or a pouch (Fig. 89*C*) serving as seminal receptacle; and it appears that in some cases the seminal receptacle is a copulation canal that has lost its surface connection.

The egg after leaving the ovary is immediately fertilized, becomes surrounded by yolk cells (not in *Gyrodactylus*), and enters the ootype where

[1] As the term vagina has been defined as the terminal part of the main female canal, it cannot be used in this connection.

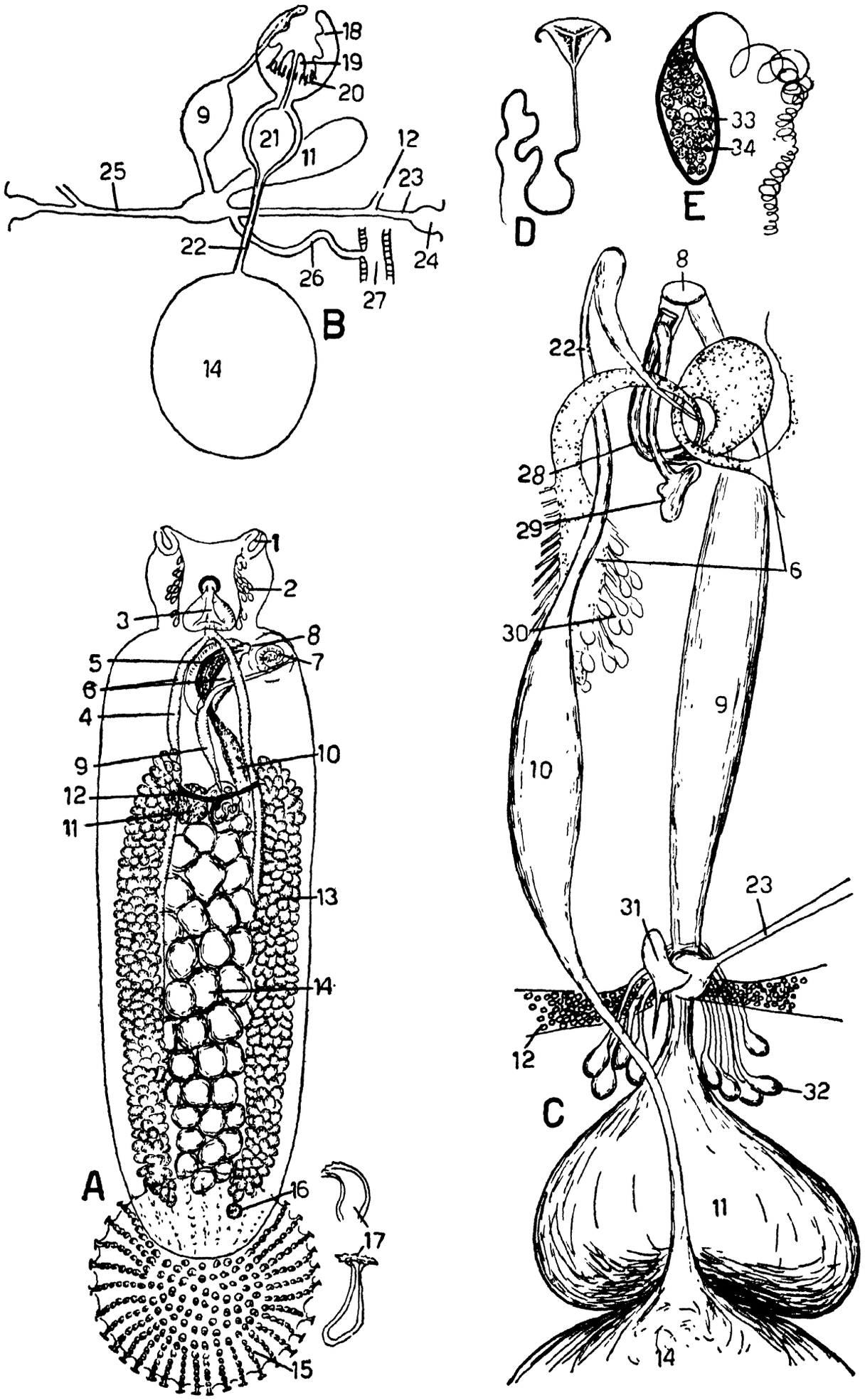

FIG. 89.—Reproductive system, Monogenea. *A. Acanthocotyle*, from life, Puget Sound, showing general features of reproductive system. *B.* Polystomoid type of reproductive system with penis papilla (*after Stunkard*, 1917). *C.* Gyrodactyloid type of reproductive system with penis stylet (*after Goto and Kikuchi*, 1917). *D.* Capsule of *Benedenia*

it pauses while the shell is formed. The shell or capsule is formed chiefly or wholly from droplets in the yolk cells. The so-called shell glands appear to play no role in its formation in most cases, although Dawes (1940) observed that in *Hexacotyle* these glands secrete a rudimentary capsule on which the yolk cells deposit their droplets. The secretion of Mehlis's glands probably functions mainly to lubricate the passage of the capsules along the uterus. The shell has an operculum at one end and often bears at one or both ends a long filament for attachment to the host (Fig. 89*D*, *E*). The capsules are usually held for some time in the uterus, which, contrary to the condition in the Digenea, contains only one or a few at a time.

The uterus and male apparatus open into a common genital antrum that exits by a common gonopore constantly situated on the ventral surface near the anterior end close to the crural fork.

b. Aspidobothria.—The reproductive system of the Aspidobothria is similar to that of the Monogenea (Fig. 97*C*). The male system comprises one or two testes and a straight or sinuous sperm duct that runs to the copulatory organ, usually a cirrus sac. The female system differs from that of the Monogenea chiefly in that the uterus may be long and coiled. A copulation (Laurer's) canal is frequently but not always present. In some forms, the beginning of the oviduct is provided with valves of unknown purpose. Sperm duct and uterus unite to a common antrum and gonopore on the ventral surface near the anterior end; the terminal part of the uterus may be thickened muscularly to form a *metraterm.*

c. Digenea.—The Digenea usually have two rounded testes situated side by side (Fig. 114*D*) or one behind the other (Fig. 82*A*); but some have one testis and others several testes (*Gorgodera*, Fig. 112*A*; *Schistosoma*, Fig. 124*B*). The testes may be lobed or branched as in the liver flukes (Fig. 116*A*) and *Opisthorchis* (Fig. 114*A*) or long and tubular (Didymozoonidae, Figs. 111, 112*C*; *Heronimus*, Fig. 125*A*). From each testis a sperm duct extends to meet its fellow, forming the common sperm duct. This pursues a straight or sinuous course, may enlarge as a spermiducal vesicle, and enters the copulatory apparatus, which varies from a simple muscular tube to an enlarged highly muscular *cirrus sac.* The distal portion of this, unarmed or armed with spines, scales, thorns, etc., is eversible as a cirrus (Fig. 90*A*, *B*). A seminal vesicle and also prostatic

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(*after Jahn and Kuhn*, 1932). *E.* Capsule of *Dip'ozoon* (*after Zeller*, 1872b). 1, lateral suckers; 2, adhesive glands of same; 3, mouth; 4, intestinal crura; 5, cirrus sac; 6, prostatic vesicles; 7, termination of uterus; 8, gonopore; 9, uterus; 10, spermiducal vesicle; 11, ovary; 12, yolk ducts; 13, yolk glands; 14, testes; 15, pseudohaptor; 16, larval haptor; 17, haptorial hooks, enlarged; 18, penis bulb; 19, penis papilla; 20, thorns; 21, seminal vesicle; 22, sperm duct; 23, copulation canal; 24, opening of same on surface; 25, common genitovitelline canal; 26, genitointestinal canal; 27, crus of intestine; 28, penis stylet; 29, accessory piece of stylet; 30, prostatic glands; 31, seminal receptacle; 32, Mehlis's glands; 33, egg; 34, yolk cells.

glands with or without a prostatic vesicle may be contained within the cirrus sac (Fig. 90*A*). A cirrus is lacking in a number of families as the Paramphistomidae (Fig. 107*C*), Didymozoonidae (Fig. 111), Schistosomatidae (Fig. 124*B*), and others. A true penis papilla is occasionally present as in the family Microphallidae (Fig. 115).

The single ovary is usually of rounded form but may be lobed (*Prosthogonimus*, Fig. 113*B*) or branched (*Fasciola*, Fig. 116*A*) or tubular (Didymozoonidae, Figs. 111, 112*C*). The oviduct very shortly after leaving the ovary receives the common yolk duct and the copulation (Laurer's) canal, then widens slightly (Fig. 90*C*) to form the ootype, encircled by Mehlis's glands (also called shell glands), and then continues to the genital antrum as a widened, usually very long coiled tube, the uterus, full of capsules. The vitellaria usually occur as numerous clusters on each side extending most of the body length (Fig. 109*C*) but may take the form of simple or branched tubes (Fig. 118*A*) or of small branched bodies, and some flukes possess only one vitellarium. Where the yolk glands consist of clustered follicles, small ducts from the clusters join a longitudinal yolk duct on each side that at the level of the ovary gives off a transverse yolk duct toward the median line. These two join with or without the formation of a small enlargement, the *yolk reservoir*, and from this or the junction the short common yolk duct extends to the oviduct, which thereafter should be termed ovovitelline duct (Fig. 90*C*). The yolk cells contain shell-forming droplets in at least many cases. A seminal receptacle (Fig. 90*C*) may be attached to the oviduct near the ovary or may occur along the course of Laurer's canal, or rarely the oviduct itself may be widened to serve as a seminal receptacle.

The homology of Laurer's canal has been the subject of much debate. This muscular tube leaves the oviduct between the ovary and the entrance of the common yolk duct and proceeds directly to the dorsal surface where it opens in the middorsal line or to one side. The opening has no relation to the gonopore. Laurer's canal seems to correspond to the copulation canal of Turbellaria which extends from the copulatory or seminal bursa to the surface with or without the concomitant disappearance of the bursa. It is found in some polyclads and a few land and marine planarians. Laurer's canal in flukes was formerly considered to serve as exit for superfluous sperm and yolk cells but is now known to function in copulation. It is absent in a considerable number of flukes.

The uterus (= ovovitelline duct), whose beginning may serve as a seminal receptacle in the absence of any other, is a simple tube, usually greatly coiled and much longer than the body length, that fills the spaces between the other organs, often concealing them from view (Fig. 82*A*). When the gonopore is anterior, the uterus usually runs to the posterior end, then turns and proceeds anteriorly; if the gonopore is posteriorly

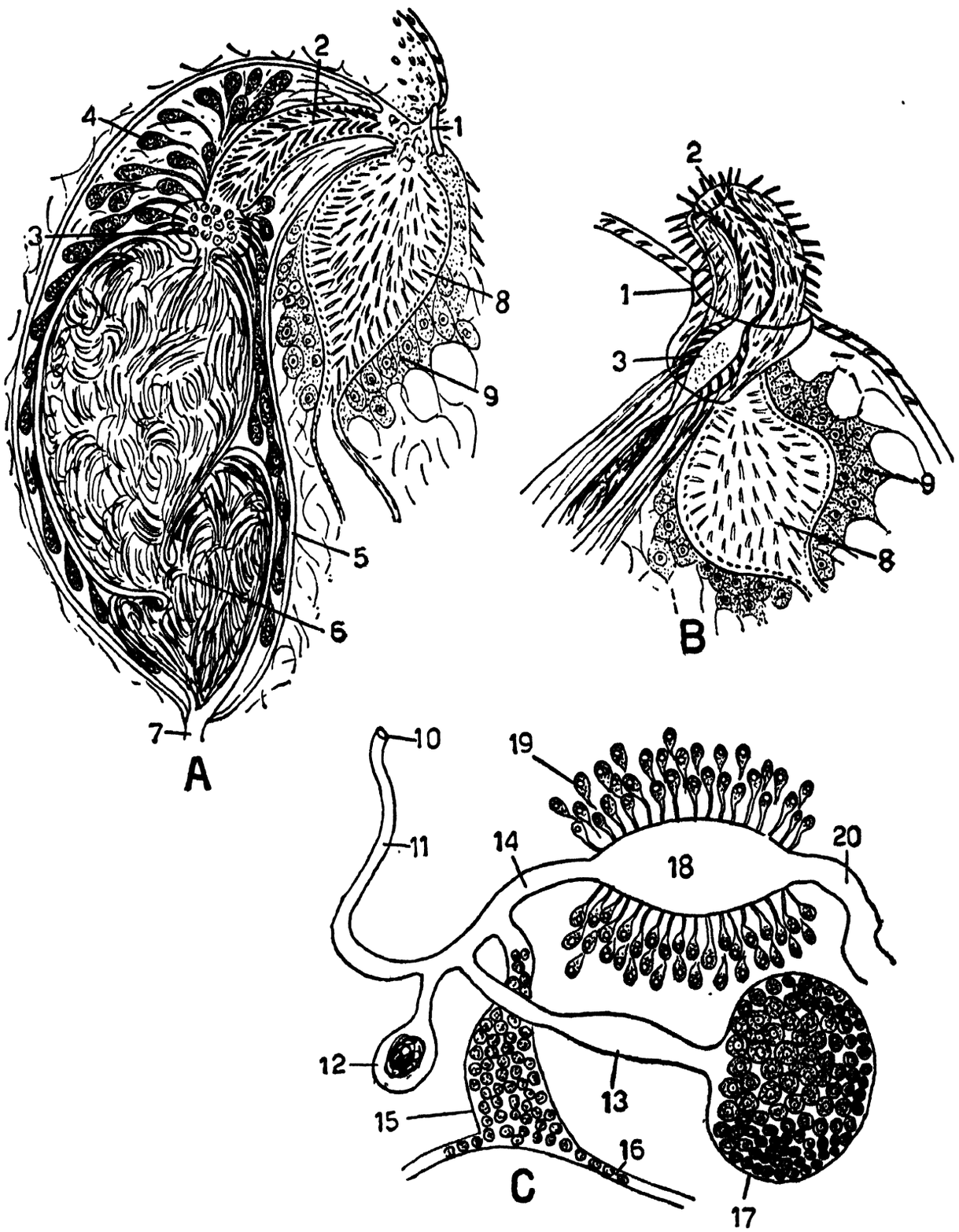

FIG. 90.—Reproductive system, Digenea. *A*. Terminal part of male system. *B*. Same, with cirrus everted. (*A*, *B after Looss*, 1894). *C*. Scheme of female system of the Digenea. 1, gonopore; 2, cirrus; 3, prostatic vesicle; 4, prostatic glands; 5, cirrus sac; 6, seminal vesicle; 7, sperm duct; 8, metraterm armed with spines; 9, gland cells of same; 10, pore of Laurer's canal; 11, Laurer's canal; 12, seminal receptacle; 13, oviduct; 14, ovovitelline duct; 15, yolk reservoir; 16, yolk ducts; 17, ovary; 18, ootype; 19, Mehlis's glands; 20, beginning of uterus.

located, the uterus often runs forward and then backward. This development of the ovovitelline duct into a long coiled uterus is the chief difference between the reproductive systems of the trematodes and the turbellarians. The formation of the uterus is correlated with a characteristic feature of entoparasitism, namely, the production of enormous quantities of eggs. Where the uterus contains but one capsule at a time as in blood

flukes, it is a short enlarged tube as in the Monogenea (Figs. 123*A*, 124*A*). The terminal part of the uterus in flukes that lack a Laurer's canal functions to receive the cirrus in copulation and for this purpose may be greatly strengthened by a layer of circular muscles, armed with spines, scales, etc., and provided with gland cells. Such an altered termination of the uterus is called *metraterm*.

The sperm duct and uterus may open separately to the exterior (*Sanguinicola*, Fig. 123*A*), but usually they enter a common genital antrum (or atrium), either separately or after fusion to a common canal. The antrum is usually a small chamber but may be a large shallow to deep pit or pocket (Fig. 119*B*), or a muscular tube into the bottom of which the genital ducts open. The gonopore commonly occurs anteriorly in the mid-ventral line between mouth and acetabulum but can be situated laterally (Fig. 113*A*) or even dorsally and in some families occurs at or near the posterior end (Bucephalidae, Figs. 84*C*, 106*D;* Strigeidae, Figs. 119*B*, 120*A*). The gonopore is sometimes encircled by a sucker-like structure, the *genital sucker* (Fig. 107*C*), or sometimes by the acetabulum itself. The terminal parts of the reproductive system are lined with cuticle.

Upon leaving the ovary the eggs are fertilized and become surrounded in the ootype by yolk cells that thereupon emit their shell-forming droplets. These harden into the characteristic shell or capsule, usually yellow or brown, of oval shape, and mostly with an operculum at one end or sometimes a filament or spine (Figs. 110*E*, 114*C*). Stephenson (1947) has shown for the liver fluke that the shell-forming droplets of the yolk cells contain protein and a phenol, that this phenol is oxidized to a quinone in the beginning coils of the uterus, and that the quinone then acts to tan the protein, producing a hard resistant combination termed sclerotin similar to leather. Probably these findings apply to all platyhelminth capsules as shown for Turbellaria by Vialli (1933). The function of the clear secretion of Mehlis's glands discharged into the ootype is very uncertain; some think this fluid lubricates the passage of the capsules along the uterus (Goldschmidt, 1909; Ujiie, 1936; Kouri and Nauss, 1938). As the capsules proceed along the coils of the uterus they undergo more or less alteration and eventually are discharged into the digestive or urinary tract of the host (although they can be emitted otherwise as through the gills of fish) whence they reach the exterior in the feces or urine, examination of which for capsules constitutes the usual method of diagnosis of the presence of flukes. The capsules of the various flukes of economic and medical importance are recognizable through differences in size, shape, and other features. It is customary in the literature of helminthology to talk about "eggs" when the capsules are meant. As development has usually already begun, even the contents should not be termed "egg"; they will here be called *encapsulated* or *ovic embryos*.

11. Copulation.—Although self-fertilization is possible in flukes through sperm wandering from the male into the female canal or through autocopulation, cross-fertilization is the usual method. Monogenetic flukes in copulation hang onto the substratum by their opisthaptors and entwine their anterior ends (Fig. 91*A*), bringing the gonopores in contact with mutual insemination; or the gonopore of one makes contact with the opening of the other's copulation canal when this is present and a probably

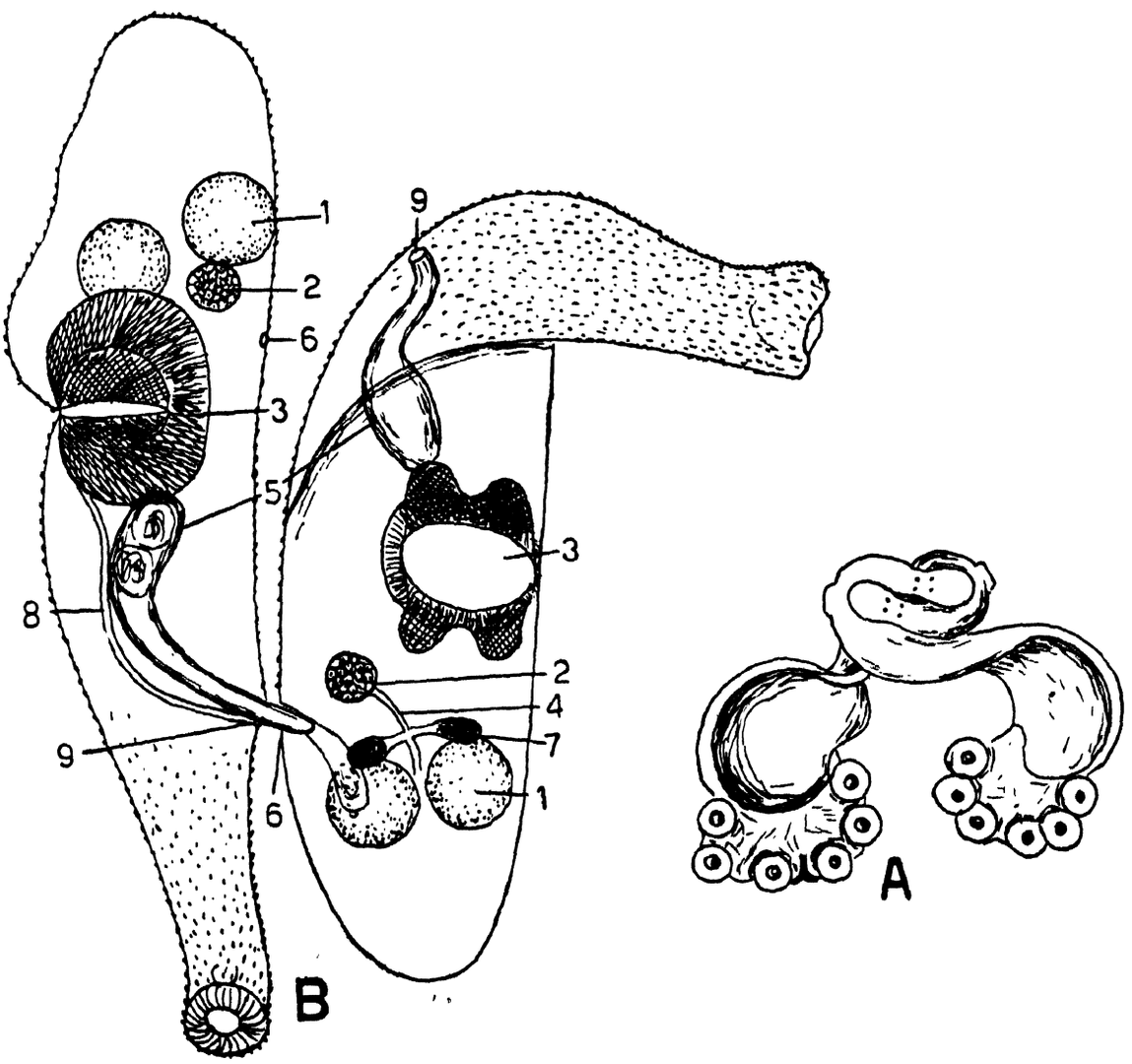

FIG. 91.—Copulation. *A*. Monogenetic fluke *Polystoma* in copulation (*after Zeller*, 1876). *B*. Digenetic fluke *Diphterostomum* (family Zoogonidae) copulating one-sidedly by way of Laurer's canal (*after Palombi*, 1932a). 1, testes; 2, ovary; 3, acetabulum; 4, oviduct; 5, cirrus sac; 6, opening of Laurer's canal; 7, yolk glands; 8, uterus; 9, gonopore.

one-sided insemination ensues (MacCallum, 1913). In the Digenea, copulation is either one-sided by way of Laurer's canal (Fig. 91*B*) or reciprocal by way of the metraterm (Leon, 1927; Palombi, 1932a). The sperm are stored in the seminal receptacle.

12. Order Monogenea.—The monogenetic trematodes are mostly ectoparasites that typically inhabit the gills, sometimes the skin, of freshwater and marine fishes; a few occur on crustaceans or cephalopods. Some tend to entoparasitism, going into structures that open to the exterior, as the nasal and pharyngeal cavities and the urinary bladder and ureters of fish, amphibians, and reptiles. Only one is known to

inhabit the interior of the host, *Dictyocotyle*, found in the coelom of a ray (Nybelin, 1941). The Monogenea move about on their hosts by looping in a leech-like manner, alternately attaching pro- and opisthaptors. They feed on slime, epithelial cells, and blood exuding from places damaged by their hooks and may seriously and even fatally injure the gills of the host, especially in the case of young fish.

The Monogenea have been monographed by Price (1937–1943) with special reference to the North American species. His arrangement and synonymy are followed here.

a. Suborder Monopisthocotylea.—In this suborder an oral sucker is generally absent but may be weakly developed. The prohaptor consists of a pair of small lateral suckers or pits supplied by adhesive glands or simply of a cluster of adhesive glands on each side opening singly or through one to several thickened bulbous ends known as *head organs* (Fig. 92*A*). These head organs often shape the anterior margin into two or more lobes. The opisthaptor is a simple or subdivided disk usually provided with one to three pairs of large hooks (*anchors*) and 2 to 16 marginal hooks (*hooklets*) (Fig. 92*B*). The two anchors of a pair may be connected by a crosspiece termed *bar*. The opisthaptor in this suborder always lacks separated suckers. Eyes are usually present. A genitointestinal canal is absent.

The Monopisthocotylea consist of two groups (superfamilies), the *gyrodactyloid* and *capsaloid* Monogenea. The former are worms of elongated form in which the prohaptor consists of glands opening through head organs (Fig. 92*A*) and the opisthaptor is armed with one or two pairs of anchors nearly always supported by bars (Fig. 92*B*). Some representative genera are: *Gyrodactylus*, viviparous, with one pair of anchors and 16 hooklets (Fig. 83*A*); *Dactylogyrus* with one pair of anchors and 14 hooklets (Fig. 92*A*, *B*); *Tetraonchus* with two pairs of anchors supported by one bar and 16 hooklets; *Ancyrocephalus*, similar but with 2 bars and 14 hooklets; *Amphibdella* with stalked lobed opisthaptor bearing two pairs of anchors without bars and 14 hooklets; *Diplectanum* (Fig. 92*C*) with a dorsal and a ventral *squamodisk* (these are disks near the opisthaptor bearing concentric circles of spines, scales, or ridges); and *Calceostoma* with greatly lobed anterior end. In the capsaloid Monogenea, the prohaptor may consist of glands with head organs (Fig. 83*B*) as in the gyrodactyloid group but more usually takes the form of a weak oral sucker or a pair of lateral pits or suckers (Fig. 92*D*). The opisthaptor is generally a large muscular disk with or without hooks and divided or not by septa. Some capsaloid genera are: *Monocotyle* (Fig. 83*B*) and *Heterocotyle* with an armed opisthaptor divided into one central and eight marginal depressions; *Microbothrium* with prohaptor of two adhesive pits opening into the oral cavity and a very reduced opisthaptor; *Acan-*

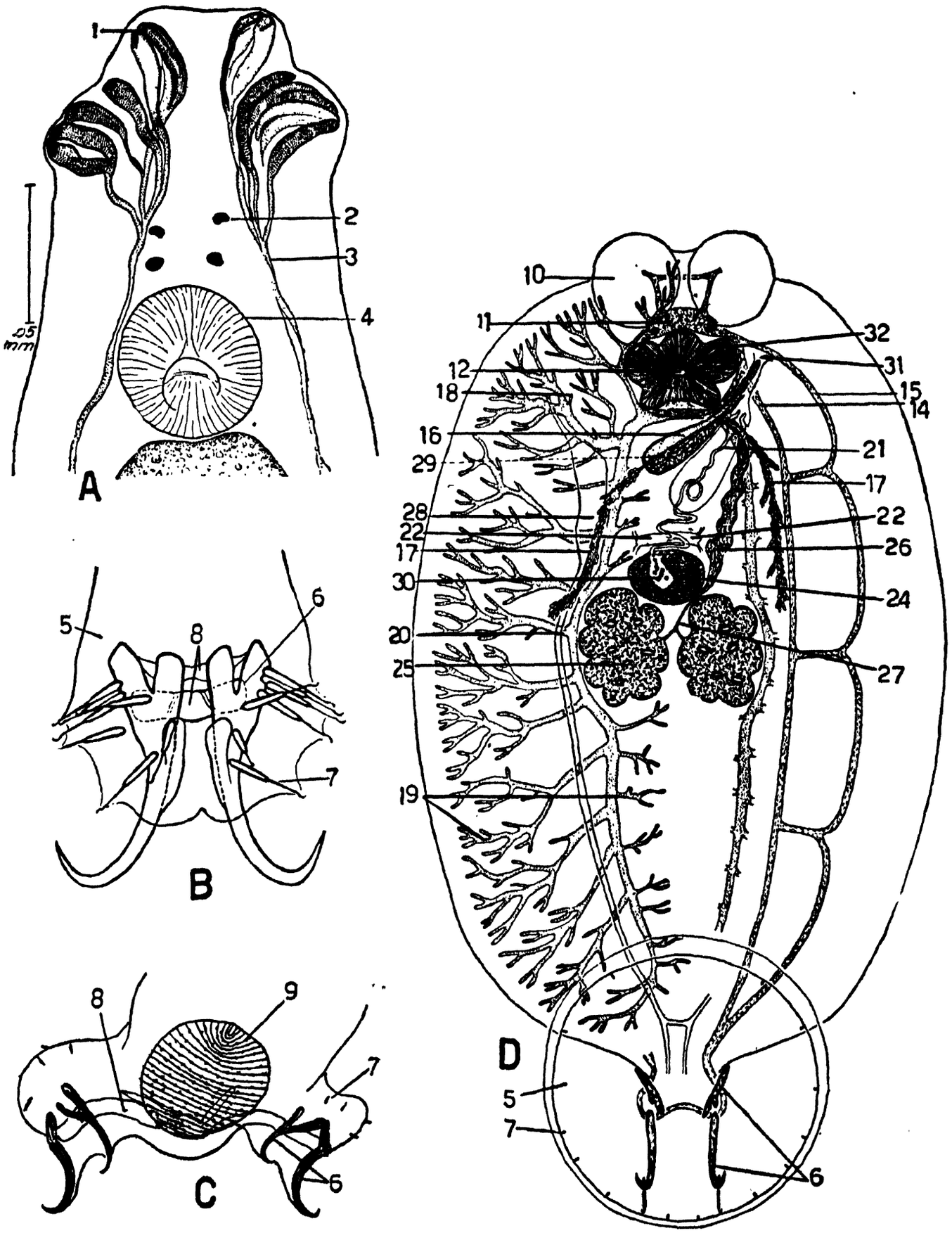

FIG. 92.—Further examples of Monogenea. *A*. Anterior end of *Dactylogyrus*, showing the head organs. *B*. Posterior end of *Dactylogyrus*, showing the opisthaptor. (*A*, *B*, *after Mueller and Van Cleave*, 1932.) *C*. Opisthaptor of *Diplectanum*, showing a squamodisk (*after Johnson and Teigs*, 1922). *D*. *Benedenia* (= *Epibdella*) *melleni* (*after Jahn and Kuhn*, 1932) showing general structure. 1, head organs; 2, eyes; 3, ducts of adhesive glands; 4, pharynx; 5, opisthaptor; 6, anchors; 7, marginal hooks; 8, bars; 9, squamodisk; 10, prohaptor; 11, brain; 12, mouth; 13, pharynx; 14, ventral cords; 15, lateral cords; 16, cirrus sac; 17, prostatic glands; 18, nephridiopore; 19, branches of intestine; 20, nephridial tubule; 21, uterus; 22, yolk reservoir; 23, oviduct; 24, ovary; 25, testes; 26, spermiducal vesicle; 27, sperm duct; 28, bladder; 29, seminal vesicle; 30, seminal receptacle; 31, gonopore; 32, oral sucker.

thocotyle in which the original opisthaptor has been replaced by a very large *pseudohaptor* bearing radiating rows of spines (Fig 89*A*); *Udonella* with two anterior suckers and a large unarmed undivided opisthaptor; *Benedenia* (= *Epibdella* in part), similar to *Udonella*, but with armed opisthaptor (Fig 92*D*); and *Capsala* and *Tristoma* (Fig 93*A*) with a pair of conspicuous anterior suckers and a large armed opisthaptor with one central and seven marginal depressions

b Suborder Polyopisthocotylea.—In this suborder, the prohaptor has the form of an oral sucker encircling the mouth or of two suckers opening into the oral cavity or of two pits. The opisthaptor is armed or not but always bears separate suckers or else sucker-like projections containing cuticularized supports resembling clamps Eyes are generally absent and there is a genitointestinal canal The suborder is also divisible into two superfamilies: the *polystomoid* forms with an oral sucker, and the *diclidophoroid* forms with two small anterior suckers opening into the oral cavity. The polystomoid Monogenea are characterized by an opisthaptor bearing six armed suckers. In *Polystoma* and related genera the circular opisthaptor with six suckers lacks an appendage (Fig 94*A*) Only two suckers are present in *Sphyranura* (Fig. 93*D*). In another group of genera exemplified by *Hexabothrium* (= *Onchocotyle*), *Erpocotyle* (= *Squâlonchocotyle*), and *Rajonchocotyle* (Fig 83*C*), the opisthaptor in addition to the six suckers has a tail-like appendage that bears a pair of terminal suckers also provided with hooks These types are found mostly on elasmobranch fishes. The diclidophoroid Monogenea usually have two rows of suckers or of sucker-like projections supported by a complicated framework of cuticularized pieces. In this group belong the curious *Diplozoon* (Fig. 93*C*) with eight suckers (see below) and types like *Microcotyle* (Fig 84*B*) with two rows and *Axine* with one row of many small adhesive clamps.

13. Development and Life History of the Monogenea.—The capsules of the Monogenea are mostly of fusiform shape and generally provided at one or both ends with short to long filaments for attachment to hosts (Fig. 89*D*, *E*). The egg develops into a ciliated larva of gyrodactyloid appearance and with a gyrodactyloid opisthaptor (Fig. 95*B*) that quickly fastens to a host of the same sort, where it grows and alters to the adult form; hence the name Monogenea in reference to the simple life history which does not involve a change of host. The details of the embryology are known in only a few cases, best in *Polystoma integerrimum* (Halkin, 1901). This fluke inhabits the urinary bladder of frogs and breeds in spring, exuding its eggs into the bladder whence they exit into the water with the feces. Inside the shell are found one egg and a number of yolk cells. The egg undergoes total unequal cleavage into a mass of blastomeres in which the smaller cells enclose the larger ones by a sort of

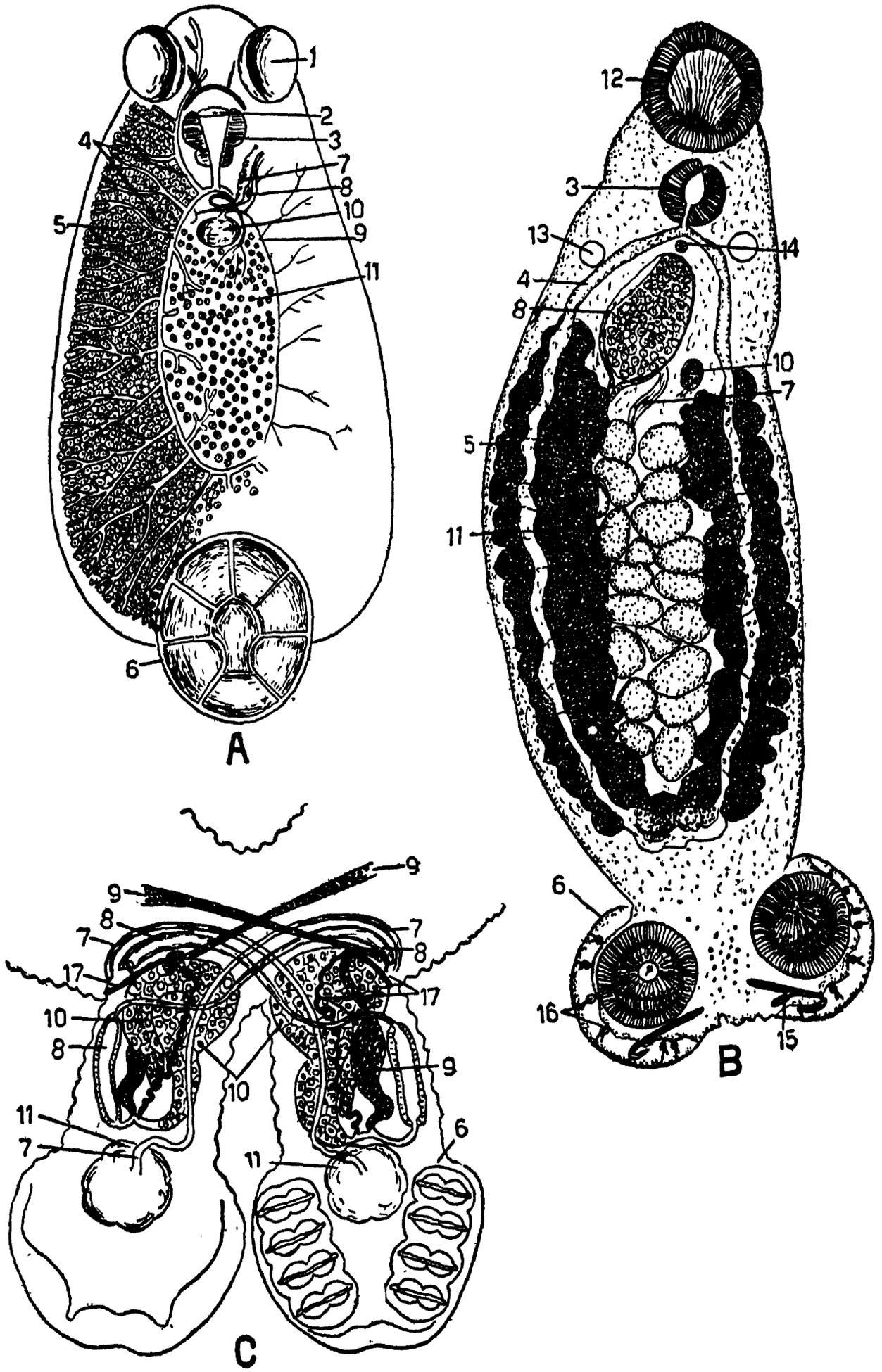

FIG. 93.—Types of Monogenea (continued). *A. Tristoma* (*after Goto*, 1894). *B. Sphyranura* (*after Alvey*, 1936). *C.* Rear end of two *Diplozoon* in permanent copulation (*after Zeller*, 1888). 1, prohaptor; 2, mouth; 3, pharynx; 4, branches of intestine; 5, yolk glands; 6, opisthaptor; 7, sperm duct; 8, uterus; 9, yolk ducts; 10, ovary; 11, testes; 12, oral sucker; 13, bladders; 14, gonopore; 15, anchors; 16, marginal hooks; 17, copulation canal.

epiboly (Fig. 94*B*). Some of the peripheral cells flatten out to an epidermis (Fig. 94*C*) that later develops a ciliation. In the interior mass of cells a cavity arises by cell degeneration beginning at a posterior dorsal point where an opening to the exterior is established and progressing anteriorly. This cavity is the lumen of the intestine, and the cells bordering it become the intestinal epithelium (Fig 94*D*). In the mid-ventral region a ball of cells differentiates into a pharynx and establishes with the ventral surface a connection that becomes the mouth. Cells in contact with the pharynx differentiate into the cerebral ganglia (Figs 94*D*, 95*A*). The remaining cells of the interior mass furnish the mesenchyme, muscles, gland cells, etc., and later the reproductive system. The embryo elongates, and at its posterior end appears a gyrodactyloid opisthaptor, in the form of a disk armed with a circle of 16 hooklets (Fig. 95*A*). Each hooklet originates as a secretion between two cells The resemblance of this embryology to that of the Rhabdocoela with its lack of germ layers and formation of organs from cell masses is obvious. The formation of an anal pore (this soon closes) is, however, puzzling and has not been explained.

The development requires four or more weeks, after which the embryo hatches as a larva with four eyes, cilia in transverse bands, a pair of protonephridia, and a hooked opisthaptor as described above (Fig 95*B*) It soon attaches to the gills of a late tadpole and there slowly grows and alters. When the tadpole metamorphoses into a frog, the young flukes pass down the digestive tract into the bladder where they lodge and complete their development; or possibly may infect the frog by way of the anus (Paul, 1938). "The alteration to the adult state includes loss of the eyes, disappearance of the ciliated epidermis, and transformation of the opisthaptor to the *Polystoma* type. „ The six suckers appear two at a time, some of the larval hooks become incorporated into the suckers, and one or two pairs of anchors appear (Fig. 95*C–E*). Ordinarily up to 3 years are required for the attainment of sexual maturity but if the fluke larvae attach to younger tadpoles, they may develop sexually, although otherwise immature, to a condition in which they lay eggs in a few weeks after attachment (Gallien, 1932, 1934; Paul, 1938). Such neotenic forms never mature further nor do they get into the bladder. In the American variety of *P. integerrimum*, it seems probable that the neotenic branchial form alternates with the mature bladder form, i e , that the latter are produced from larvae of the branchial form that invade the frog directly by the anus (Paul, 1938). The close correlation between the maturing and egg laying of the bladder form and that of its host suggests some hormonal control by the latter.

In *Gyrodactylus*, common on the gills of fresh-water fishes, the naked egg lacks yolk cells, obtaining yolk by fusing with sister eggs, and develops

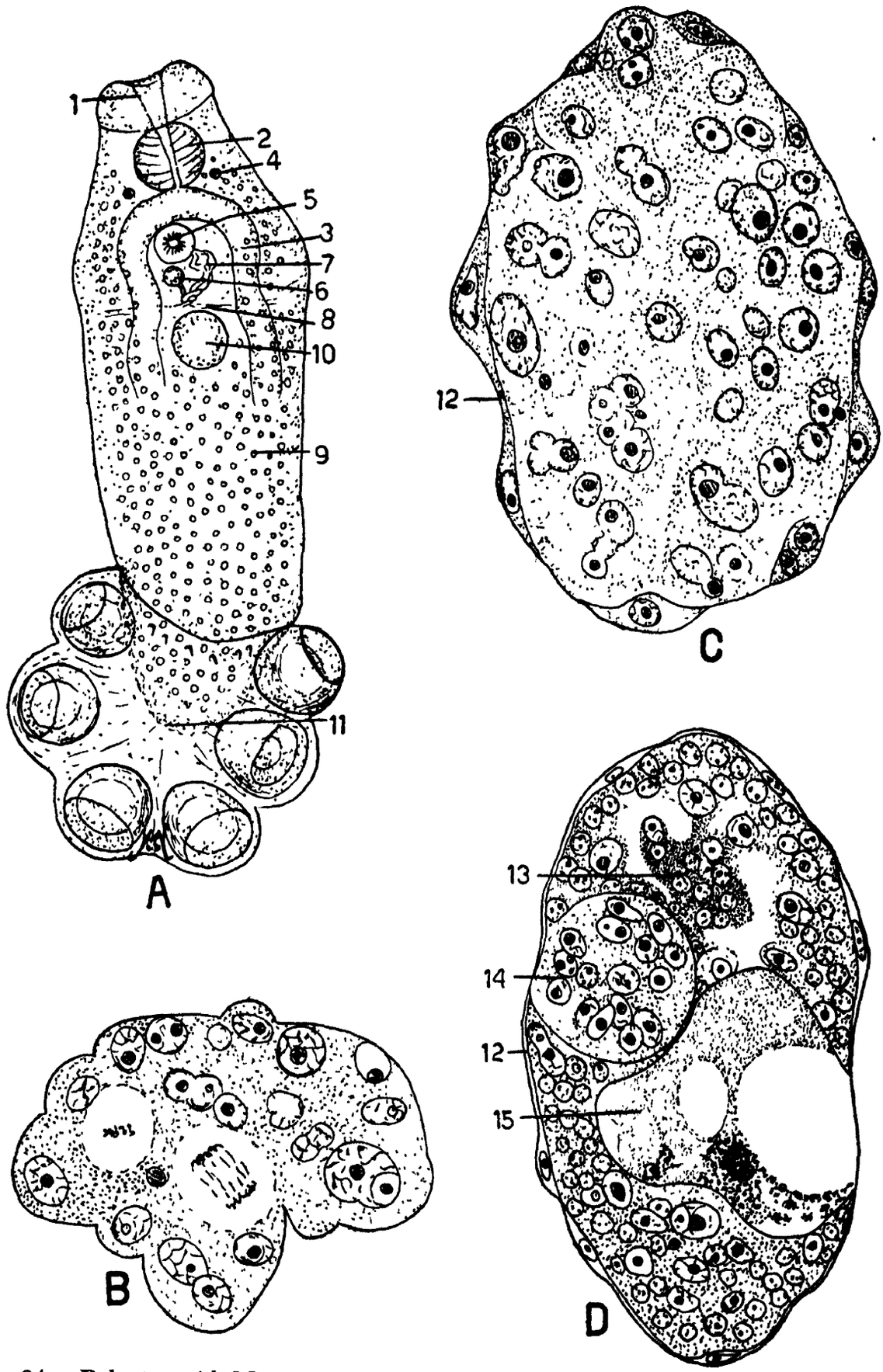

FIG. 94.—Polystomoid Monogenea, development. *A. Polystomoides* (*after Stunkard*, 1917). *B–D.* Development of *Polystoma* (*after Halkin*, 1901). *B.* Early stage showing epiboly. *C.* Later stage, epidermis separating from cell mass. *D.* Organs forming from cell masses, cavity becomes digestive lumen. 1, mouth funnel; 2, pharynx; 3, intestine; 4, nephridiopores; 5, gonopore; 6, ovary; 7, uterus; 8, yolk ducts; 9, yolk glands; 10, testis; 11, opisthaptor with six suckers; 12, epidermis; 13, brain ganglion; 14, primordium of pharynx; 15, lumen of intestine.

in the uterus (Fig. 83*A*). The development is remarkable in that very early a second embryo appears inside the first one, a third inside the second, and even a fourth inside the third. Only the early embryology has been described, and this resembles that of *Polystoma* through the epiboly process (Kathariner, 1904). The successive embryos appear to arise by a kind of polyembryony. When the first embryo has completed its development it passes to the exterior, still enclosing the other embryos, and attaches directly to a host fish.

In the curious genus *Diplozoon*, the capsule attached by a long tangled filament (Fig. 89*E*) to the host gills hatches into a ciliated larva provided with two eyes, digestive system, and a pair of suckers at each end This larva soon loses cilia and eyes and becomes a *Diporpa* larva that must attach to fish gills for further development The Diporpa develops a small sucker near the mid-ventral region and a dorsal papilla; two Diporpae then unite into an X-shape through the grasping of the dorsal papilla of one by the ventral sucker of the other (Fig 96*A*) The two animals grow permanently together in this position and apparently can survive only as such fused pairs When the reproductive system develops, the sperm duct of each opens directly into the yolk duct of the other by a connection probably representing a copulation canal, so that the two flukes are in a permanent state of copulation (Zeller's account, 1872a). Meantime additional suckers have been added to the opisthaptor which in the adult consists of paired ovals, each bearing a row of four suckers supported by cuticularized pieces (Fig 93*C*).

Life cycles have been described for a number of other Monogenea: *Dactylogyrus* (Wilde, 1936; Groben, 1940), *Benedenia* (= *Epibdella*, Jahn and Kuhn, 1932), *Ancyrocephalus* (Siwak, 1931), *Acolpenteron* (Fischthal and Allison, 1941), *Sphyranura* (Alvey, 1936), *Polystomoides* (Paul, 1938), and *Microcotyle* (Remley, 1942). In general the mature fluke lays capsules throughout its life singly at the rate of one every 5 to 10 minutes or at least a few daily. These hatch, usually in several days but requiring up to a month in some species, to a free-swimming larva provided with eyes, cilia usually in the form of three or more incomplete transverse bands, and an opisthaptor of the gyrodactyloid type (Figs. 95*B*, 96*B*). The larvae of *Sphyranura* are not ciliated, however, and creep about to find their host (*Necturus*); they also already have indications of the two adult suckers (Fig. 96*C*). The larva must locate and attach to a host of the same kind within a few hours or it perishes. After attachment, the larva sheds the ciliated epidermis and gradually alters to the adult state. The larval opisthaptor generally alters into the adult opisthaptor but in *Microcotyle* is shed and the adult opisthaptor is a new development. The same probably applies to other Monogenea with complicated type of opisthaptor (Fig. 89*A*). The adult worm probably has a short existence.

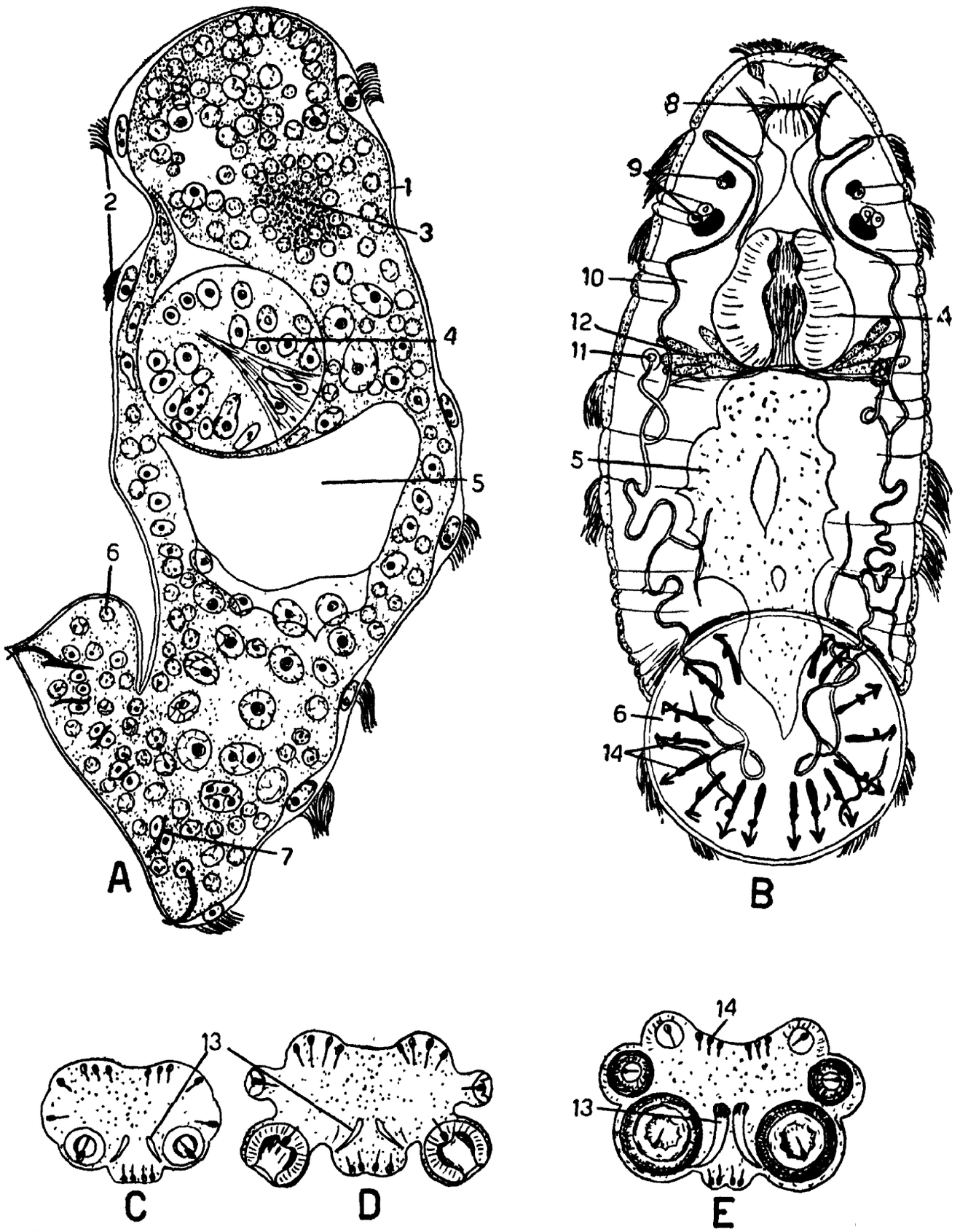

FIG. 95.—Development of *Polystoma* (continued). *A*. Late stage (*after Halkin*, 1901) *B*. Larva of *Polystoma* (*after Halkin*, 1901). *C–E*. Stages in the development of the opisthaptor of *Polystoma* (*after Zeller*, 1872). 1, epidermis; 2, ciliary rings; 3, brain; 4, pharynx; 5, intestine; 6, opisthaptor; 7, haptorial hook developing between two cells; 8, mouth; 9, eyes; 10, nephridium: 11, nephridiopore; 12, pharyngeal glands; 13, anchors; 14, marginal hooks.

Groben estimates the duration of life of *Dactylogyrus* from egg to death at 10 to 12 days, but other forms probably live a month or two, and as noted above *Polystoma* from the frog bladder may have a cycle lasting 3 years.

14. Order Aspidobothria.—The members of this order have long been of uncertain status, being included by some workers in the Monogenea, by others in the Digenea They were separated from both these groups as early as 1856 by Burmeister under the name Aspidobothrii The same separation under the name Aspidocotylea was made by Monticelli in 1892, but later authors again incorporated them into the Digenea. However, recent work (Faust and Tang, 1936, Williams, 1942) again favors regarding them as a distinct group of trematodes, and hence they are here considered an order coordinate with Monogenea and Digenea under Burmeister's name slightly altered.[1]

The order comprises two families, Aspidogastridae and Stichocotylidae, of which the former includes the more typical and best known members.

The Aspidogastridae are characterized by the enormous circular, oval, or elongated sucker divided by septa into one, three, or four longitudinal rows of depressions termed *alveoli* (Figs 84*A*, 97*A*, *B*). This sucker occupies the greater part of the ventral surface and is somewhat set off from the body. The narrowed anterior end of the body has a terminal or slightly subterminal mouth, usually a large funnel-like opening, not provided with an oral sucker although sometimes with muscularized walls (Fig 97*A*). It leads usually by way of a small pharynx into the simple rounded or elongated intestinal sac. Between mouth and pharynx there may be a long buccal tube ("prepharynx") The protonephridia have separate bladders and separate or a common nephridiopore situated dorsally near the posterior end. The reproductive system resembles that of the Digenea except that usually there is a single testis, a Laurer's canal may be present (Fig. 97*C*). Characteristic sense organs occur along the margins of the sucker embedded between the outer ends of the alveoli They are protrusible flask-like bodies with a canal leading to the surface (Fig. 97*D*); each consists of a granular oval mass embedded in fibrous tissue and supplied by a nerve bundle. In the genus *Lophotaspis* the septa of the sucker bear numerous projecting papillae presumably of sensory nature (Fig. 98*A*, *B*).

[1] Faust and Tang have proposed a new name Aspidogastraea for the group on the ground that the name has to be derived from the genus *Aspidogaster*. This ground is mistaken. There are no rules governing the formation of names of higher taxonomic categories, and the creator of an order or class is at liberty to select any name he pleases. The author is strongly opposed to the invention of new names for groups for which names already exist.

The members of this family are entoparasitic in the mantle and pericardial and renal cavities of clams and snails and in the digestive tract of fish and turtles and the bile passages of fish, occurring in both fresh-water and marine hosts. The best known genus *Aspidogaster* has four rows of alveoli; *A. conchicola* is common in the pericardial and renal cavities of fresh-water clams (Fig. 97*A*). *Cotylaspis* (Fig. 97*B*) with three rows of alveoli occurs in the branchial cavity of clams and the intestine of turtles. *Cotylogaster* from the intestine of fishes also has three rows of alveoli of which the middle row is much elongated transversely (Fig. 84*A*); in this

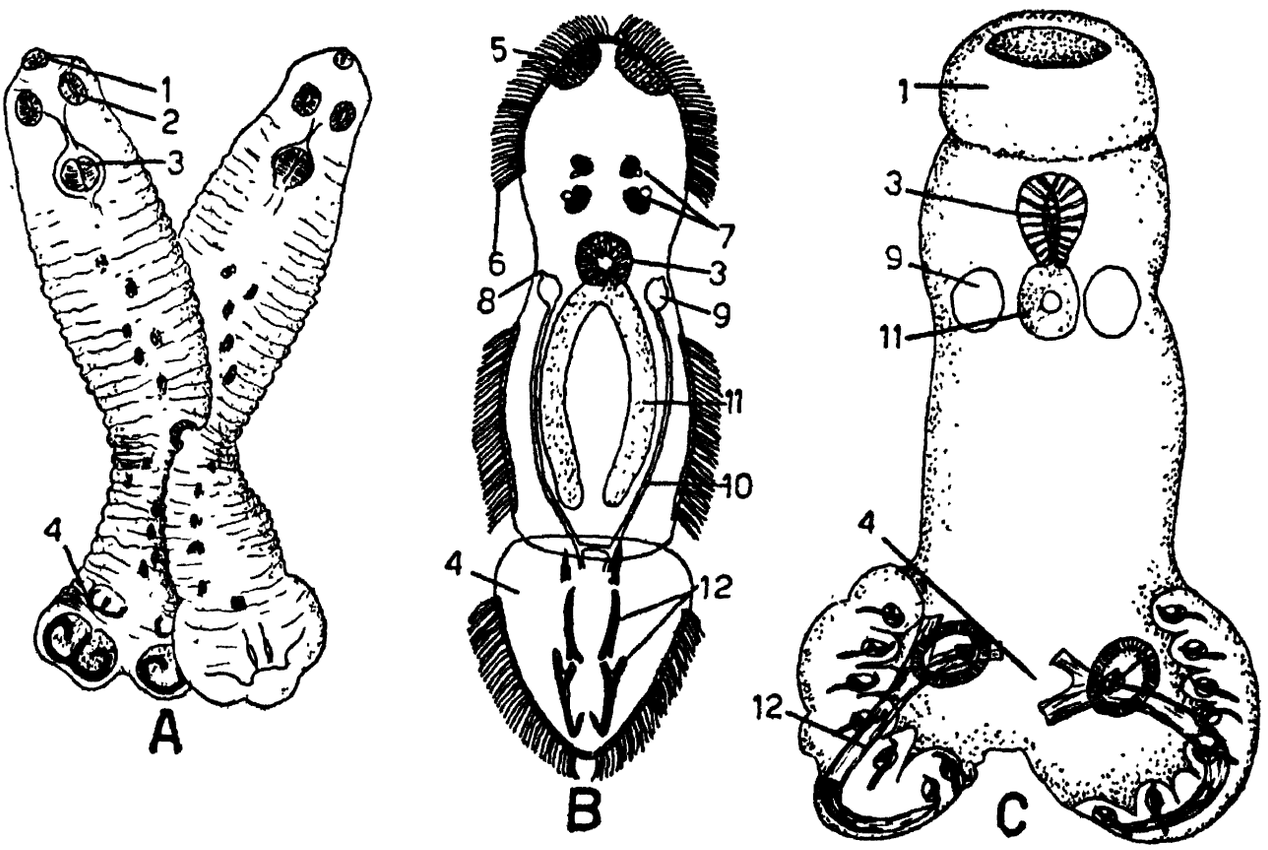

FIG. 96.—Other larval types of Monogenea. *A*. Diporpae larvae of *Diplozoon* (*after Zeller*, 1872). *B*. Larva of *Benedenia* (= *Epibdella*) (*after Jahn and Kuhn*, 1932). *C*. Larva of *Sphyranura* (*after Alvey*, 1936). 1, oral sucker; 2, lateral suckers; 3, pharynx; 4, opisthaptor; 5, anterior adhesive areas; 6, ciliary rings; 7, eyes; 8, nephridiopore; 9, bladder; 10, protonephridium; 11, intestine; 12, anchors.

genus there are also two testes. Other genera are the very long slender *Macraspis* with a single row of alveoli, *Lobatostoma* with lobed mouth rim, and *Lophotaspis* (Fig. 98*A*, *B*) with the papillae mentioned above.

The life cycle of the Aspidogastridae is generally simple, without alternation of hosts. The egg hatches into a fluke-like larva with both oral and posterior suckers or only the latter (Nickerson, 1902; Williams, 1942; Fig. 97*E*). This larva develops directly into the adult by expansion of the posterior sucker into the adult sucker (Fig. 97*F*) and makes its way into other individuals of the same kind of host. Probably aspidogastrids get into fish and turtles through the eating of clams and snails by these vertebrates; but the vertebrate host is not necessary for the completion of the life cycle, for several aspidogastrids occur in the mature state in both

clams and cold-blooded vertebrates. However, *Lophotaspis* apparently has a digenetic type of cycle with a young stage in a marine snail and the adult stage in turtles (Wharton, 1939).

The family Stichocotylidae comprises the single genus *Stichocotyle*, very elongated slender worms around 10 cm. in length that inhabit the bile passage or spiral valve of skates. Of the two known species, one, *S. nephrops*, has a row of up to 30 separated alveoli along the ventral surface. In the other species, *S. cristata*, there is a short row of alveoli anteriorly, and then the rest of the ventral surface bears a continuous longitudinal row of alveoli thrown into ridges and depressions (Faust and Tang, 1936, Fig. 98*C*). The life cycle is partly known for *S. nephrops;* immature worms occur encysted on the intestine of lobsters and presumably develop to maturity only when ingested by skates (Cunningham, 1887; Nickerson, 1894; Odhner, 1910). The cycle is therefore a complex one, involving at least two hosts.

15. Order Digenea: Embryology and Life Cycle.—The digenetic trematodes comprise a bewildering array of families, genera, and species that differ in shape and size, number, location, and size of suckers, length of intestinal crura, flame-bulb arrangement, and especially details of the reproductive system. New species are described almost daily, and investigation of almost any vertebrate not hitherto examined for this purpose is certain to yield new forms.

The Digenea with rare exceptions are entoparasites of vertebrates, fresh-water, marine, and terrestrial. In the adult stage they occur primarily in the digestive tract, particularly the intestine, and in various appendages of the digestive tract, such as lungs, liver, gall-bladder and bile passages, and urinary bladder; other sites are the kidneys and ureters, air sacs of birds, other parts of the respiratory system, coelom, eye, and various head cavities. Several families represented by the genera *Sanguinicola*, *Spirorchis*, and *Schistosoma* (old name, *Bilharzia*), flukes of elongated form, inhabit the blood of fish, turtles, birds, and mammals A tendency to ectoparasitism is exhibited by a few Digenea that live on the gills of fishes or in the mouth and pharyngeal cavities, or around the anus, etc. In the adult stage, the Digenea are capable of little movement and remain at the site of attachment.

As the main features of the anatomy were given above, it remains here to consider the life cycle. The Digenea, as the name implies, have complicated life cycles, involving typically four larval forms and three, sometimes four, different hosts. That the life cycle of the Digenea involves an alternation of hosts and that cercariae, previously considered to be adult animals, are a larval stage of the Digenea, was first recognized by Steenstrup in 1842. Many contributions to digenetic life cycles followed (for an annotated bibliography of this period see Braun, 1879–

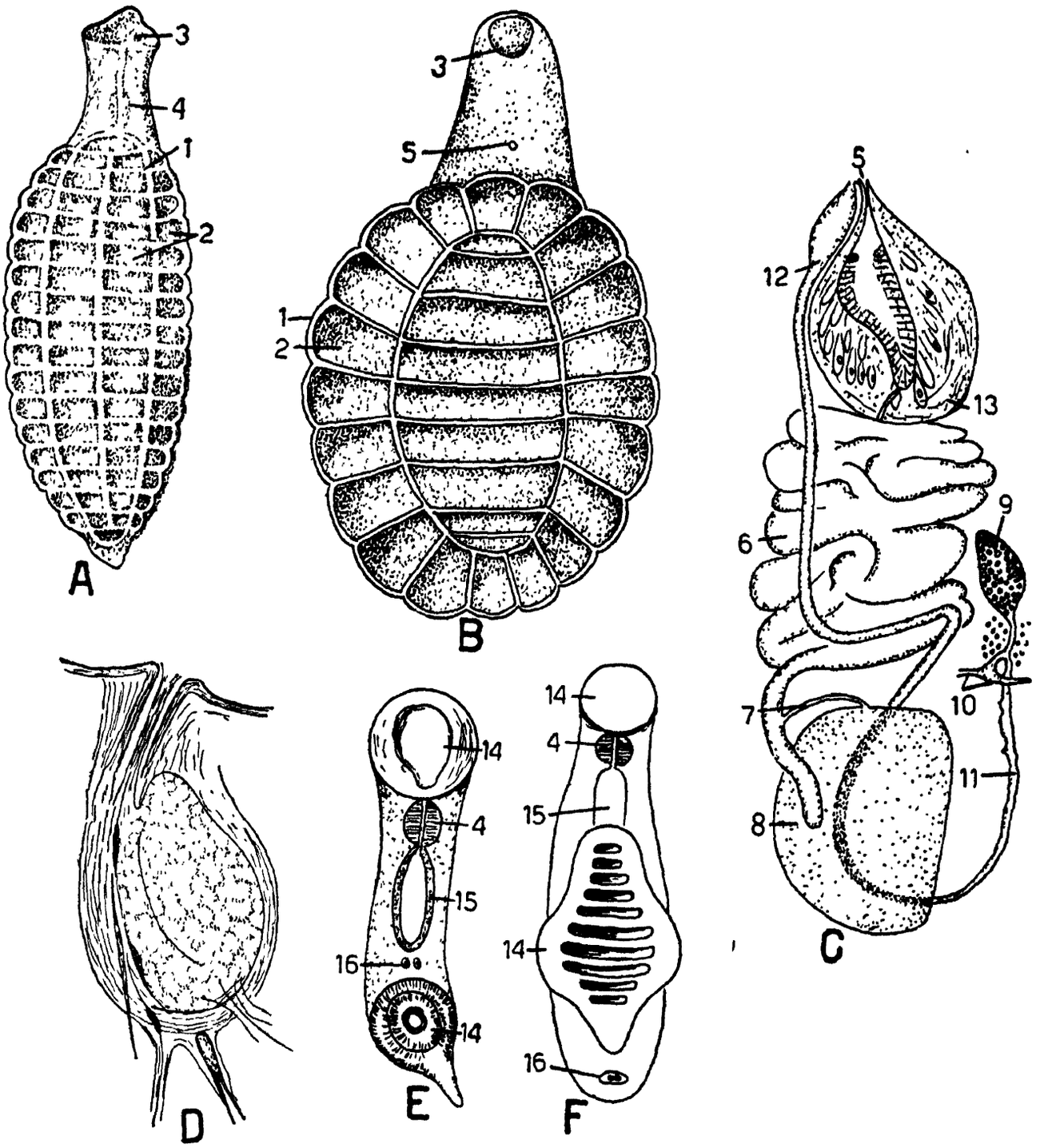

FIG. 97.—Types of Aspidobothria. *A. Aspidogaster conchicola* (*after Monticelli*, 1892). *B. Cotylaspis* (*after Osborn*, 1903). *C.* Reproductive system of *Cotylaspis* (*after Stunkard*, 1917). *D.* Longitudinal section of sense organ of sucker margin of *Cotylogaster* (*after Nickerson*, 1902). *E, F.* Larval stages of *Aspidogaster* (*after Voeltzow*, 1888). *E.* Newly hatched larva. *F.* Later stage, definitive sucker developing from larval posterior sucker. 1, sucker; 2, alveoli; 3, mouth funnel; 4, pharynx; 5, gonopore; 6, seminal vesicle; 7, sperm duct; 8, testis; 9, ovary; 10, yolk ducts; 11, ovovitelline duct; 12, uterus; 13, cirrus sac; 14 larval suckers; 15, intestine; 16, nephridiopore.

1893), but the first complete account of the cycle was that of the liver fluke of the sheep by A. P. Thomas in 1883, an article that has become a zoological classic. Following the lead given by Thomas many life cycles were worked out, and research on trematode life histories constitutes today an active branch of investigation throughout the world.

a. Embryology.—Development usually proceeds while the capsules are passing along the uterus and out of the host but may be deferred until the exterior is reached. Hence newly laid capsules may contain

any stage from the uncleaved egg to the finished larva, and hatching of capsules may require a few hours or less up to several weeks. Sometimes the larva has already hatched within the parent uterus (Cyclocoelidae). Although the embryonic development of the Digenea was described in several older papers (Schauinsland, 1883; Looss, 1892; Goldschmidt, 1905; Schubmann, 1905; Ortmann, 1908), the best and most exact accounts are those of Ishii (1934), P. D. Chen (1937), and Rees (1940). As these are in substantial agreement although concerned with different species, they may be taken as generally applicable to the group.

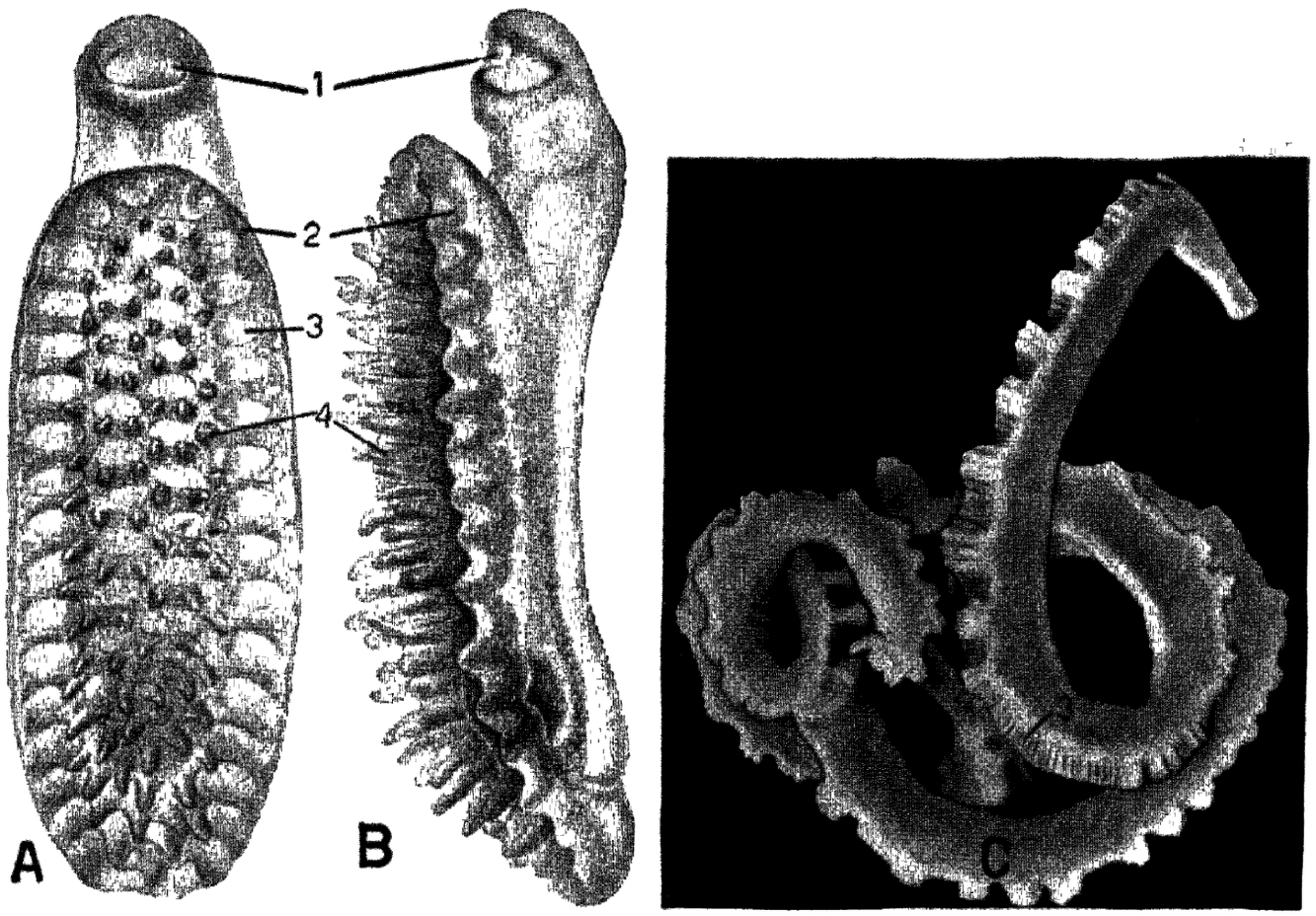

FIG. 98.—Aspidobothria (continued). *A. Lophotaspis*, ventral view. *B. Lophotaspis*, lateral view. (*A*, *B*, *after Ward and Hopkins*, 1931.) *C. Stichocotyle cristata* (*after Faust and Tang*, 1936). 1, mouth; 2, sucker; 3, alveoli; 4, papillae.

The egg cleaves into a *propagatory* cell and a slightly larger *somatic* cell (Fig. 99*A*). The latter divides to form a ball of unequally sized cells (Fig. 99*B*) of which certain small cells pass to the periphery forming just inside the capsule a vitelline membrane that encloses embryo and yolk cells (Fig. 99*C*). The propagatory cell, distinguishable by certain cytological details, now divides repeatedly and at each division one daughter retains the characteristics of the propagatory cell while the other is a somatic cell contributing to the embryo. The ball of cells elongates and differentiates into the first larval form, the *miracidium* (Fig. 99*D*). Its surface cells differentiate into an epidermis, later ciliated. An anterior mass of cells produces the brain and other parts of the nervous system. From a strand of cells arises a pair of protonephridia. The propagatory

cell remaining after the divisions mentioned above retires into the rear part of the embryo (Fig. 99*D*) where it divides to form a number of cells that produce the next larval type. It will be perceived that there is no formation of germ layers in this development and that the embryology in general resembles that of ectolecithal Turbellaria.

b. Miracidium.—As just noted, the embryo differentiates directly into a ciliated larval form, termed the *miracidium.* This escapes from the capsule by butting against the operculum until the latter opens; gland secretions probably also aid the escape. As the miracidium is a swimming larva requiring an aquatic environment it occurs in typical form only when the capsules are shed into water as is usually the case.

The miracidium (Fig. 100) is a minute oval creature that darts about rapidly seeking a suitable host. It is clothed in a flattened ciliated epidermis consisting of a definite number of cells, usually 18 to 21, arranged in four or five tiers (Fig. 99*E, F*). A table of the known arrangements is given by Bennett (1936); the most common types are 6, 8, 4, 2 for amphistomes; 6, 6, 4, 2 for echinostomes; 6, 8, 4, 3 for strigeids; and 6, 6, 3, 4, 2 for liver flukes. The numbers give the number of cells in each tier from the anterior end backward. The anterior tip of the larva is devoid of cilia and forms a mobile protrusible *apical papilla* or *terebratorium* (Fig. 100) that in some cases is sufficiently firm and muscular to constitute a *rostrum.* This papilla may be armed with a protrusible stylet and also bears the openings of glands, all structures associated with host penetration. Two, sometimes three, eyes are often present over the brain. In the groove between the first and second tiers of epidermal cells there usually occurs on each side a *lateral papilla,* presumably sensory, although some observers have seen drops of secretion exuding from them. In some miracidia there are additional sensory papillae (up to 24) in a circle in this groove (Fig. 99*F*), and similar papillae may occur in the groove between the third and fourth tiers (Rees, 1940).

Beneath the epidermis is found a thin subepidermal musculature of outer circular and inner longitudinal fibers, and beneath this is a layer called the subepithelium. This in some miracidia forms a definite one-layered epithelium (Fig. 100*A*) but in others is more like mesenchyme; probably it represents the mesenchyme. The interior of the larva contains glands, the nervous system, the nephridia, and the propagatory cells and balls (Fig. 100). Attached by a stalk to the center of the apical papilla is a large rounded multinucleate sac of coarsely granular cytoplasm. This was formerly considered to be a rudimentary gut but is now regarded as a gland. Probably this *apical gland* is homologous with the frontal gland of the Turbellaria. There also often open on the apical papilla one to several pairs of large unicellular *cephalic* or *penetration* glands. The brain is a large mass behind the apical gland; usually nerves

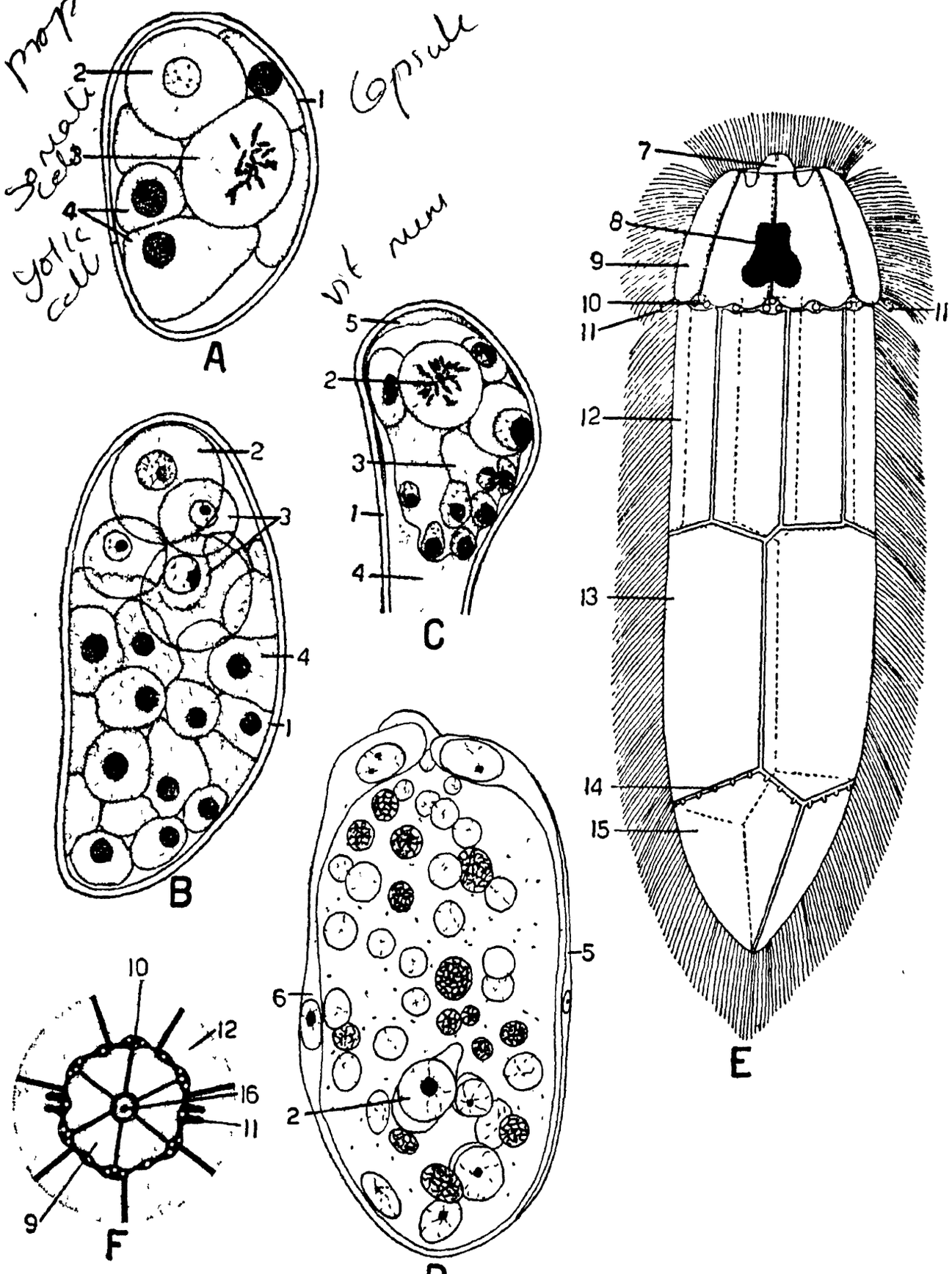

FIG. 99.—Development of Digenea. *A–C* Early development of *Parorchis* (*after Rees*, 1940). *A* First cleavage of fertilized egg into propagatory cell and somatic cell, entire capsule shown. *B* Entire capsule showing stage of four blastomeres. *C* Later stage, only part of capsule shown. *D* Late embryo, *Paragonimus*, epidermis differentiated (*after Chen*, 1937). *E* Miracidium of *Parorchis*, showing epidermal cells. *F* Anterior end of miracidium of *Parorchis*. (*E*, *F*, *after Rees*, 1940.) 1, capsule, 2, propagatory cell, 3, somatic cell; 4, yolk cells, 5, vitelline membrane, 6, epidermis, 7, apical papilla, 8, eyes, 9, first tier, 6 cells; 10, ring of sensory papillae, 11, lateral papilla, 12, second tier, 7 cells, 13, third tier, 3 cells, 14, ring of papillae between third and fourth tiers, 15, last tier, 3 cells; 16, opening of apical gland.

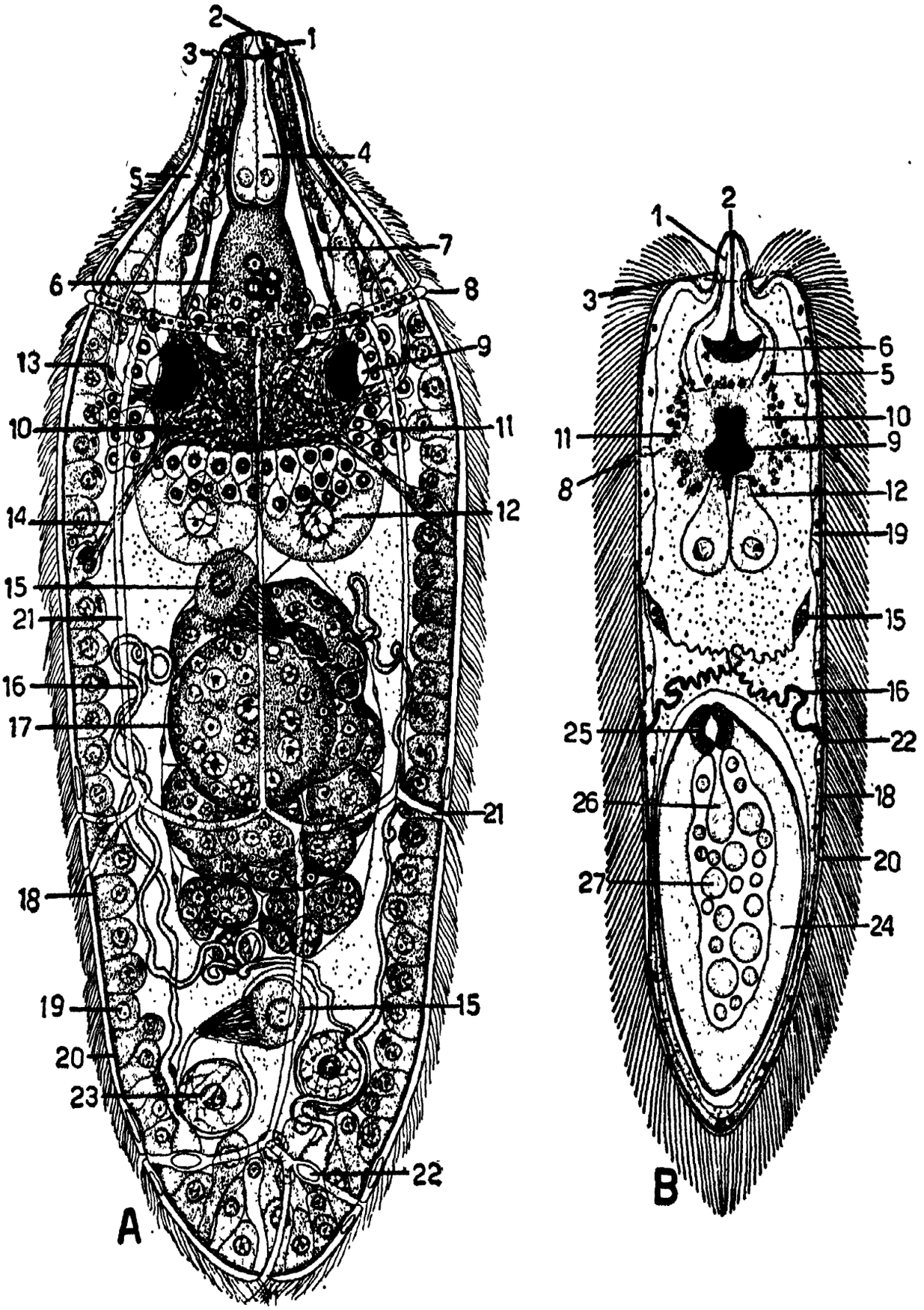

FIG. 100—Structure of the miracidium. *A*. Miracidium of *Heronimus* (*after Lynch*, 1933). *B*. Miracidium of *Parorchis* (*after Rees*, 1940), type containing fully developed redia. 1, apical papilla; 2, opening of apical gland; 3, opening of penetration glands; 4, additional glands of uncertain nature; 5, duct of penetration glands; 6, apical gland; 7, anterior nerve; 8, lateral sensory papilla; 9, eyes; 10, brain; 11, nerve cells; 12, penetration glands; 13, lateral nerve; 14, posterior nerve; 15, flame bulb; 16, nephridium; 17, germ balls; 18, epidermis; 19, subepithelium; 20, subepidermal musculature; 21, boundary of epidermal cells; 22, nephridiopore; 23, athrocyte; 24, redia; 25, pharynx of redia; 26, intestine of redia; 27, germ balls of redia.

may be seen proceeding from it. There is a pair of protonephridia, each with one or two flame bulbs; each is a sinuous tube proceeding to a nephridiopore situated laterally between the last two tiers of cells or penetrating the third or fourth tier. In the rear part of the larva are found a number of propagatory cells, some or all of which may have divided to form balls of cells known as *germ balls;* these are in reality embryos.

Very peculiar miracidia occur in the families Bucephalidae (= Gasterostomidae) and Brachylaimidae. In these the epidermis lacks cilia, and instead the cilia are borne on projecting rods (Fig. 106*B*, Woodhead, 1929; Allison, 1943).

Further details of miracidial structure with figures will be found in such articles as those of Coe (1896), Cort (1919), Lynch (1933), the Hunters (1935b), Bennett (1936), Yamaguti (1940), and Willey (1941).

Unless the miracidium finds a suitable host within a few to 24 hours it perishes. This host, called the first intermediate host, is practically always a mollusk, usually a snail, less often a bivalve. Only one exception is known, a case in which the first intermediate host is a polychaete annelid (Linton, 1915; Martin, 1944). Host specificity varies greatly, i.e., in some flukes only one particular species of mollusk is suitable, but in most more than one species will serve; and trematodes transported into new countries may become adapted to new species of mollusks as intermediate hosts. The miracidium adheres to the mollusk by its apical papilla and with the aid of the flesh-dissolving secretions of its apical and penetration glands rapidly passes (Fig. 126) into the mollusk, often by way of the latter's branchial apparatus, and lodges in almost any organ or tissue, most commonly the digestive gland ("liver") or the gonads. The miracidium sheds its ciliated epidermis either during its passage through the host epidermis (Fig. 126) or shortly after attaining the interior of the mollusk where it undergoes extensive alteration into the next larval stage, the *sporocyst* or *germinal sac.*

c. Sporocyst.—This is a rounded, elongated, or vermiform (to 25 mm. long) hollow structure (Fig. 101) covered with a thin cuticle beneath which is the miracidial muscle layer and mesenchyme (Fig. 101*A*). Other structures of the miracidium generally disappear except the protonephridia. The hollow interior contains propagatory cells and germ balls (Fig. 101*C*) or else these are embedded in the mesenchymal layer of the wall. The germ balls may multiply by dividing up into other germ balls. In some families (Bucephalidae, Brachylaimidae), the sporocyst branches and ramifies through the host tissue (Fig. 101*E*). The sporocyst moves about more or less in the host tissue from which it absorbs nutrition and to which it is often highly destructive and its germ balls develop either into daughter sporocysts or into the next larval stage,

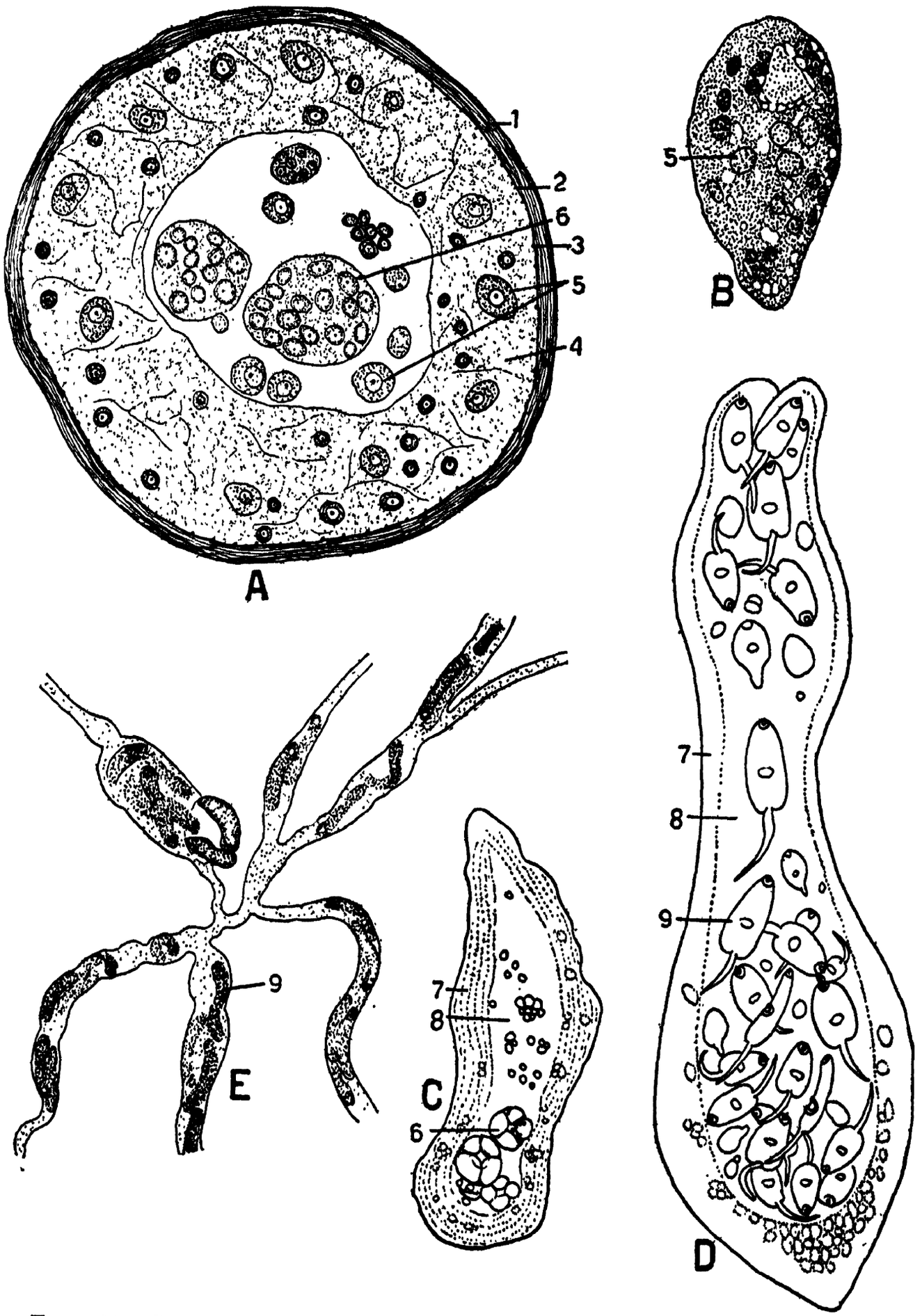

FIG. 101.—Sporocyst. *A*. Section through a sporocyst (*after Tennent*, 1906). *B*. Very young sporocyst (of the amphistome, *Cotylophoron*, *after Bennett*, 1936). *C*. Young sporocyst (plagiorchid fluke, *Renifer*). *D*. Mature daughter sporocyst (*Renifer*), filled with cercariae. (*C*, *D*, *after Byrd*, 1935). *E*. Branching type of sporocyst of the gasterostomes (*after Palombi*, 1934). 1, cuticle; 2, circular muscle layer; 3, longitudinal muscle layer; 4, mesenchyme; 5, propagatory cells; 6, germ balls; 7, wall; 8, hollow interior; 9, cercariae.

the redia. If daughter sporocysts are formed, then rediae are lacking from the life cycle and the final larval form, the cercaria, arises directly in the daughter sporocysts (Fig. 101*D*). Hence mature sporocysts may be filled either with daughter sporocysts or with rediae or with cercariae.

d. Redia.—The redia develops from a propagatory cell or germ ball in practically the same manner as the miracidium does from the egg and propagatory cells are again set aside for the formation of the cercariae or else germ balls for this purpose are split off from preexisting germ balls. The redia (Fig. 102*A*, *C*) is of elongated form usually with two ventral projections near the posterior end and a birth pore near the anterior end, where there also may be a collar-like welt (Fig 102*C*). The body wall consists of the usual cuticle, muscular and mesenchymal layers. The mouth at the anterior end leads into a muscular pharynx followed by a simple sacciform intestine. Penetration glands are sometimes present There is a pair of cerebral ganglia at the sides of the pharynx from which nerves extend. Protonephridia with flame bulbs are present (Fig 102*B*). The hollow interior is filled with germ balls in process of development (Fig 102*A*). The rediae escape from the sporocyst and move about in the host tissues on which they feed. They give rise either to a new generation of rediae, rarely more than one, or to cercariae and in any event cercariae are the final product of the redial generations (Fig. 102*C*). The cercariae are typically swimming larvae, they escape from the redia (by way of the birth pore when this is present) and exit from the molluscan host into the surrounding water. The time that elapses between the penetration of a miracidium into the host and the emergence of cercariae is naturally variable, depending on external factors, especially temperature, but generally occupies some weeks or even months.

e. Cercaria.—The development of a cercaria from a germ ball is similar to that of the preceding stages, and propagatory cells of direct descent from the original propagatory cell are again set aside to furnish the reproductive system of the adult fluke. As already noted, cercariae develop either in rediae or in daughter sporocysts; they sometimes leave the parent at an early stage and complete their development in the host tissues. The cercaria has a higher grade of organization than any of the preceding stages and already considerably resembles an adult fluke (Figs. 102, 103, 104). It consists of a broad to elongated oval body and a simple or forked tail. In early stages the cercaria is covered by a thin epidermis, but this is soon shed and replaced by a cuticle. This is often spiny in whole or in part or may bear bristles; a crown of larger spines may occur on the anterior tip. A shoulder girdle of spines is characteristic of echinostome cercariae but may be lacking in some species. Beneath the cuticle is found the usual muscle layer and a number of gland cells, the *cystogenous glands* (Fig. 103*A*). Oral sucker and acetabulum

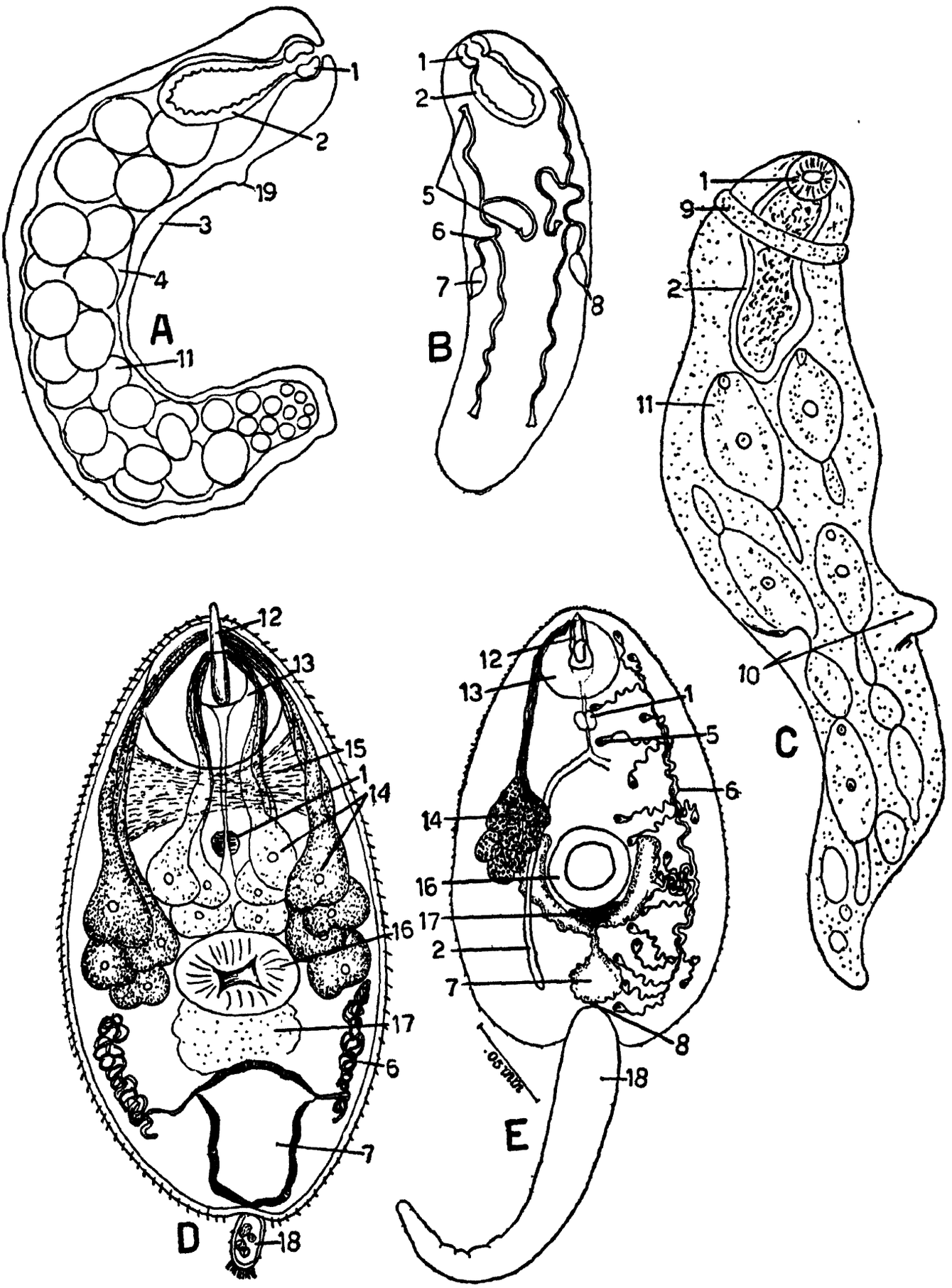

FIG. 102.—Rediae, types of cercariae. *A*. Redia of the amphistome *Cotylophoron*, type without collar or appendages. *B*. Same showing excretory system. (*A*, *B*, *after Bennett*, 1936.) *C*. Redia of the liver fluke (*after Ross and McKay*, 1929); birth pore does not show. *D*. Microcercous cercaria of *Paragonimus* (*after Ameel*, 1932). *E*. Stylet cercaria of a plagiorchid reniferine fluke (*after Byrd*, 1935). 1, pharynx; 2, intestine; 3, wall; 4, central hollow containing young cercariae; 5, flame bulbs; 6, protonephridia; 7, bladder; 8, nephridiopore; 9, collar; 10, lateral projections; 11, cercariae; 12, stylet; 13, oral sucker; 14, penetration glands; 15, brain; 16, acetabulum; 17, primordium of reproductive system; 18, tail; 19, birth pore.

are present except in monostome cercariae, which lack an acetabulum. The digestive system resembles that of adult flukes, consisting typically of buccal cavity encircled by the oral sucker, pharynx, esophagus, sometimes very long, and bifurcated intestine, but parts are often lacking. The anterior end may be armed with a protrusible stylet and bears the openings of the penetration glands, large gland cells occurring in a cluster in either side of the body with long necks running forward (Fig 102*D*, *E*). There is a pair of protonephridial tubules, each provided with a number of flame bulbs (Fig. 102*E*) whose grouping has been considered in recent years of great taxonomic importance (Faust, 1932). However, it is probably not so diagnostic as considered by some, and the same arrangement may be found in unrelated forms The two tubules meet at the posterior end of the body in a bladder from which a single stem proceeds along the tail; this then usually divides into two forks each of which opens by a pore on the side of the tail (Fig 103*E*). In fork-tailed cercariae, the tubule divides where the tail forks and each branch then extends to the tip of the fork (Fig. 124*D*). The development of the tubules has been followed in a number of digenetic cercariae (Komiya, 1938, Hussey, 1941) and found to be similar in all. There first appear two tubules each with one or two flame bulbs and a pore as in the miracidium. As the tail develops the pores and terminal parts of the tubules are usually drawn into the tail, and fusion of the two tubules occurs at the rear end of the cercarial body where the fused portion also develops a bladder (Fig. 105) When the tail is shed the bladder is thus left at the rear end of the definitive fluke where a new common pore is established. The nervous system is similar to that of the adult; two, rarely three, eyes similar to those of the miracidium, are often present. The tail, formed by outgrowth, is of various shapes (see below) and is provided with muscles and often also with gland cells and hairs or spines.

Various types of cercariae occur, and these have been classified by Luhe (1909), Cort (1915b), Faust (1919), Sewell (1922), and others. They are broadly grouped into gasterostome, monostome, amphistome, echinostome, holostome, and distome cercariae on the same characters as give these names to adult flukes. The very numerous distome cercariae have been named on the basis of tail features, although these do not necessarily express taxonomic relationship. Distome cercariae with heavy broad tails are termed *rhopalocercous;* with very small tails, *microcercous* (Fig. 102*D*); with a cup-like tail, really a sucker provided with adhesive glands, *cotylocercous* or *cotylomicrocercous* (Fig. 103*F*, McCoy, 1929a; Palombi, 1938; Dobrovolny, 1939; Neuhaus, 1940; Hunninen and Cable, 1941, 1943); *furcocercous* with forked tails (Fig. 120*C*, H. M. Miller, 1926); *pleurolophocercous* when the tail has a fin (Fig. 103*A*, Lundahl, 1941; Cable and Hunninen, 1942a); *trichocercous* when the tail is beset with

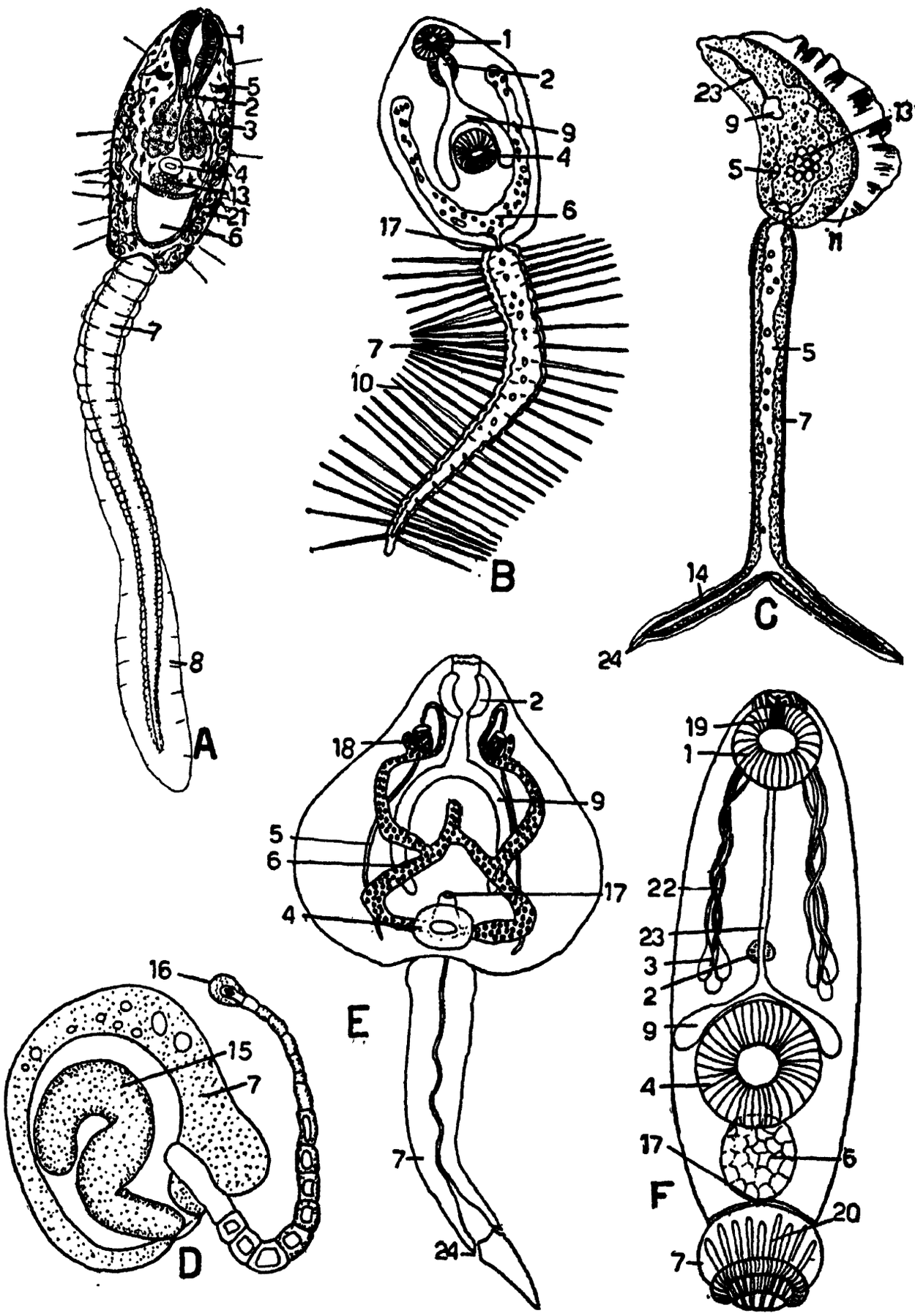

FIG. 103.—Types of cercariae (continued). *A*. Pleurolophocercous cercaria of *Opisthorchis sinensis* (*after Komiya and Tajimi*, 1940). *B*. Trichocercous cercaria (*after Palombi*, 1934). *C*. Lophocercous furcocercous cercaria of *Sanguinicola* (*after Ejsmont*, 1925). *D*. Cystophorous cercaria of *Halepegus* (*after Rankin*, 1944a). *E*. Amphistome cercaria of *Cotylophoron* (*after Bennett*, 1936). *F*. Cotylocercous cercaria (*after Palombi*, 1938). 1, oral sucker; 2, pharynx; 3, penetration glands; 4, acetabulum; 5, protonephridium; 6, bladder; 7, tail; 8, tail fin; 9, intestine; 10, bristles on tail; 11, body fin; 12, esophagus; 13, primordium of reproductive system; 14, tail forks; 15, body of cercaria; 16, appendage; 17, nephridiopore; 18, eyes; 19, stylet; 20, adhesive glands; 21, cystogenous glands; 22, ducts of penetration glands; 23, esophagus; 24, larval nephridiopore.

bristles (Fig. 103*B*, Palombi, 1932b; Martin, 1938; Cable and Hunninen, 1942b); and *cystocercous* when the proximal end of the tail contains a cavity into which the cercarial body can be withdrawn (Figs. 103*D*, 104). Furcocercous cercariae are characteristic of the families Strigeidae and Schistosomatidae; the stem may be long and the forks short (*brevifurcate*) or vice versa (*longifurcate*). The most peculiar of all cercariae are the cystocercous forms. These really consist of three types (Horsfall, 1934; E L. Miller, 1936). In the cystocercous type proper, also called *mirabilis* type, the tail is large and thick with two anchoring flaps at the rear (Fig. 104*B*); this kind of cercaria belongs to the family Azygiidae (Ward, 1916; Faust, 1918c; Smith, 1932; Horsfall, 1934). The *macrocercous* or *gorgoderine* cercariae, typical of the family Gorgoderidae, have simple, often long tails (Fig. 104*A*, *D*) with or without a vesicular swelling containing the cercarial body (Krull, 1934a; E. L. Miller, 1936; Steelman, 1939, Baker, 1943). The most peculiar are the *cystophorus* types in which the tail consists of a rounded vesicle bearing various long appendages (Fig. 103*D*, Cort and Nichols, 1920; Thomas, 1939; Hunninen and Cable, 1943b; Rankin, 1944a). Cystophorous cercariae are characteristic of the family Hemiuridae and related forms. When the body of the cercaria bears a dorsal fin, the name *lophocercous* (Fig. 103*C*) is applied. A considerable number of cercariae are armed at the anterior end with a boring spine and are termed *stylet* or *xiphidiocercariae* (Fig. 102*E*). Cercariae that lack a tail are known as cercariaea (Fig. 104*C*). Special types of cercariae occur in the gasterostomes and holostomes (see later). Very curious are the marine *rattenkonig* cercariae which are united into a writhing ball by the tips of their long tails (Fig. 104*E*). While the family and even the genus to which a cercaria belongs may be recognizable through its structure, this is often not the case, and large numbers of cercariae have been described and named of which the adult is unguessed

The number of cercariae produced is often prodigious. Infected snails may give off hundreds of cercariae daily over long periods of time. Thus Rothschild (1942) records an individual of the common shore snail *Littorina littorea* that gave off cercariae of *Cryptocotyle lingua* for 7 years at the rate of about 1,000,000 per year, or about 830 daily. This snail was presumably infected with more than one sporocyst, but reinfection was prevented. The number of cercariae coming from a single miracidium (hence from one fertilized egg) varies according to the details of the life cycle from as few as 50 to 200 up to a million in strigeids (discussion in Cort, 1944); probably the usual figure is ten to fifty thousand.

Innumerable studies of cercariae have been published; among the more extensive ones may be mentioned those of Cort (1915b), Faust (1918b, 1918d), H. M. Miller (1925–1928), Wesenberg-Lund (1934),

E. L. Miller (1936), Porter (1938), Palombi (1934, 1938, 1940), Brooks (1943).

When fully developed, the cercariae leave the redia or daughter sporocyst, bore through the host tissues, and escape into the water where they swim about for a few minutes to 2 or 3 days. They may encyst on plants or inert objects; but more often they penetrate or are eaten by a new host, the second intermediate host, in or on which they encyst. Unless the suitable host is found they perish. The second intermediate host may be a medusa, turbellarian, annelid, crustacean, mollusk, insect larva, or vertebrate, mostly fish and amphibians. Penetration into animals is accomplished by boring movements of the anterior tip aided by the stylet if present and particularly by the flesh-dissolving action of the secretion of the penetration glands. As the cercaria passes into the host it sheds its tail by a sudden jerk. The cyst is usually a thick-walled sphere (Fig. 106*A*) secreted by the cystogeneous glands but may consist wholly or partly of host connective tissue. Rarely encystment occurs by the tail coiling about the cercarial body (Palombi, 1937a). The encysted cercaria must be eaten by the final or definitive host before it can develop into the adult fluke. In rare cases there is a third intermediate host so that there are two successive encysted stages (*Alaria*, see under family Strigeidae).

f. Metacercaria.—The encysted larva, termed *metacercaria*, is a juvenile fluke. The typical larval organs such as eyes, stylet, cystogenous and penetration glands, etc., disintegrate gradually following encystment and the metacercaria develops the general structural features of the adult fluke (Fig. 106*A*). The reproductive system, however, remains rudimentary and its differentiation and other changes take place after the metacercaria has entered the definitive host. Following ingestion of the encysted metacercariae or of the animals containing them, the cyst wall dissolves in the host's digestive tract, chiefly in the intestine, and the young fluke migrates to the location typical of the species. During this migration and after attachment to the selected site the fluke continues to grow and mature; several to a number of days are required for the attainment of sexual maturity.

g. Variations of the Life Cycle.—The foregoing recounts the usual life cycle, but many variants occur as adaptive short cuts. Not uncommonly the miracidium does not lead a free existence but hatches only after the capsules have been ingested by the proper host; such miracidia may be devoid of cilia and may be provided with an apical crown of thorns for easier invasion of host tissue (Fig. 111*B*). Cycles of this type occur not only in flukes that have all their stages in terrestrial animals but are also found where aquatic hosts are involved. A few cases are known in which the miracidium already contains a fully developed redia (Fig. 100*B*),

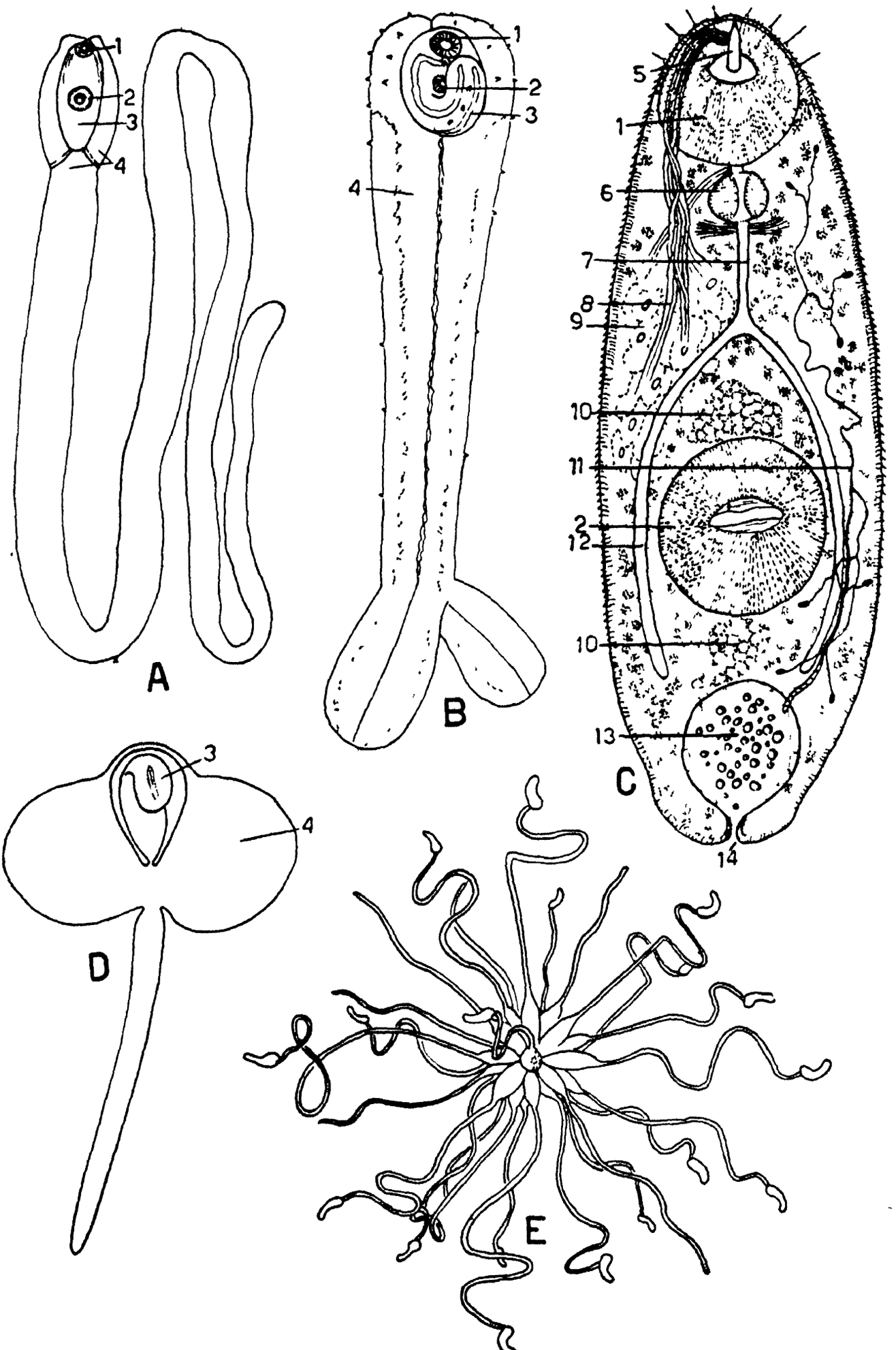

FIG. 104.—Types of cercariae (continued). *A* Macrocercous cercaria of a gorgoderine fluke (*after Krull*, 1934a). *B*. Cystocercous cercaria of the Azygiidae (*after Horsfall*, 1934). *C*. Cercariaeum, Zoogonidae (*after Stunkard*, 1943). *D*. Another kind of macrocercous

sometimes provided with penetration glands, so that the sporocyst stage is skipped (*Typhlocoelum*, Szidat, 1932b; Stunkard, 1934; *Parorchis*, Stunkard and Cable, 1932; Rees, 1940; *Stichorchis*, Bennett and Humes, 1939). The cercariae of the Schistosomatidae and some other blood flukes penetrate the definitive host directly and omit the encysted stage, hence do not require a second intermediate host. Cercariaea (tailless cercariae) may occur in either aquatic or terrestrial hosts and may or may not be encysted; they usually do not lead a free existence but remain in the snail host without further development until the latter is eaten by the second intermediate or the definitive host.

h. The Nature of the Digenetic Life Cycle.—The type of reproduction involved in the larval stages of the Digenea has been the subject of discussion for over a hundred years. The different views that have been held are reviewed by P. D. Chen (1937), Rees (1940), and Cort (1944) and as they are mostly of historical interest will not be recounted here. A widely accepted theory was that the reproductive processes in the sporocyst and rediae are parthenogenetic in nature, i.e., that the propagatory cells are eggs that undergo parthenogenetic development, and maturation processes were described by some authors. Under the influence of this theory, the following terms were introduced into the literature and received wide usage: *parthenitae* for the sporocysts and rediae, *adolescariae* for cercariae and metacercariae, and *maritae* for adult flukes. As it is now practically certain that the parthenogenesis theory is erroneous, these terms will pass out of the literature and hence have not been employed here. According to the best work on digenetic life cycles, that of Ishii (1934), Chen (1937), and Rees (1940), the reproductive processes in the sporocysts and rediae are of the nature of *polyembryony*, a simple multiplication of propagatory cells by mitosis or of germ balls by breaking up into other germ balls. The digenetic life cycle is therefore similar to that of hydroid coelenterates, comprising a period of asexual multiplication during immature stages followed by sexual reproduction in the mature stage. Although some regard this cycle as constituting an alternation of asexual and sexual generations it is better to view it simply as a continuous ontogeny involving asexual multiplication in larval stages.

16. Some Families of the Digenea and Their Life Cycles.—The Digenea are classified into a large number of families, mainly on the basis of details of the reproductive system; only the more interesting and important of these can be considered here.

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gorgoderine cercaria (*after Baker*, 1943). *E.* Rattenkönig (ball of cercariae attached by their tail ends) (*after Ward*, 1916). 1, oral sucker; 2, acetabulum; 3, body of cercaria; 4, tail of cercaria; 5, stylet; 6, pharynx; 7, esophagus; 8, ducts of penetration glands; 9, penetration glands; 10, primordium of reproductive system; 11, nephridium; 12, intestine; 13, bladder; 14, nephridiopore.

a. Family Bucephalidae (= *Gasterostomidae*) —This family, known as gasterostomes, is distinguished from all other Digenea by the location of the mouth at the middle of the body (Fig. 106*D*) and hence is often separated as a suborder Gasterostomata from the remaining digenetic families, constituting the suborder Prosostomata, in which the mouth is at the anterior end. This classification is considered of doubtful validity at present. The anterior end bears a simple (*Bucephalopsis*) or lobed (*Bucephalus*) oral sucker or has a generally lobed hood-like extension (*Rhipidocotyle*, Fig 84*C*) or instead of a sucker has a protrusible piston-like muscular cushion (*Prosorhynchus*, Fig. 106*D*). The mouth leads by way of a pharynx into a small sacciform intestine; this digestive system

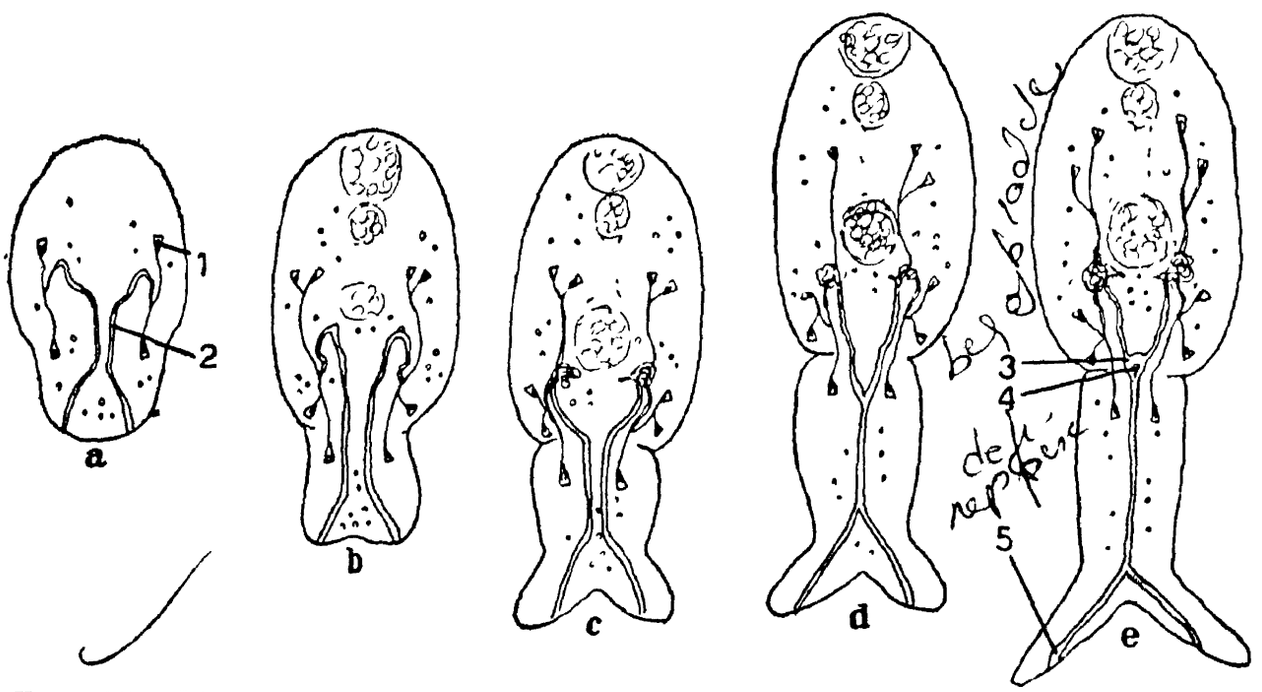

FIG. 105 —Five stages in the development of the excretory system and the forked tail of a strigeid cercaria (*after Komiya*, 1938) 1, flame bulbs, 2, protonephridium, 3, beginning of bladder, 4, definitive nephridopore, 5, nephridiopores of cercaria

is considered by some as a primitive feature reminiscent of rhabdocoels while others maintain that the original digestive system has degenerated and the present one is a modified acetabulum. An acetabulum is lacking; the genital pore is posterior. The adults, under 1 mm. long, inhabit the digestive tract of carnivorous fish (Ozaki, 1928b; Eckmann, 1932). The peculiar miracidia (Fig. 106*B*, Woodhead, 1929) bear their cilia on projecting rods. They penetrate fresh-water clams of the family Unionidae or marine bivalves such as the oyster and there grow into highly branched sporocysts (Fig. 101*E*) that produce cercariae directly (Woodhead, 1929, 1930; Tennent, 1906). The cercariae, known as oxhead cercariae (whence the name *Bucephalus*) have a pair of long tails, often extremely long, that give them a resemblance to an oxhead with a pair of horns (Fig. 106*C*, Woodhead, 1936). The cercariae have the typical gasterostome digestive tract and are hence easily recognizable as belonging to the family. The second intermediate host, comprising small

fishes, is attained by the entanglement of the cercarial tails in the fins. The cercariae encyst under the scales, mostly of the fins, and develop to adults when the fish carrying them are eaten by larger fish.

b. Family Paramphistomidae (= *Amphistomidae*).—This family comprises the amphistome flukes, i.e., those having the acetabulum, sometimes very large, at the posterior end of the body, considered to be the primitive position (Figs. 107, 108). In *Homalogaster* (Fig. 108*B*) and *Gastrodiscus* the ventral surface is papillate in whole or part, and in some genera the interior of the acetabulum is papillate (Fig. 108*A*). The anterior end, often provided with minute sensory papillae, is devoid of an oral sucker and bears the mouth; this leads into a very muscular pharynx often provided with two pouches (Fig. 108*A*). The posterior end of the slender esophagus is often thickened to form a muscular bulb (Fig. 109*A*). The family has a lymphatic system (page 230). The gonopore, situated in the anterior body half, and provided in some genera with a genital sucker (Fig. 108*A*), leads into a roomy antrum, often very muscular and provided with a sphincter, into which the sex ducts open on a protrusible papilla that may be encircled by a sphincter (Fig. 107*C*). In the genus *Gastrothylax* (Fig. 80*C*) there is a very deep ventral pouch considered by some to represent an enlarged antrum, into the anterior part of which the genital ducts open. The nephridiopore is dorsal in front of the acetabulum, and the mouth of Laurer's canal lies near by (Fig. 107*C*). This family has been treated extensively by Fischoeder (1903), Stiles and Goldberger (1910), Maplestone (1923), Fukui (1929), Travassos (1934), and Näsmark (1937). The adults, ranging from 3 to 20 mm., are parasites of the digestive tract of vertebrates, especially large herbivorous mammals. Some representative genera are *Microrchis* in fish, *Diplodiscus* (Fig. 109*A*) in the rectum of frogs, *Allassostoma* in the cloaca of turtles, *Ophioxenos* in garter snakes, *Zygocotyle* in ducks, *Stichorchis* in the beaver, *Cladorchis* (Fig. 108*A*) in tapirs, *Gastrodiscus* in the horse tribe, *Chiorchis* in aquatic mammals of the order Sirenia, *Nilocotyle* and *Buxifrons* in the hippopotamus, *Brumptia* and *Pseudodiscus* in elephants, *Watsonius* in man and monkeys, and *Paramphistomum* (Fig. 107), *Cotylophoron* (Fig. 88*B*), *Gastrothylax* (Fig. 80*C*) *Homalogaster* (Fig. 108*B*), *Gigantocotyle*, and others in ruminants (cattle, sheep, goats, antelopes, deer, etc.), especially in the rumen. *Gastrodiscoides hominis*, normally a parasite of pigs, is the only amphistome parasitizing man to any extent, inhabiting the colon; it occurs in India and Indo-China, where 40 per cent of the natives may be infected (Buckley, 1939). *Watsonius watsoni*, normally in monkeys, is rarely found in man (Stiles and Goldberger, 1910).

The life cycle is thoroughly known for only a few species. Miracidia, sporocysts, and rediae offer no peculiarities except that in *Stichorchis* the

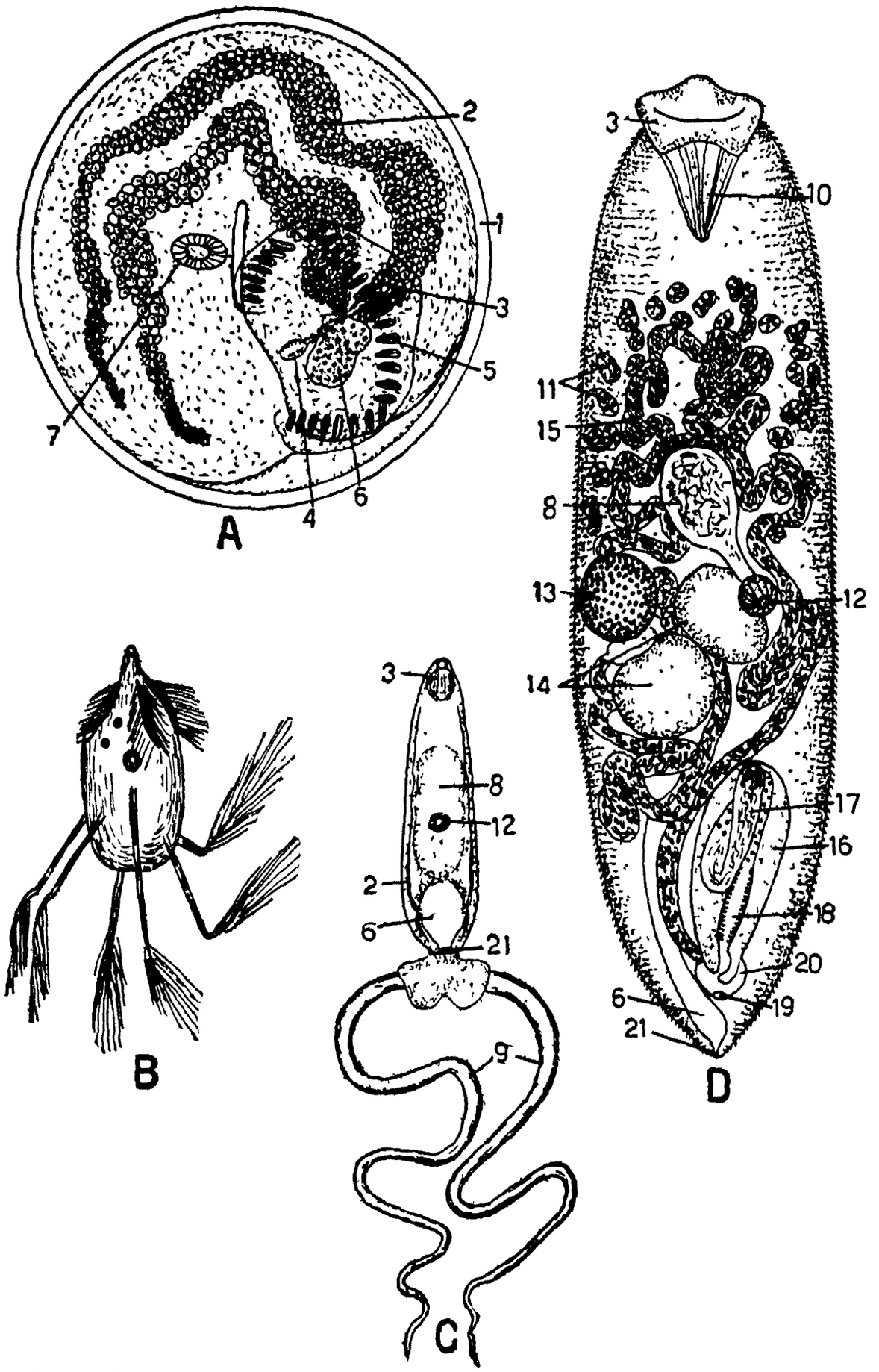

FIG. 106. Metacercaria, family Bucephalidae *A* Metacercaria of an echinostome (*after Palombi*, 1934) *B*. Miracidium of the Bucephalidae (*after Woodhead*, 1929). *C*. Oxhead cercaria of the Bucephalidae (*after Palombi*, 1934). *D* A gasterostome fluke *Prosorhynchus* (*after Ozaki*, 1928b). 1, cyst wall, 2, protonephridia filled with excretory spherules; 3, oral sucker; 4, pharynx; 5, collar of thorns, 6, bladder, 7, acetabulum; 8, intestine; 9, tails; 10, rhynchus, 11, yolk glands; 12, mouth; 13, ovary; 14, testes; 15, uterus; 16, cirrus sac; 17, seminal vesicle; 18, cirrus; 19, gonopore; 20, genital antrum; 21, nephridiopore.

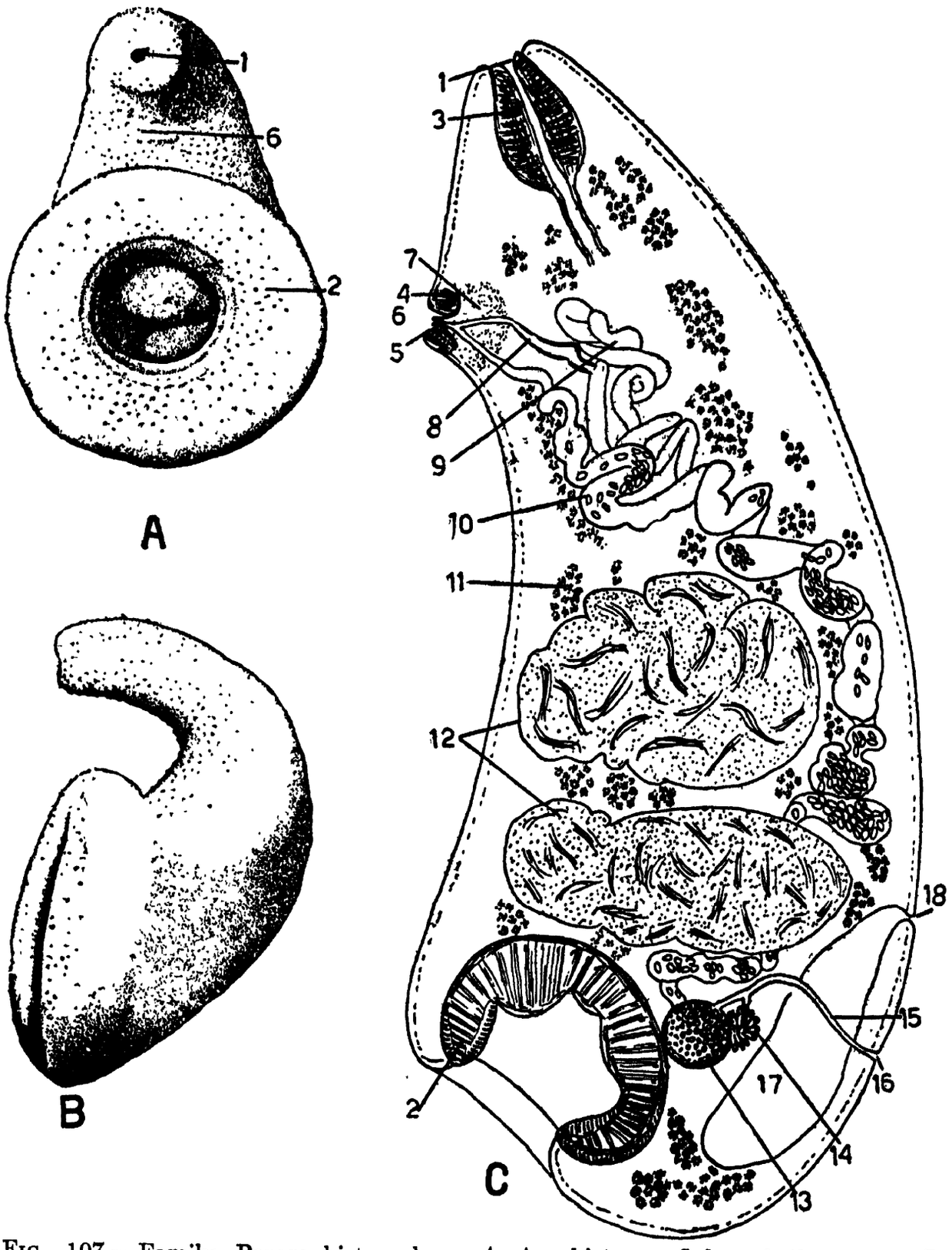

FIG. 107.—Family Paramphistomidae. *A*. Amphistome fluke of the genus *Paramphistomum*, ventral view. *B*. Same, seen from the side. (*A*, *B*, *after Fukui*, 1929.) *C*. Longitudinal section of *Paramphistomum* (*after Fischoeder*, 1903, *and Näsmark*, 1937). 1, mouth; 2, acetabulum; 3, pharynx; 4, genital sphincter; 5, genital papilla; 6, gonopore; 7, prostatic glands; 8, sperm duct; 9, seminal vesicle; 10, uterus; 11, yolk glands; 12, testes; 13, ovary; 14, ootype with Mehlis's glands; 15, Laurer's canal; 16, pore of same; 17, bladder; 18, nephridiopore.

miracidium contains a fully developed redia (Bennett and Humes, 1939). The cercariae have the amphistome construction (Fig. 103*E*) and hence are easily recognized as belonging to the family. They emerge from snails that harbor the sporocysts and rediae. In *Diplodiscus temperatus* (Fig. 109*A*) from American frogs, the cercariae encyst on bottom debris

and on the surface of tadpoles and frogs. Infection ensues when debris or shed skin bearing the cysts is eaten by tadpoles or frogs (Krull and Price, 1932). According to Beaver (1929), the cercariae of *Allassostoma* encyst on tadpoles and crayfish which are then eaten by the definitive hosts (turtles, bullfrogs). In the case of amphistomes of large herbivorous mammals, the cercariae probably encyst on grasses and other vegetation, as was determined for *Cotylophoron cotylophorum* (Bennett, 1936) and *Paramphistomum cervi* (Szidat, 1936), both from ruminants.

c. Family Zoogonidae.—These are small distomes with spiny cuticle, short intestinal crura, and yolk glands reduced to one or two small masses so that the eggs lack proper shells, being enclosed in the vitelline membrane. At the time of laying, the miracidium is fully developed. Life cycles have been worked out for *Zoogonus lasius* and *Zoogonoides laevis* (Fig 109*B*) from the New England coast (Stunkard, 1938a, 1943) and for *Diphterostomum brusinae* from the Mediterranean (Palombi, 1930). The miracidia penetrate marine snails such as *Nassa*, *Ilyanassa* and *Natica*, in which the sporocyst produces cercariae directly. These cercariae are of the cercariaeum type, i e , without tails (Fig 104*C*). In *Zoogonus* and *Zoogonoides* these are emitted and crawl about on the bottom until they make contact with the second intermediate host, chiefly the polychaete *Nereis*, in which they encyst. In *Diphterostomum*, they encyst within the mother sporocyst, and these cysts are then discharged from the snail and fall on various sessile animals or on plants The definitive hosts are a variety of marine fishes.

d. Family Allocreadiidae.—These are small distomes that parasitize the intestine of marine and fresh-water fishes, being among the common parasites of salmon, trout, perch, pike, bass, sunfish, catfishes, etc. In the genera *Crepidostomum* and *Bunodera* the oral sucker has six muscular papillae (Fig 109*C*). The known life cycles are of three different types (Hopkins, 1934). In *Crepidostomum* and *Allocreadium*, the rediae, found in small bivalves of the family Sphaeriidae, produce ophthalmoxiphidiocercariae (i.e., with eyes and stylet) and the metacercariae encyst in May fly nymphs, amphipods, crayfish, or bivalves (Hopkins, 1934; Ameel, 1937; Crawford, 1943). A different cycle obtains for such genera as *Hamacreadium* (McCoy, 1929a, 1930) and *Plagioporus* (Sinitsin, 1931a; Dobrovolny, 1939); the sporocysts inhabit snails and produce cotylocercous cercariae (Fig. 103*F*) that encyst in various animals as crayfish, snails, or small fish or encyst directly in the sporocyst so that there is no second intermediate host. Still a different history is known for *Lepocreadium* and *Pharyngora*. The trichocercous cercariae (Fig. 103*B*), produced in rediae in snail hosts (Dollfus, 1925; Palombi, 1931, 1937b; Hopkins, 1937), attach to various hosts and transform into metacercariae without encysting. Thus *Pharyngora* metacercariae occur naked

attached to medusae (Lebour, 1916) awaiting ingestion by the final fish host. The variability in the cycles indicates that the family is artificial and requires breaking up into several families.

e. Family Azygiidae.—These are flukes with opaque muscular bodies, found in the esophagus and stomach of fishes. The family is discussed by Odhner (1911a), Manter (1926), and Dickerman (1934). Some

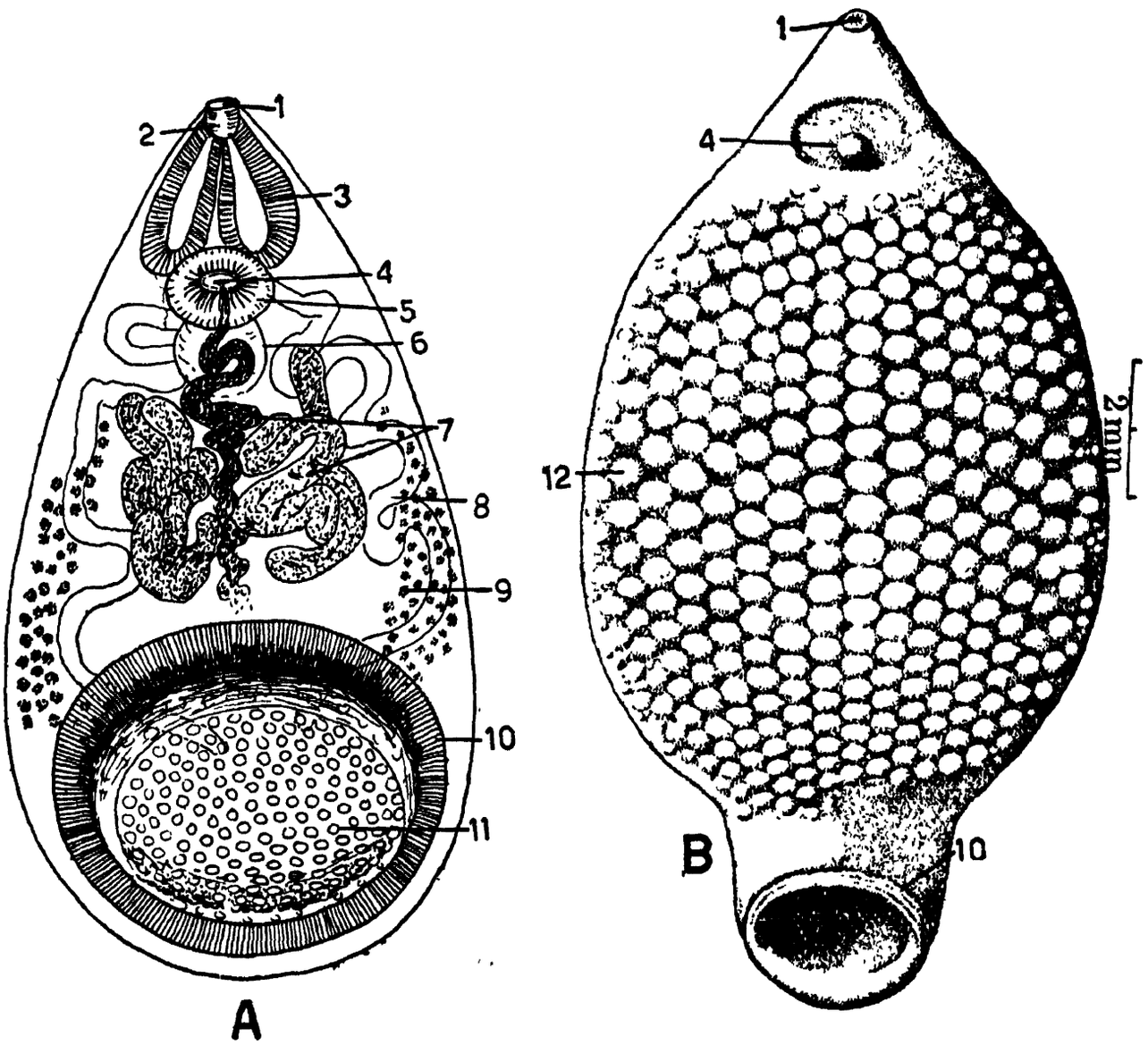

FIG. 108.—Paramphistomidae (continued). *A. Cladorchis* from the tapir, with pharyngeal sacs (*after Fischoeder*, 1903). *B. Homalogaster* from ruminants, with ventral papillae (*after Fukui*, 1929). 1, mouth; 2, pharynx; 3, pharyngeal sacs; 4, gonopore; 5, genital sucker; 6, cirrus sac; 7, uterus; 8, intestine; 9, yolk glands; 10, acetabulum; 11, papillae in acetabulum; 12, papillae on ventral surface.

genera as *Azygia* in fresh-water fishes and *Otodistomum* from elasmobranches (Fig. 110*A*, Mühlschlag, 1914; Manter, 1926) are of long slender form, up to 125 mm. in length; whereas *Proterometra* from centrarchid fishes is oval. Life cycles are known for *Azygia* (Szidat, 1932a) and *Proterometra* (Smith, 1934, 1936; Dickerman, 1934, 1945). The capsules containing the unciliated miracidia are eaten directly by snails; the miracidium is armed with four anterior bristle plates for penetrating the snail's intestinal wall. The cercariae are of the cystocercous type (Fig.

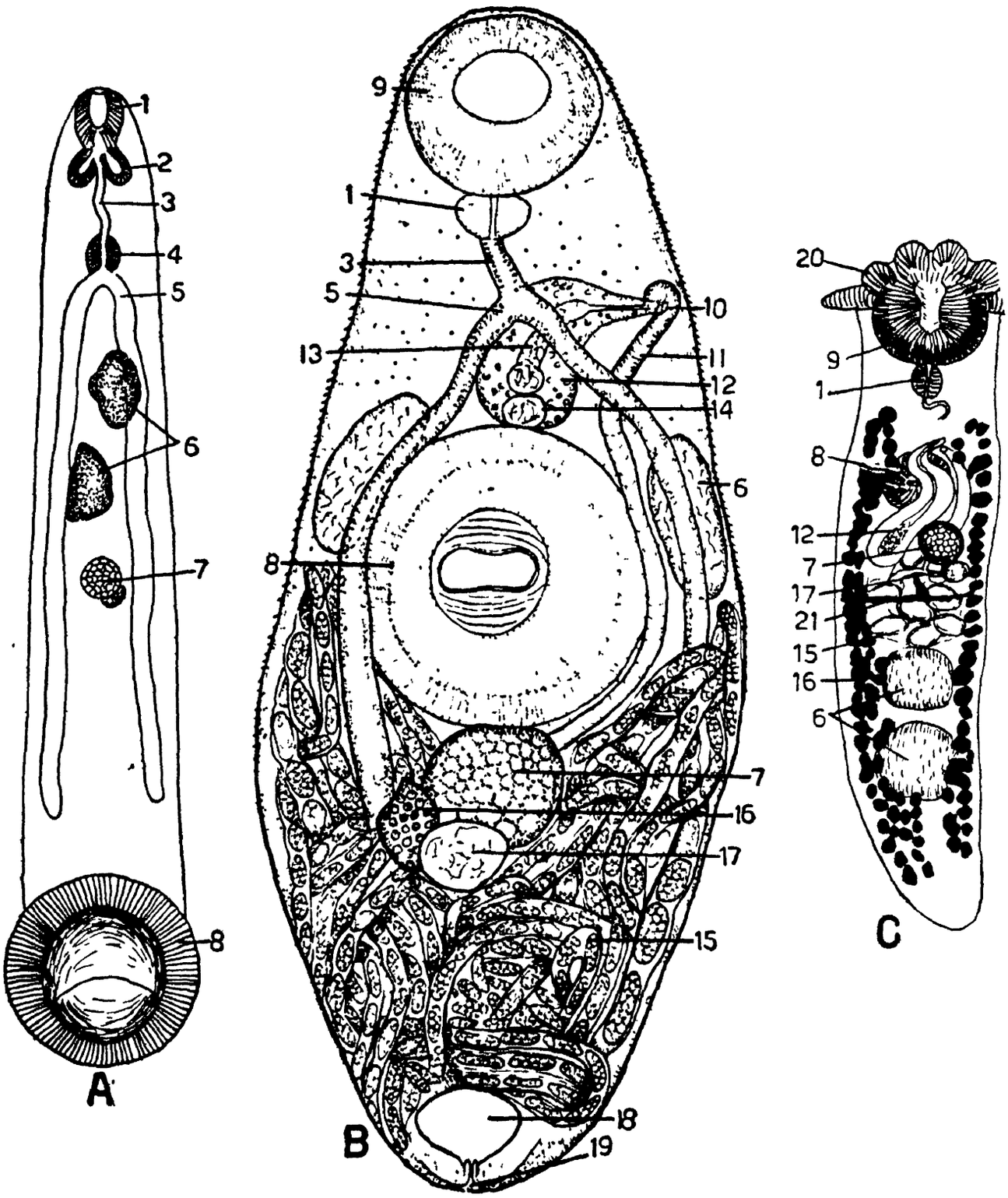

FIG. 109 —Paramphistomidae, Zoogonidae, Allocreadiidae. *A. Diplodiscus temperatus*, amphistome from the rectum of frogs, from life. *B. Zoogonoides* (*after Stunkard*, 1943), from fish intestine. *C. Crepidostomum cornutum* (*after Van Cleave and Mueller*, 1934), allocreadiid from the intestine of fresh-water fish. 1, pharynx, 2, pharyngeal sacs, 3, esophagus; 4, esophageal bulb, 5, intestine, 6, testes, 7, ovary, 8, acetabulum, 9, oral sucker; 10, gonopore; 11, metraterm, 12, cirrus sac, 13, cirrus; 14, seminal vesicle, 15, coils of uterus; 16, yolk gland; 17, seminal receptacle; 18, bladder, 19, nephridiopore, 20, papillae, 21, yolk ducts.

104*B*) and notable for their relatively gigantic size (up to 16 mm.); they are eaten directly by the definitive fish host.

f. Family Hemiuridae.—This is a distome family of varied appearance. The typical members, known as *appendiculate* flukes, are slender cylindroid forms, up to 15 mm. in length, that inhabit the esophagus and

stomach, less often the pharynx and intestine, of marine fishes. The rear part of the body, up to one-half the body length, can be telescoped into the anterior part, from which it is demarcated by a constriction marking the ring of attachment of the retractor muscles accomplishing the withdrawal (Fig. 110*B*, *C*). The anterior part has a thick, often ringed, cuticle whereas the posterior part is thin-walled and hence supposed to serve for respiration, absorption etc. Some representative appendiculate genera are *Hemiurus* (Fig. 110*B*, *C*), *Dinurus*, *Sterrhurus* and *Lecithochirium* (Pratt, 1898; Lühe, 1901; Lander, 1904; Looss, 1908). The life cycle is not known except that metacercarial stages have been found in copepods (Pratt, 1898).

The nonappendiculate hemiurids, represented by such genera as *Derogenes*, *Hirundinella*, and *Halipegus* (Rankin, 1944a), are smaller and of normal form. *Halipegus* (Fig. 110*D*) differs from the rest of the family in parasitizing fresh-water hosts, frogs and salamanders, where it is found chiefly in the buccal cavity and related parts. The life cycle of *Halipegus*, worked out by Krull (1935) and Thomas (1939), includes a nonciliated miracidium escaping only after ingestion of the capsules by snails, sporocyst and redial stages in snails, and cystophorous cercariae (Fig. 103*D*) that are eaten by copepods or dragonfly and damsel fly nymphs; or possibly copepods are the second and these nymphs the third intermediate hosts.

g. Family Didymozoonidae.—The members of this curious family live in pairs in cysts on the surface, gills, operculum, or on the walls of the oral cavity or pharynx of marine fishes, seldom in the interior. Studies on the family have been made by Odhner (1907), the MacCallums (1916), Dollfus (1933), and Ishii (1935). Although some forms are hermaphroditic, there is a tendency in the family toward gonochorism through degeneration of the organs of one sex, and this is accompanied by sexual dimorphism and assumption of peculiar body shape. Characteristic of the family are the demarcation of a slender or spoon-like forebody from the cylindroid, plump, or rounded hindbody, and the long slender tubular shape of ovary, testis, and yolk gland (Figs. 81, 111). *Nematobothrium* is extremely long and slender up to a meter in length. In *Didymozoon* (Fig. 112*C*) the hindbody is plump and cylindroid, and in *Didymocystis* (Fig. 111) it has shortened to a reniform shape from which the slender forebody protrudes. These genera are hermaphroditic. *Wedlia* (Fig. 81) in which the peculiar body form reaches its climax is dioecious; the small male hindbody is lodged in a depression in the large rounded female hindbody from which the two small spoon-shaped forebodies protrude. Throughout the hindbody of the members of this family wind the coils of the long slender ovary, yolk gland (single), and uterus. The Didymozoonidae have an oral sucker, but an acetabulum is wanting so that they classify

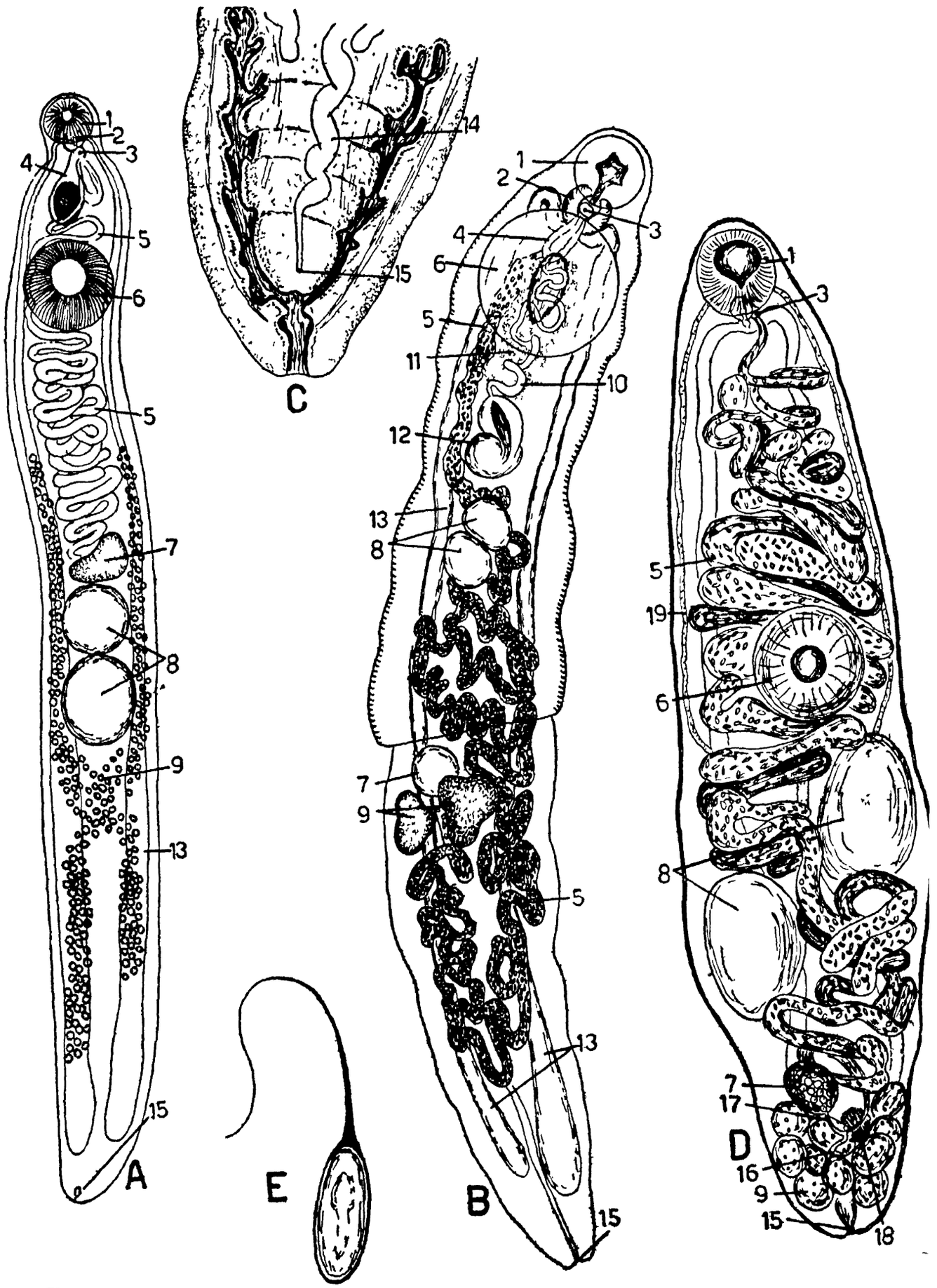

FIG 110.—Azygiidae, Hemiuridae. *A. Otodistomum*, to 100 mm long, from the stomach of a skate, from life. *B Hemiurus* (after Looss, 1908) with rear end extended. *C.* Rear part of same with rear end telescoped into the interior (*after Looss*, 1908). *D Halipegus*, nonappendiculate hemiurid, from the oral cavity of frogs *E.* Capsule of *Halipegus* (*D* and *E*, *after Krull*, 1935) 1, oral sucker, 2, pharynx; 3, gonopore, 4, cirrus sac; 5, uterus; 6, acetabulum; 7, ovary; 8, testes; 9, yolk glands; 10, sperm duct; 11, prostatic glands; 12, seminal vesicle; 13, intestine; 14, bladder; 15, nephridiopore; 16, yolk duct, 17, oviduct; 18, ootype, 19, nephridium.

as monostomes. The pharynx is often reduced or absent. The life cycle is not known, but the miracidia lack cilia and are armed with an anterior crown of thorns (Fig. 111*B*), whence it may be inferred that the capsules hatch only after being eaten by the intermediate host, presumably a marine snail.

h. Family Gorgoderidae.—This is a distome family parasitic in the ureters and urinary bladder of fish, amphibians, and reptiles. The best known genera are *Gorgoderina* with two testes, *Gorgodera* (Fig. 112*A*) with nine testes, and *Phyllodistomum* (Fig. 112*B*, Lewis, 1935) with expanded rear part, all common in the urinary bladder of frogs and salamanders. The life cycle of these genera, first worked out by Sinitsin (1907), has been verified by Krull (1934a), Rankin (1939b), Crawford (1940), and Goodchild (1943). The laid capsules already contain the miracidium which enters small bivalves of the family Sphaeriidae. The cercariae, developing directly in sporocysts, are of the macrocercous type (page 262) with long broad tails or very long and slender tails (Fig. 104*A*, *D*). Wriggling of the tails induces ingestion by the second intermediate host, usually a damsel fly nymph or other aquatic insect larva, less often a snail or tadpole. Enclosure of the cercarial body in the tail base is believed to act as a protection from insect jaws. The metacercariae, after hatching in the definitive host, seem to inhabit the kidneys first, passing into the bladder as sexual maturity is attained (Odlaug, 1937).

i. Family Plagiorchidae.—These are small to moderate distomes, with a spiny cuticle, Y-shaped urinary bladder, and anterior, often lateral, gonopore (Fig. 113). The family, broadly conceived, is one of the largest digenetic families, with nearly 50 genera and hundreds of species, inhabiting the intestine of various vertebrates, chiefly those of aquatic habits; the oral cavity, esophagus, and respiratory tract of amphibians and reptiles; and less often the gall bladder and urogenital tract of reptiles and birds. The capsules on laying contain a fully developed miracidium but hatch only after ingestion by snails. The development of the sporocysts has been studied by Cort and Olivier (1943a) and Cort and Ameel (1944); the daughter sporocysts are covered with a special epithelial layer and contain a germ mass that continues to produce cercariae over a long period. The cercariae are of the stylet type (Fig. 102*E*), and have the flame-bulb formula 2[(3 + 3 + 3) + (3 + 3 + 3)], also occurring in the adults. By the scraping action of the stylet, the cercariae penetrate the surface of aquatic insect larvae, crayfish, or tadpoles in which they encyst to form metacercariae.

The family is divided into several subfamilies, of which the arrangement proposed by Travassos (1928) is probably the best. The plagiorchine group (Olsen, 1937), comprising the genera *Plagiorchis* (= *Lepoderma*), *Glyphthelmins*, *Styphlodora* (Byrd, Parker, and Reiber, 1940),

Opisthioglyphe, and others, generally inhabits the intestine of various vertebrates of aquatic habits but may be experimentally grown in mice, rats, and pigeons. The cercariae of *Plagiorchis* penetrate aquatic insect larvae (odonates, May flies, dipterans, McMullen, 1937b) or crayfish

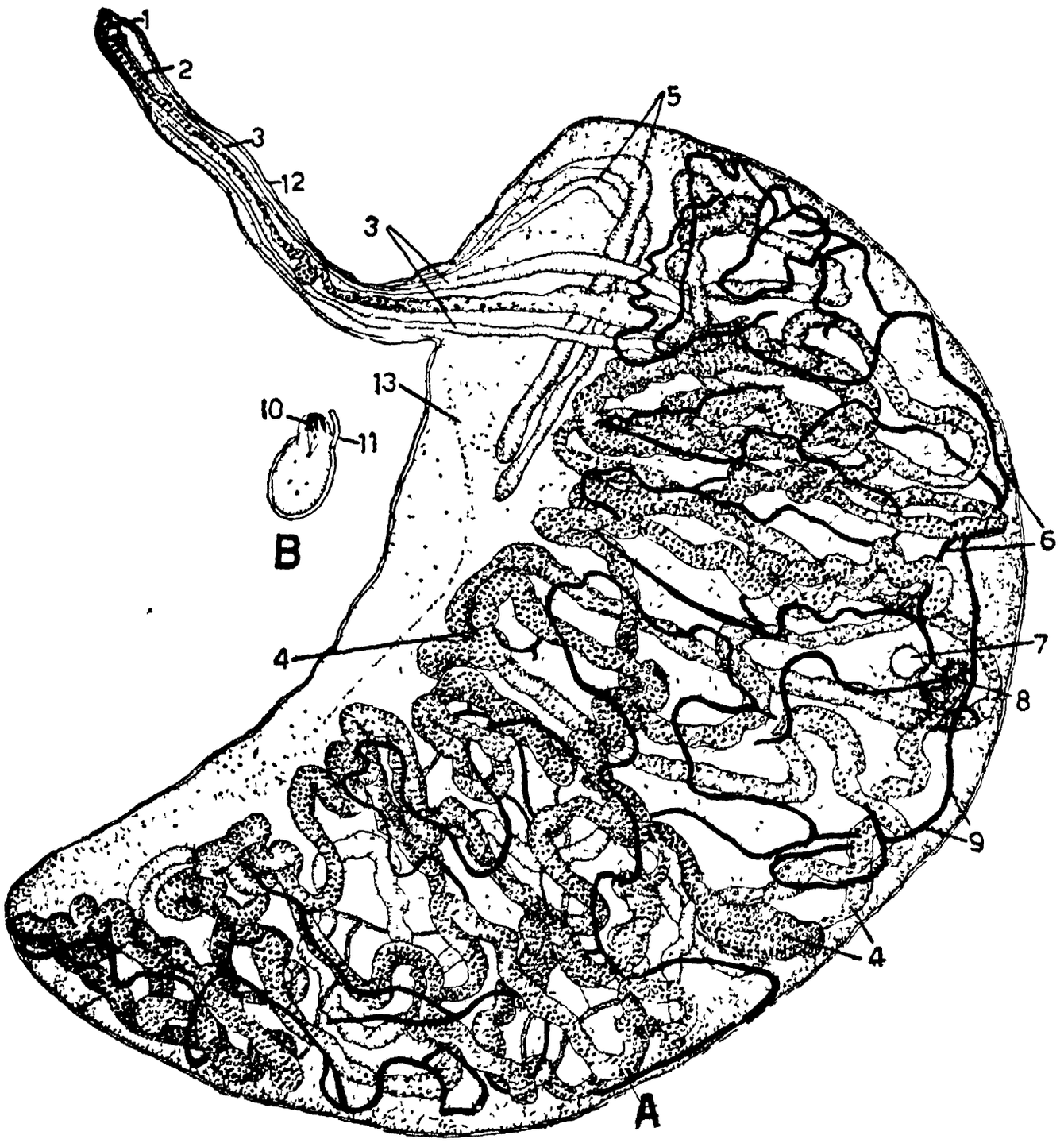

FIG. 111.—Didymozoonidae. *A. Didymocystis* (*after Nigrelli*, 1939). *B.* Capsule of same, shown crown of thorns on nonswimming miracidium. 1, oral sucker, 2, esophagus, 3, intestine; 4, uterus, 5, testes, 6, ovary; 7, seminal receptacle, 8, ootype, 9, yolk glands, 10, thorns; 11, operculum; 12, forebody; 13, hindbody.

(McCoy, 1928); those of *Glyphthelmins* encyst in the epidermis of frogs that when shed is eaten by the definitive frog host (Rankin, 1944b). Species of *Plagiorchis* occasionally occur in the human intestine (Philippines, Africa and Garcia, 1937; Java, Sandground, 1940) and *Plagiorchis muris*, naturally infecting the muskrat and aquatic birds, will take in man (McMullen, 1937c).

The reniferine plagiorchids, discussed by Talbot (1934) and Byrd and Denton (1938), include such genera as *Renifer* (Fig. 113*A*), *Neorenifer*, *Zeugorchis*, and *Dasymetra*, parasitizing snakes. The life histories of this group have been worked out by Ingles (1933), Talbot (1933), Byrd (1935), and Walker (1939). The cercariae encyst in tadpoles that are eaten by snakes in which the adults infect the oral cavity, esophagus, air passages, and lungs.

The saphaedrine group contains the familiar lung flukes of frogs, belonging to the genera *Haematoloechus* (= *Pneumoneces*,[1] Fig. 113*C*), with rounded testes and simple ovary, and *Pneumobites* with elongated testes and lobed ovary. The species of American frog lung flukes have been described and figured by Stafford (1902) and Cort (1915a). The life cycle has been elucidated by Krull (1930, 1931, 1934b). As in other plagiorchids, the capsules hatch only after ingestion by snails, and stylet cercariae are produced. These commonly encyst in dragonfly nymphs of the genus *Sympetrum* after being swept into the rectum of the nymph by its respiratory currents; but they also may employ other aquatic insect nymphs as second intermediate hosts. The metacercariae remain through the metamorphosis of the insect and attain the definitive frog host when the latter eats infected dragonflies. After hatching in the frog stomach, the young flukes travel up the esophagus to the oral cavity and then down the glottis into the lungs.

This ability of plagiorchid metacercariae to persist in an infective state through metamorphosis to the adult insect permits the spread of plagiorchid flukes to nonaquatic birds and mammals that have access to shores of ponds and lakes, and birds such as swallows that feed on insects over water. Thus plagiorchids of the genus *Prosthogonimus* (Fig. 113*B*) that have their metacercarial stage in dragonfly nymphs and adults are common in the intestine, bursa Fabricii, and oviducts not only of ducks and other aquatic birds but also of a great variety of land birds, including the domestic hen. Infection of the oviducts of the domestic hen by *Prosthogonimus* (Fig. 113*B*) in lake regions throughout the world (Macy, 1934) has become of economic importance, since it results in a great decline in egg production, formation of soft-shelled eggs, and deterioration of the health of the hen; not infrequently the flukes are found in the eggs laid by infected hens.

j. Family Dicrocoeliidae.—These are distomes of some size and of elongated flattened form with tubular excretory bladder and testes situated anterior to the ovary (Fig. 82*A*). They parasitize the liver and gall

[1] In 1902, Looss proposed to change the name *Haematoloechus* to *Pneumoneces* on the ground that the former name was too similar to the prior name *Haematoloecha*. Such similarity is not, however, a valid ground for changing generic names, and therefore *Haematoloechus* is the valid name of the common lung flukes of frogs.

bladder of reptiles, birds, and mammals, the pancreas of ruminant mammals, and the intestine of amphibians and reptiles *Dicrocoelium* (Fig. 82*A*), *Eurytrema*, and *Brachycoelium* are representative genera, and the lancet fluke, *Dicrocoelium dendriticum* (= *lanceolatum* or *lanceatum*),

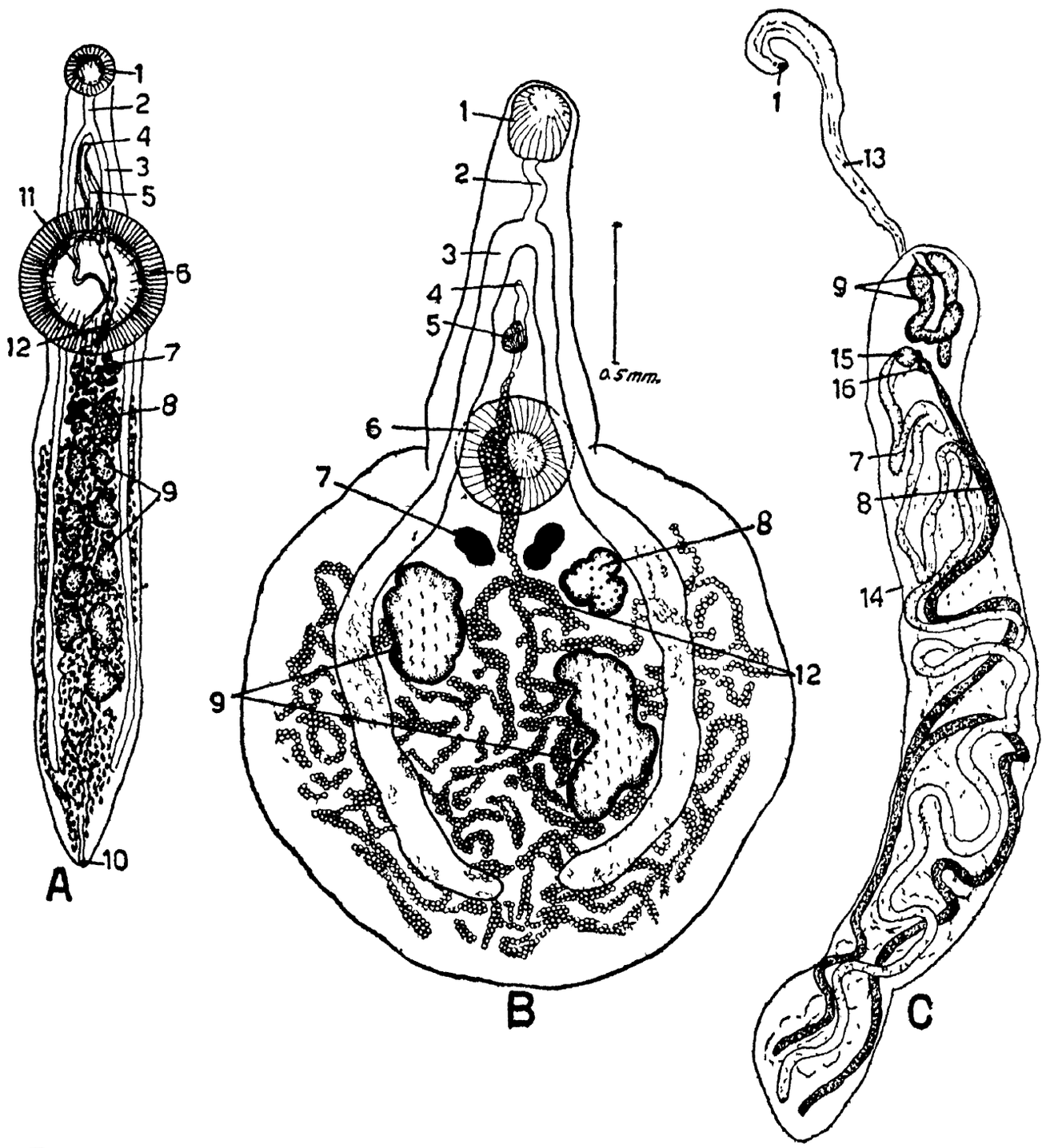

FIG 112.—Didymoozonidae, Gorgoderidae *A. Gorgodera*, frog rectum, from life *B Phyllodistomum* (*after Van Cleave and Mueller*, 1934) *C Didymozoon* (*after Ishii*, 1935). 1, oral sucker, 2, esophagus, 3, intestine, 4, gonopore, 5, cirrus sac, 6, acetabulum, 7, yolk glands, 8, ovary, 9, testes, 10, nephridiopore, 11, sperm duct, 12, uterus, 13, forebody, 14, hindbody, 15, seminal receptacle, 16, ootype.

found in the bile passages of sheep, cattle, and other herbivorous mammals, is one of the best known flukes. Its life cycle was worked out by Mattes (1936) and Neuhaus (1936, 1938). The capsules hatch only after ingestion by certain land snails in which two generations of sporocysts occur. The cercariae exit through the pulmonary sac into the mantle

cavity of the snail host where they form an adhesive cyst. These cysts stick together to form balls containing hundreds of metacercariae that fall on vegetation and debris. After ingestion by the definitive host, the metacercariae hatch in the intestine and bore through the intestinal wall

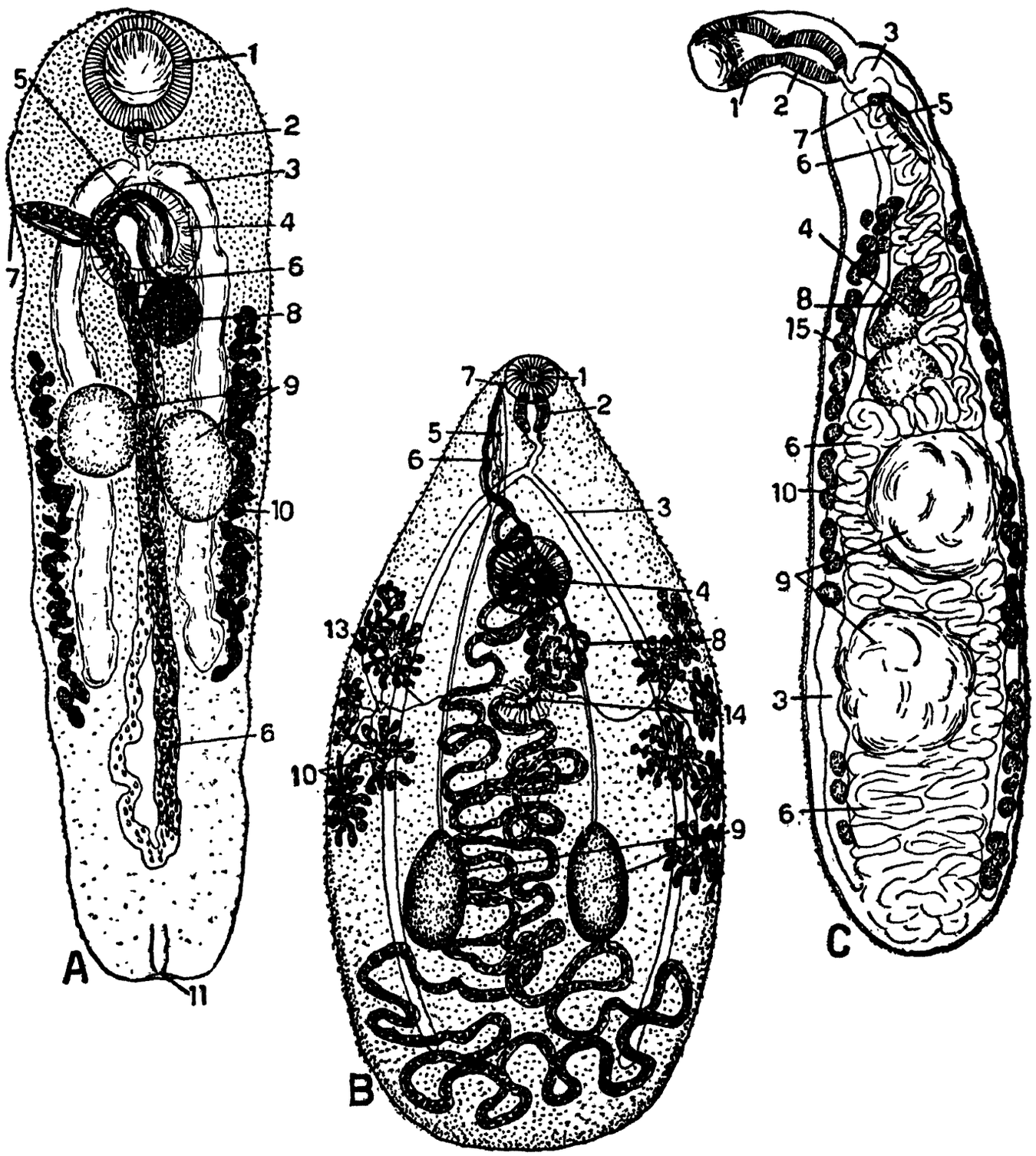

FIG. 113.—Plagiorchidae. *A. Renifer*, oral cavity of snakes, original. *B. Prosthogonimus macrorchis*, oviduct of hen, original. *C. Haematoloechus* (= *Pneumoneces*), frog lung, original. 1, oral sucker; 2, pharynx; 3, intestine; 4, acetabulum; 5, cirrus sac; 6, uterus; 7, gonopore; 8, ovary; 9, testes; 10, yolk glands; 11, nephridiopore; 12, sperm ducts; 13, yolk ducts; 14, ootype; 15, seminal receptacle.

into the branches of the portal system which carries them to the liver; here they finally pass from the portal vein into the bile passages. Similar cycles obtain for *Eurytrema* from the pancreas and bile passages of mammals (Denton, 1944) and *Brachylecithum* from the bile passages of pas-

serine birds (Denton, 1945), except that a second intermediate host seems to be required. *Dicrocoelium* and *Eurytrema* sometimes occur in man, probably as a result of eating infected mammalian livers.

k. Family Opisthorchidae.—These are distomes of small to considerable size with flat semitransparent bodies, small suckers, Y-shaped excretory bladder, posterior testes, and gonopore just in front of the acetabulum. They inhabit the bile passages of fish-eating reptiles, birds, and particularly mammals. The best known members of the family are *Opisthorchis felineus* and *O.* (= *Clonorchis*) *sinensis* (Fig. 114*A*) from the bile passages of cats, dogs, man, and other mammals. These two species have very similar life cycles. The small oval capsules (Fig. 114*C*) contain a complete miracidium that hatches only after ingestion by operculate snails of the genus *Bythinia* and related genera. In the snail the mother sporocyst gives rise to one generation of rediae without birth pore or projections, and these produce cercariae of the pleurolophocercous type (Fig. 103*A*). The cercariae penetrate fresh-water fish of the family Cyprinidae in which they encyst under the skin or in the musculature. The definitive host becomes infected by eating raw or insufficiently cooked fish. The metacercarial cyst after partial dissolution by the gastric juice is finally dissolved in the small intestine, and the metacercariae make their way up the bile duct. *Opisthorchis sinensis* is an important human parasite in local areas of Japan, China, and French Indo-China and may cause serious symptoms through blocking the bile passages. A comprehensive study of this parasite was made by Faust and Khaw in 1927, but it appears they confused the larval forms of three different species of flukes. The cercariae (Fig. 103*A*) and metacercariae (Fig. 114*B*) have been well studied and figured by Yamaguti (1935) and Komiya and Tajimi (1940). *O. felineus*, whose cycle was fully elucidated by Vogel (1934), and other species of *Opisthorchis* occur in man in areas where raw fish are eaten. Some other genera of the family, found in fish-eating mammals, are *Amphimerus*. *Metorchis*, and *Pseudamphistomum* (Schuurmans-Stekhoven, 1931).

l. Family Heterophyidae.—This family comprises small distomes or monostomes, mostly not more than 2 to 3 mm. long, of oval or pyriform shape with motile contractile anterior region contrasting with the heavier rear containing the whole of the reproductive system. The cuticle, at least anteriorly, is spiny or scaly. Other characters are a long esophagus, the lack of a cirrus, and the presence in the genital antrum of a muscular protrusible cushion or tubercle termed the gonotyl (Fig. 114*D*). The acetabulum is often reduced and incorporated into the genital antrum and is altogether lacking in some genera (*Stictodora*, *Monorchitrema*). The heterophyids inhabit the intestine of birds and mammals, usually those of aquatic, fish-eating habits, and also occur commonly in the

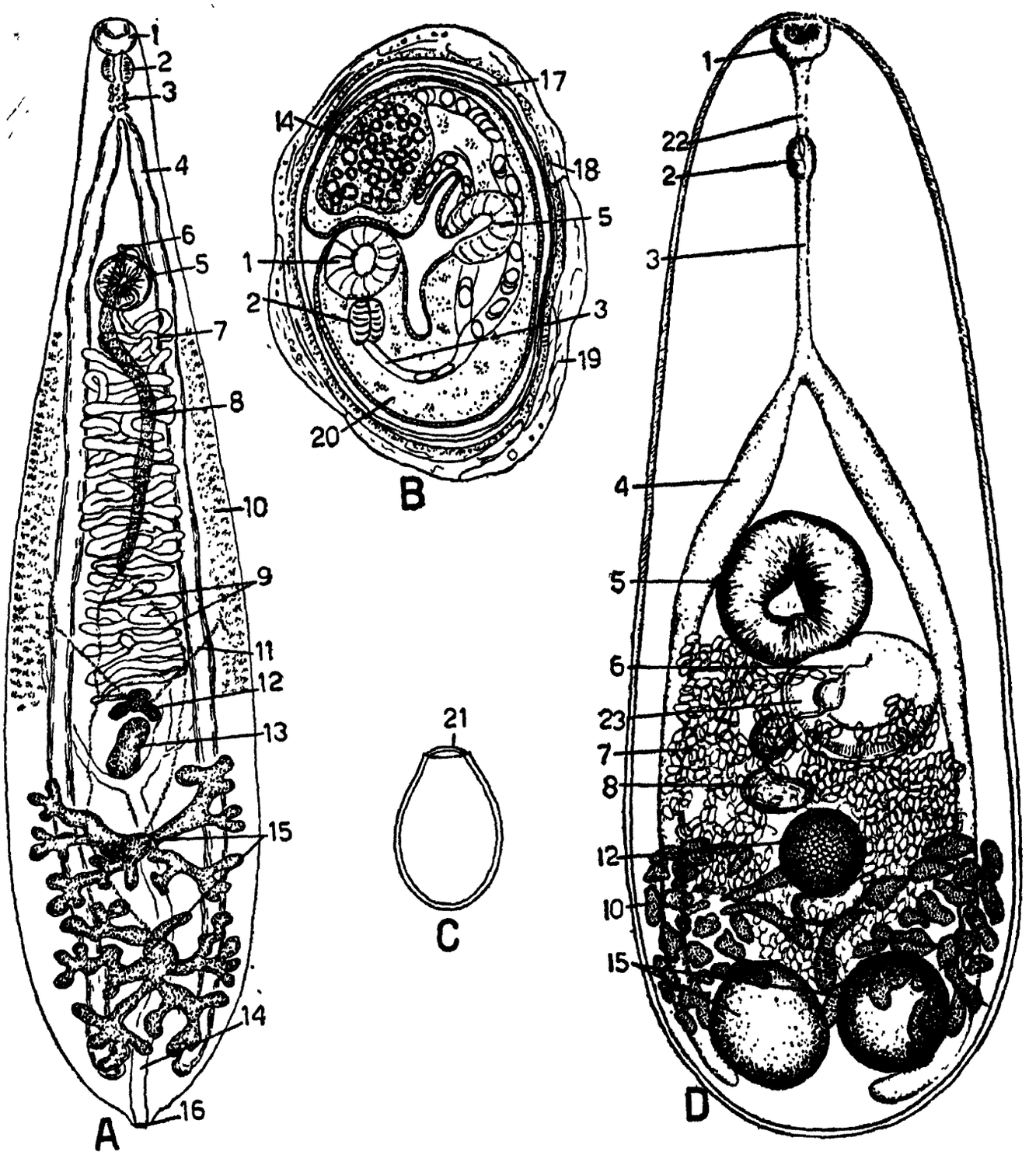

FIG. 114.—Opisthorchidae, Heterophyidae. *A. Opisthorchis sinensis* (*from slide, courtesy A. E. Galigher*), human liver fluke. *B.* Metacercaria of *O. sinensis* (*after Komiya and Tajimi*, 1940). *C.* Capsule of *O. sinensis* (*after Looss*, 1907a). *D. Heterophyes heterophyes* (*after Witenberg*, 1929), intestinal fluke of mammals. 1, oral sucker; 2, pharynx; 3, esophagus; 4, intestine; 5, acetabulum; 6, gonopore; 7, uterus; 8, seminal vesicle; 9, sperm ducts; 10, yolk glands; 11, yolk ducts; 12, ovary; 13, seminal receptacle; 14, bladder; 15, testes; 16, nephridiopore; 17, inner cyst wall; 18, outer cyst wall; 19, host part of cyst wall; 20, metacercaria coiled in cyst; 21, operculum; 22, buccal tube; 23, gonotyl.

intestine of man, dogs, and cats. The family has been reviewed by Ransom (1920) and Witenberg (1929). The life cycle is similar to that of the Opisthorchidae; the capsules are eaten by operculate snails in which one generation of sporocyst and one or two generations of rediae develop, and the pleurolophocercous cercariae, distinguished from opisthorchid cercariae mostly by a spiny armature on the anterior end, encyst in fish. The genus *Heterophyes* is characterized by the occurrence of a

well-developed acetabulum adjacent to the gonotyl (Fig. 114*D*). Several species of this genus, of which the most common is *Heterophyes heterophyes* (Fig. 114*D*), occur in the intestine of dogs, cats, and man in Egypt, Palestine, and other Asiatic regions. A similar distribution and host relationship obtains for *Metagonimus yokogawai*. Man appears to be a normal host for these two heterophyid flukes, and they evoke negligible symptoms. But it appears that other heterophyids, not normal to man, may develop in man from eating infected fish and may cause serious damage (Africa and Garcia, 1935, Vazquez-Colet and Africa, 1940). The genus *Euryhelmis*, parasite of the intestine of minks, differs from other heterophyids in that the metacercariae occur in frogs and tadpoles (Ameel, 1938).

m. Family Microphallidae.—These flukes resemble closely in general appearance the Heterophyidae, of which family they were formerly considered a subfamily. Differences are the short intestinal crura and the presence of a penis papilla (Fig. 115). *Microphallus* occurs in the intestine of fishes; other genera as *Spelotrema* (Fig. 115, Rankin, 1940a; Cable and Hunninen, 1940), *Levinseniella* (Rankin, 1939a; Young, 1938), and *Maritrema* inhabit the intestine of shore birds such as gulls, terns, and sandpipers. The capsules containing the miracidium are eaten by littoral snails in which sporocysts and rediae occur. The cercariae are simple monostome stylet cercariae that encyst in crustaceans such as amphipods, isopods, barnacles, sand crabs, and true crabs.

n. Family Troglotrematidae.—These are distomes or monostomes of some size, mostly of shortened oval form, with scaly cuticle, that live two or more in cysts in various organs of bird and carnivorous mammals. The family includes the important genus *Paragonimus* (Fig. 118*A*), the lung fluke of mammals, up to 20 mm. long, living in cysts about the size of a hazelnut in the lungs of various mammals and of man. In North America, where *Paragonimus* has been extensively studied by Ameel (1934), the parasite occurs mainly in the Great Lakes region where the mink is the usual definitive host, although muskrats, cats, rats, and pigs may also be infected. In the Orient (China, Korea, Japan, Formosa, Indo-Malay region, etc.), human infection, up to 50 per cent in some localities, is common, from the habit of eating raw crayfish and crabs. The capsules (Fig. 118*B*) are emitted with the sputum, and the miracidium develops in about 3 weeks if moist conditions obtain. After a brief free existence, the miracidia penetrate operculate snails in which the mother sporocyst and two generations of rediae occur. The cercaria (Fig. 102*D*) is microcercous and does not swim, crawling about in a leech-like manner and encysting in crayfish or fresh-water crabs, but not in fresh-water shrimps. After ingestion by the final host, the young flukes bore through the intestinal walls into the abdominal cavity and thence

through the diaphragm into the lungs. The number of species of *Paragonimus* has been repeatedly discussed (Ward and Hirsch, 1915; Ameel, 1934; H. T. Chen, 1940) but no agreement has been reached and it is probable that only one species, *P. westermani*, exists in man.

Some other genera of the family are *Collyriclum* and *Troglotrema*. Species of the former are rounded flukes without an acetabulum that occur in cysts in the skin of passerine birds (Cole, 1911; Jegen, 1917);

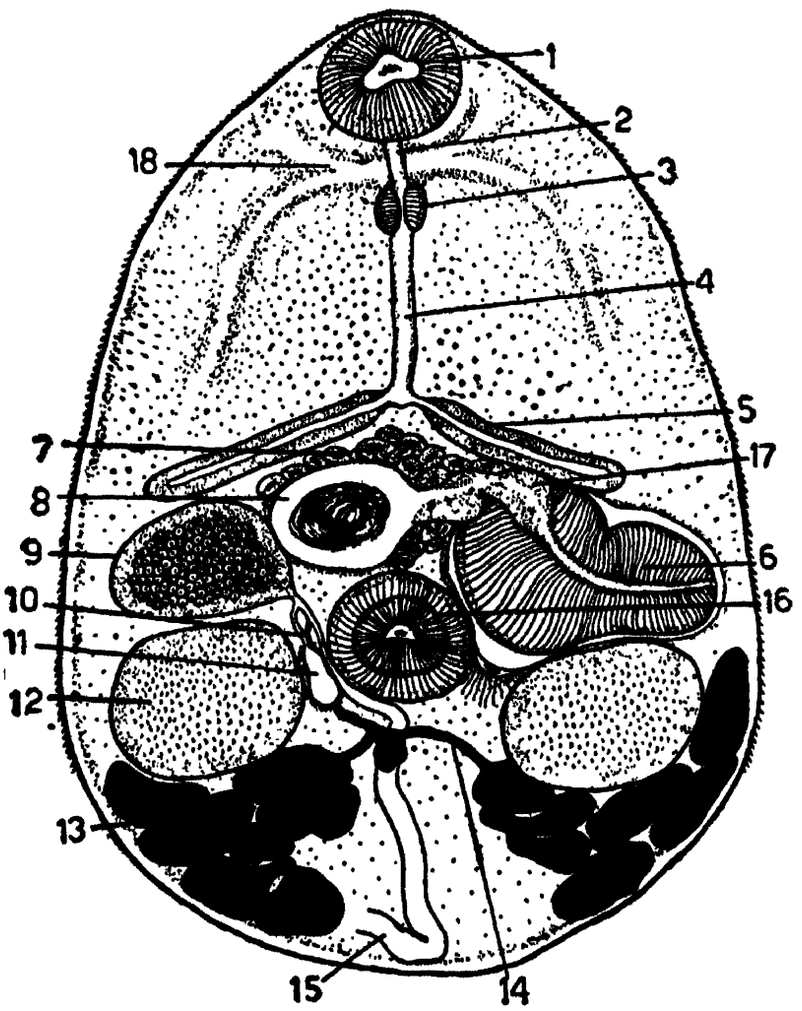

FIG. 115.—Microphallidae. *Spelotrema* (*after Rankin*, 1940a). 1, oral sucker; 2, buccal tube; 3, pharynx; 4, esophagus; 5, intestine (note short crura); 6, penis papilla; 7, prostatic gland cells; 8, seminal vesicle; 9, ovary; 10, Laurer's canal; 11, seminal receptacle; 12, testes; 13, yolk glands; 14, yolk ducts; 15, beginning of uterus (rest not shown); 16, acetabulum; 17, prostatic vesicle; 18, brain.

the life cycle is unknown. There is a tendency to sexual dimorphism, for of the two worms in each cyst, one is larger and with better development of the female system and the other smaller with male tendency (Jeger, 1917). *Troglotrema salmincola* with metacercariae in the salmon is the causative agent of a highly fatal disease of dogs termed salmon poisoning resulting from eating infected salmon (Simms, Donham, and Shaw, 1931; Witenberg, 1932). Presumably the fatal effect comes from some disease carried by the flukes, rather than from the flukes themselves.

o. Family Fasciolidae.—This family includes the well-known liver flukes of ruminants, large leaf-like flukes with acetabulum relatively close to the oral sucker, gonopore just in front of the acetabulum, and a

branched condition of crura, gonads, yolk glands, and excretory tubules (Fig. 116*A*). These flukes inhabit the liver and bile passages of sheep, goats, cattle, deer, and other ruminants, often to the great detriment of the host's health. The principal liver flukes are *Fasciola hepatica,* to 30 mm., in ruminants in Europe and America; the even longer *Fasciola gigantica.* to 75 mm., in Africa and Asia; and *Fascioloides magna,* to 100 mm , in North America (Stiles, 1894, 1895; Swales, 1935). *Fasciola hepatica* is frequently used as a textbook and class type, but the branched condition of its organs is somewhat atypical for the Digenea (Fig. 116*A*). Stephenson (1947) has made valuable contributions to the anatomy and physiology of this species; he finds that an ootype is lacking and Laurer's canal enters the oviduct, not the common vitelline duct (Fig. 116*C*). The life cycle of the liver fluke as worked out by A P. Thomas in 1883 has been confirmed for other Fasciolidae. The capsules at laying contain an uncleaved egg (Fig 117*A*) that requires some weeks to develop to a miracidium (Fig. 117*B*). This penetrates pulmonate snails of the genus *Lymnaea* and related genera, in which the sporocyst produces two generations of rediae (Fig. 102*C*) and finally somewhat long-tailed cercariae (Fig. 117*C*). These encyst on grasses or aquatic plants (Fig. 117*D*), and after ingestion by the definitive host the cysts hatch into young flukes that bore through the intestinal wall into the peritoneal cavity and thence into the liver (Schumacher, 1938; Krull and Jackson, 1943). The chief fasciolid fluke of man is *Fasciolopsis buski,* to 70 mm , inhabiting the intestine, and common in China, India, Sumatra, and similar localities in pigs as well as in man. In China the cercariae encyst on the nutlike fruits of a certain aquatic plant (Nakagawa, 1922; Barlow, 1925) that are eaten raw by the natives.

p. Family Cyclocoelidae.—This is one of the principal families of monostome flukes, although a small acetabulum is sometimes present. They are large to moderate flukes, to 15 mm , with muscular bodies, reduced or nearly absent oral sucker, and intestinal crura confluent posteriorly (Fig. 87*C*). The adults inhabit the coelom, trachea, lungs, air sacs, and nasal and other head cavities of water birds The family has been extensively treated by Kossak (1911), Harrah (1922), Witenberg (1926), and Joyeaux and Baer (1927). The last named authors reduce the number of genera to three: *Cyclocoelum, Typhlocoelum,* and *Ophthalmophagus.* The life cycle of *Typhlocoelum cymbium* from grebes and ducks has been worked out by Szidat (1932b) and Stunkard (1934). The miracidium contains a fully formed redia which escapes after penetration of snails. Within the snail the redia produces directly cercariae of the cercariaeum type that encyst in the same snail, and the eating of such infected snails by water birds completes the cycle. The cercariae are distome so that the monostome condition is here secondarily derived

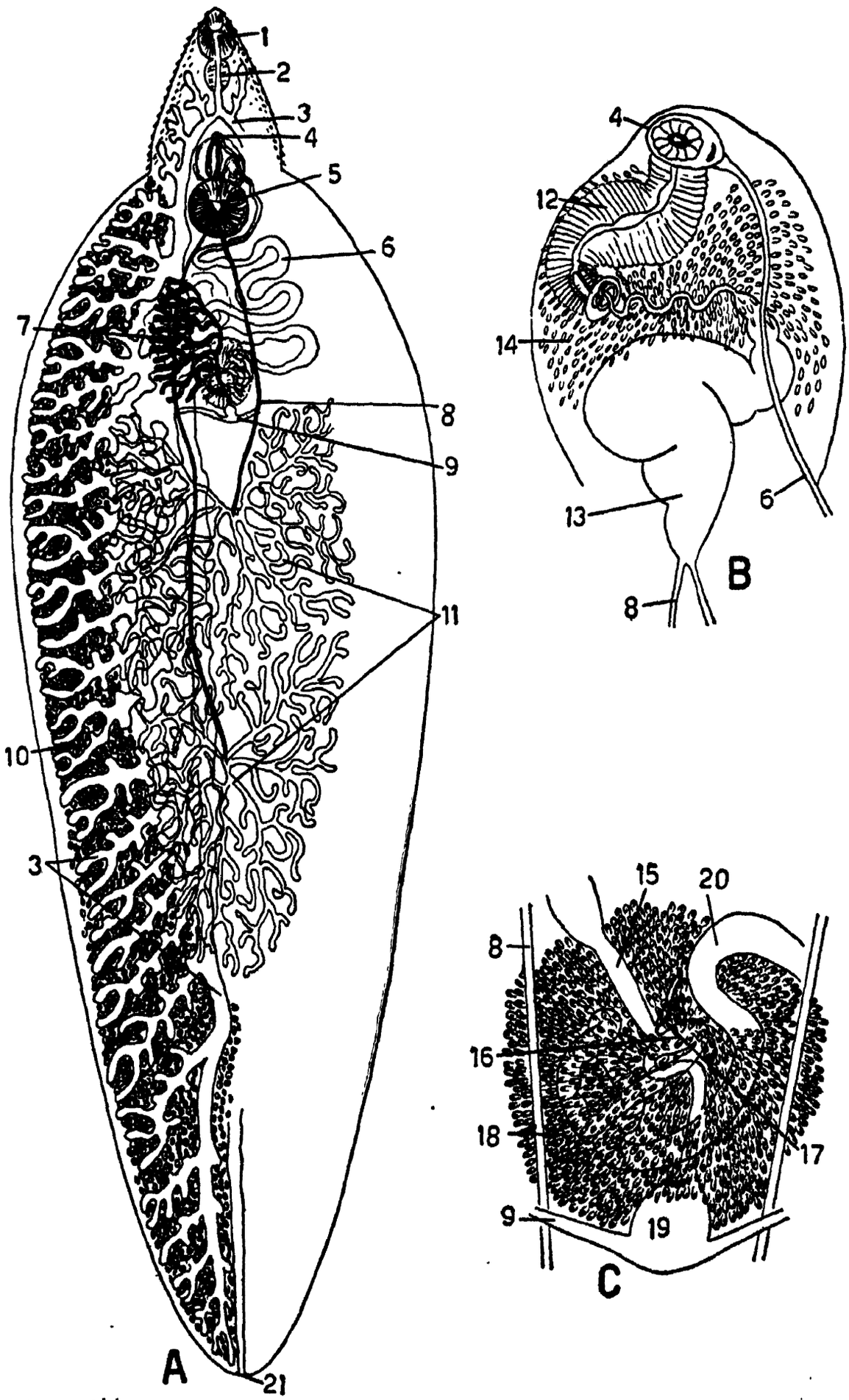

FIG. 116.—Fasciolidae. *A. Fasciola hepatica (from slide, courtesy A. E. Galigher).* *B.* Details of male system of *F. hepatica.* *C.* Details of the female system. 1, oral sucker; 2, pharynx; 3, intestine; 4, gonopore; 5, acetabulum; 6, uterus; 7, ovary; 8, sperm duct; 9, yolk duct; 10, yolk glands; 11, testes; 12, cirrus sac; 13, seminal vesicle; 14, prostatic glands; 15, oviduct; 16, beginning of uterus; 17, Laurer's canal; 18, Mehlis's glands; 19, yolk reservoir; 20, continuation of uterus; 21, nephridiopore.

from a distome ancestor. The monostomes are clearly a heterogeneous assemblage of no taxonomic status.

q. Family Clinostomatidae.—These are distomes of some size with small oral sucker, large anteriorly placed acetabulum, scantily coiled uterus, and surface network of excretory vessels. The adults inhabit the oral cavity, throat, and esophagus of fish-eating birds, especially wading birds. The best known genus is *Clinostomum*, the metacercariae of

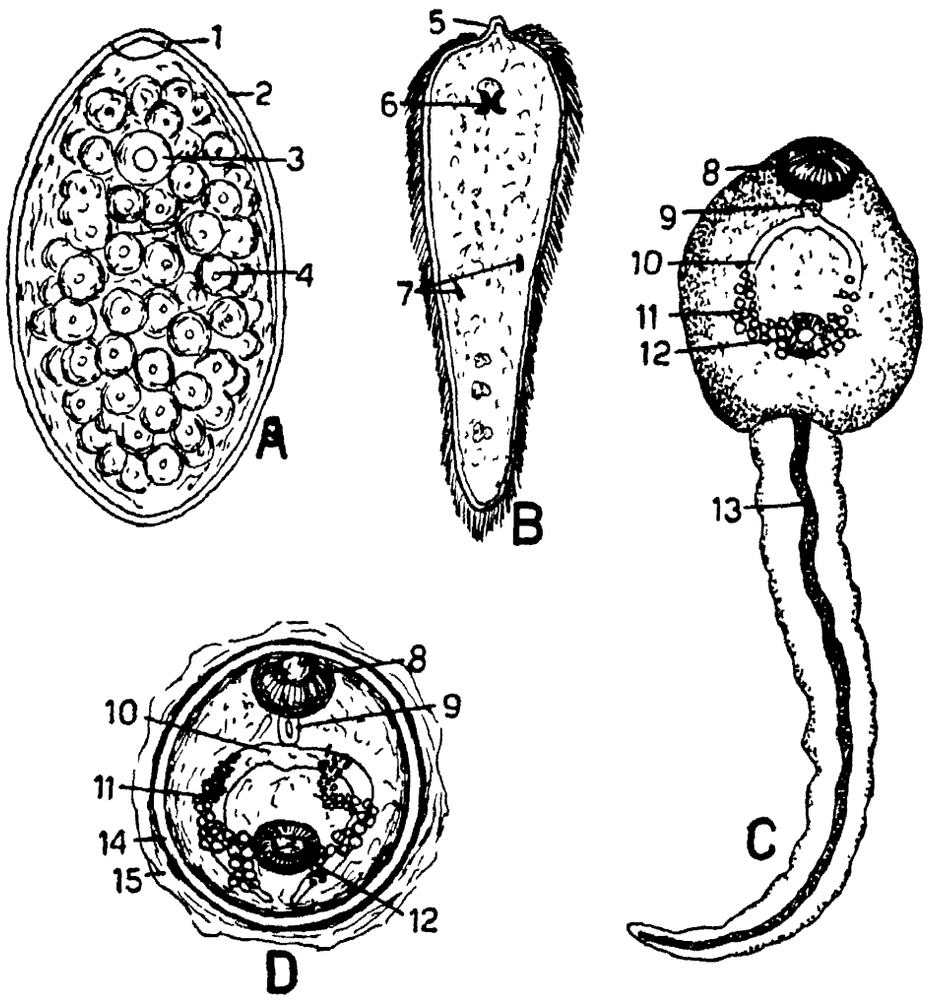

FIG. 117.—Fasciolidae, larval stages. *A*. Capsule at laying *B* Miracidium. *C*. Cercaria. *D*. Encysted metacercaria (All stages of the human intestinal fluke, *Fasciolopsis buski, after Nakagawa,* 1922) 1, operculum, 2, capsule, 3, egg, 4, yolk cells, 5, apical papilla; 6, eyes; 7, flame bulbs; 8 oral sucker, 9, pharynx, 10, intestine, 11, spherules in nephridia; 12, acetabulum; 13, nephridium in tail, 14, inner cyst wall; 15, outer cyst wall.

which, known as "yellow grubs," occur encysted in the muscles throughout the body in fish and in the coelomic lining and lymph sacs of frogs (Fig. 118*C*). These cysts, large enough to be obvious, have long been noticed by zoologists, students dissecting frogs, fishermen, and breeders of tropical fishes (Nigrelli, 1936); but the life cycle of *Clinostomum* was first elucidated in 1934 by the Hunters. The capsules drop into the water from the mouths of the bird hosts as they are fishing, and the miracidium (the Hunters, 1935), provided with two pairs of flame bulbs, hatches at once or later and penetrates snails of the genus *Helisoma*. The sporocyst produces two generations of rediae, and the cercariae are ophocercous with forked tails. The metacercarial cyst is composed

entirely of the host's connective tissue (Hunter and Dalton, 1939). It has been shown (Cort, 1913; the Hunters, 1933) that the species encysted in fish with herons as the definitive host is distinct from that encysted in frogs with the final stage in the bittern. The one is *C. complanatum* (= *marginatum*) and the other is *C. attenuatum*. The adult anatomy was extensively described by Osborn (1912).

r. Family Notocotylidae.—These are monostomes notable for the presence on the ventral surface of rows of eversible pouches into which glands open (Fig. 118*D*). The adults inhabit the intestine of aquatic birds and mammals. The majority of species belong to the notocotyline group, including the genera *Notocotylus, Quinqueserialis, Catatropis,* and *Paramonostomum*, of which the North American forms have been reviewed by Harwood (1939). The life cycle of the notocotylines comprises sporocysts and two generations of rediae in snails, cercariae of ordinary tailed type, and metacercarial encystment on vegetation and inanimate objects (Yamaguti, 1938; Herber, 1942).

s. Family Echinostomatidae.—This is a large and important distome family of mostly slender elongated form, with spiny or scaly cuticle, large acetabulum shortly behind the small oral sucker, and a collar of spines on the anterior end (Fig. 119*A*). The collar of spines is already present in cercarial and metacercarial stages (Fig. 106*A*) and serves to distinguish the family readily from all other digenetic families. The echinostomes inhabit chiefly the intestine of birds, less often the intestine of mammals. The echinostomes of birds were extensively treated by Dietz (1910), and many species were also described from Japanese birds by Yamaguti (1933–1941). Some representative genera are *Echinostoma, Echinoparyphium, Patagifer, Petasiger, Euparyphium, Himasthla, Echinochasmus*, and *Parorchis*. The life cycle of an echinostome was first worked out by Johnson (1920), and a number of cycles have since been described (Beaver, 1937; Johnston and Angel, 1941; Macy, 1942, for *Echinostoma;* McCoy, 1928; Rasin, 1933; Tubanqui and Pasco, 1933, for *Echinoparphyium;* Stunkard and Cable, 1932, for *Parorchis;* Stunkard, 1938b, for *Himasthla;* and Beaver, 1939, for *Petasiger*). The capsules at laying contain an uncleaved egg that develops into a miracidium in 2 to 5 weeks. The miracidium penetrates snails in which the sporocyst and two redial generations are passed; but in *Parorchis* (Fig. 100*B*) the miracidium already contains a fully developed redia. The cercariae swim free and encyst chiefly in other snails, also in clams, planarians, tadpoles, and fish. Echinostomes appear not to be very particular as to either intermediate or definitive hosts, and several species may infect man in common with other hosts as a result of eating raw snails and clams, in China, Java, Philippines, etc. (Vogel, 1933; Tubanqui and Pasco, 1933; Sandground and Bonne, 1940).

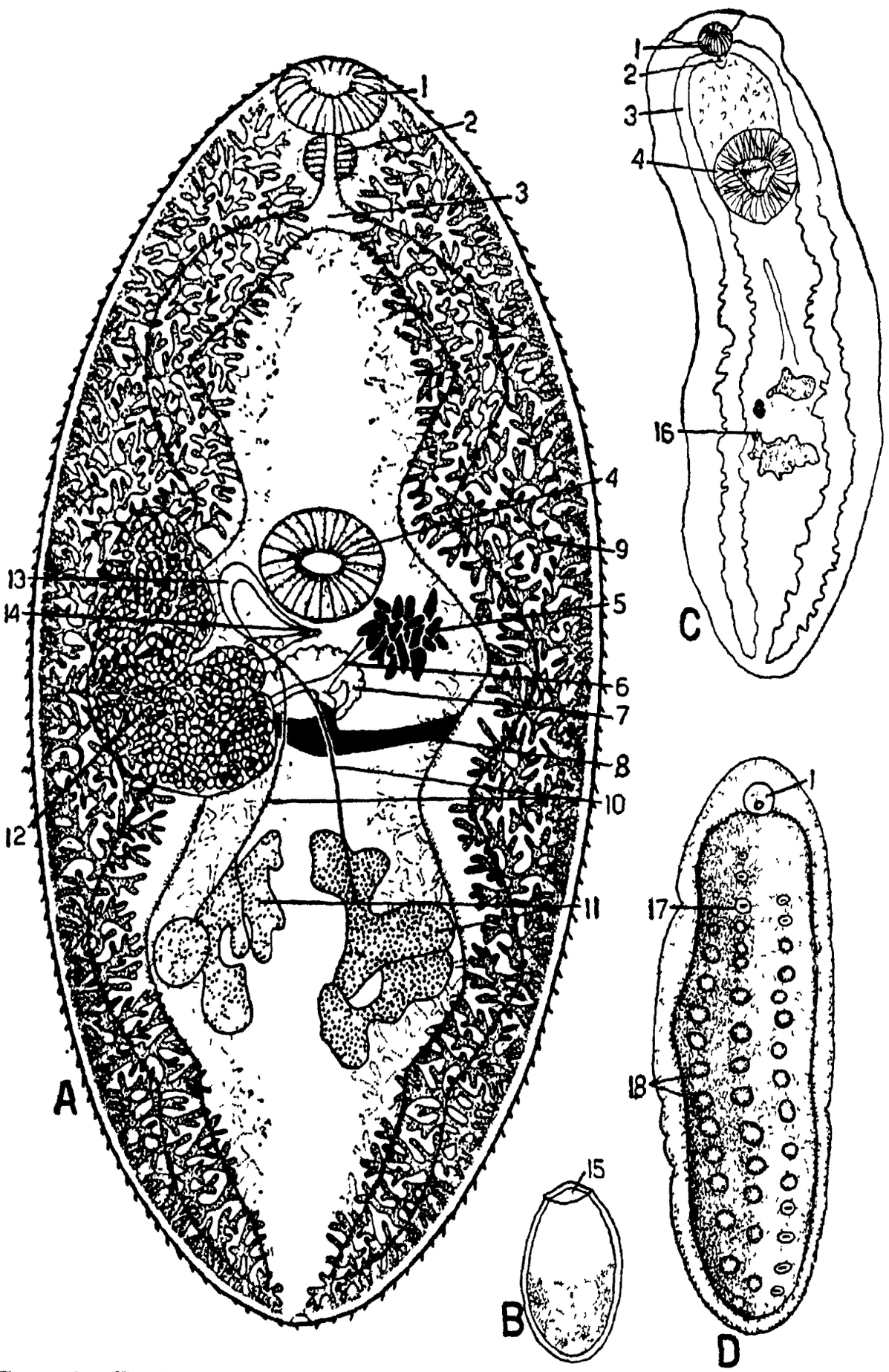

FIG. 118.—Troglotrematidae, Clinostomatidae, Notocotylidae. *A. Paragonimus* (*after Chen*, 1940) *B.* Capsule of *Paragonimus* (*after Ward and Hirsch*, 1915) *C* Metacercaria of *Clinostomum* removed from cyst (*after Cort*, 1913). *D. Notocotylus* (*after Harwood*, 1939) 1, oral sucker; 2, pharynx; 3, intestine, 4, acetabulum; 5, ovary, 6, oviduct; 7, ootype; 8, yolk ducts; 9, yolk glands; 10, sperm ducts, 11, testes, 12, uterus, 13, cirrus sac; 14, gonopore; 15, operculum; 16, primordia of reproductive system, 17, gland pockets; 18, pockets everted.

t. Family Strigeidae (= *Holostomidae*).—This is also a large and important distome family, parasitic as adults in the intestine of birds and mammals, less often reptiles. The strigeids are flukes of small to considerable size (to 20 mm.) and of peculiar body shape, being typically (but not always) divided by a constriction into a flattened, concave, spoon-like, or cup-like *forebody*, and a cylindroid *hindbody* (Figs. 80*B*, 119*C*). The relative proportions of these two regions vary greatly in different members; thus in *Nematostrigea*, *Ophiosoma* (Fig. 119*B*), and *Cardiocephalus*, the forebody is short and the hindbody very slender and elongated, whereas in *Cyathocotyle* (Fig. 120*A*) the very small hindbody is not distinctly set off. The forebody bears the small oral sucker and acetabulum and behind the latter an accessory adhesive organ termed the *holdfast* (Figs. 80*B*, 119*C*) that is without counterpart in other Digenea. This holdfast is a rounded, mushroom-like, or elongated protuberance that is often cleft or lobed or may be subdivided (Fig. 120*B*) into dorsal and ventral parts; it contains gland cells whose secretion has been conjectured to exercise a corroding effect on host tissue (La Rue, 1932). The strigeids maintain a very strong attachment on the host intestine by grasping villi between the holdfast and the side walls of the forebody. In some strigeids, especially the genus *Diplostomum* (Fig. 119*C*) and related genera, the anterior end bears to either side of the oral sucker, a small accessory sucker or sucker-like depression or ear-like projection; these are called *pseudosuckers*, *sucking cups*, etc. Another peculiar feature of strigeids is the so-called *reserve bladder*, a peripheral system of excretory channels (Fig. 121*C*) that opens into the regular protonephridial system. The reproductive system is usually lodged chiefly in the hindbody and opens at the posterior end, often into a large antrum (Fig. 119*B*). Strigeids with cup-like forebody and holdfast divided into dorsal and ventral parts are often called *holostomes;* those with leaf-like or spoon-like forebody and undivided holdfast are termed *hemistomes* and *diplostomes;* the latter may have pseudosuckers.

Extensive articles on the family have been published by Brandes (1890), Krause (1915), Szidat (1929), and Dubois (1937), and numerous studies on North American strigeids have been made at the University of Michigan by La Rue, Hughes, and Van Haitsma (1926–1931). Dubois in 1938 issued a valuable monograph in which what is here considered a family was raised to the rank of supersuperfamily Strigeida and what are usually considered subfamilies were raised to family rank. Some of the principal genera of the Strigeidae (in the broad sense) are *Alaria* (= *Hemistomum*, Fig. 80*B*) and *Pharyngostomum* in dogs, cats, foxes, and other carnivorous mammals; *Braunina* in whales and dolphins; *Neodiplostomum* and *Strigea* (= *Holostomum*) in birds of prey; *Apatemon*, *Cyathocotyle* (Fig. 120*A*), *Cotylurus* (Fig. 120*B*), and *Diplostomum* (Fig.

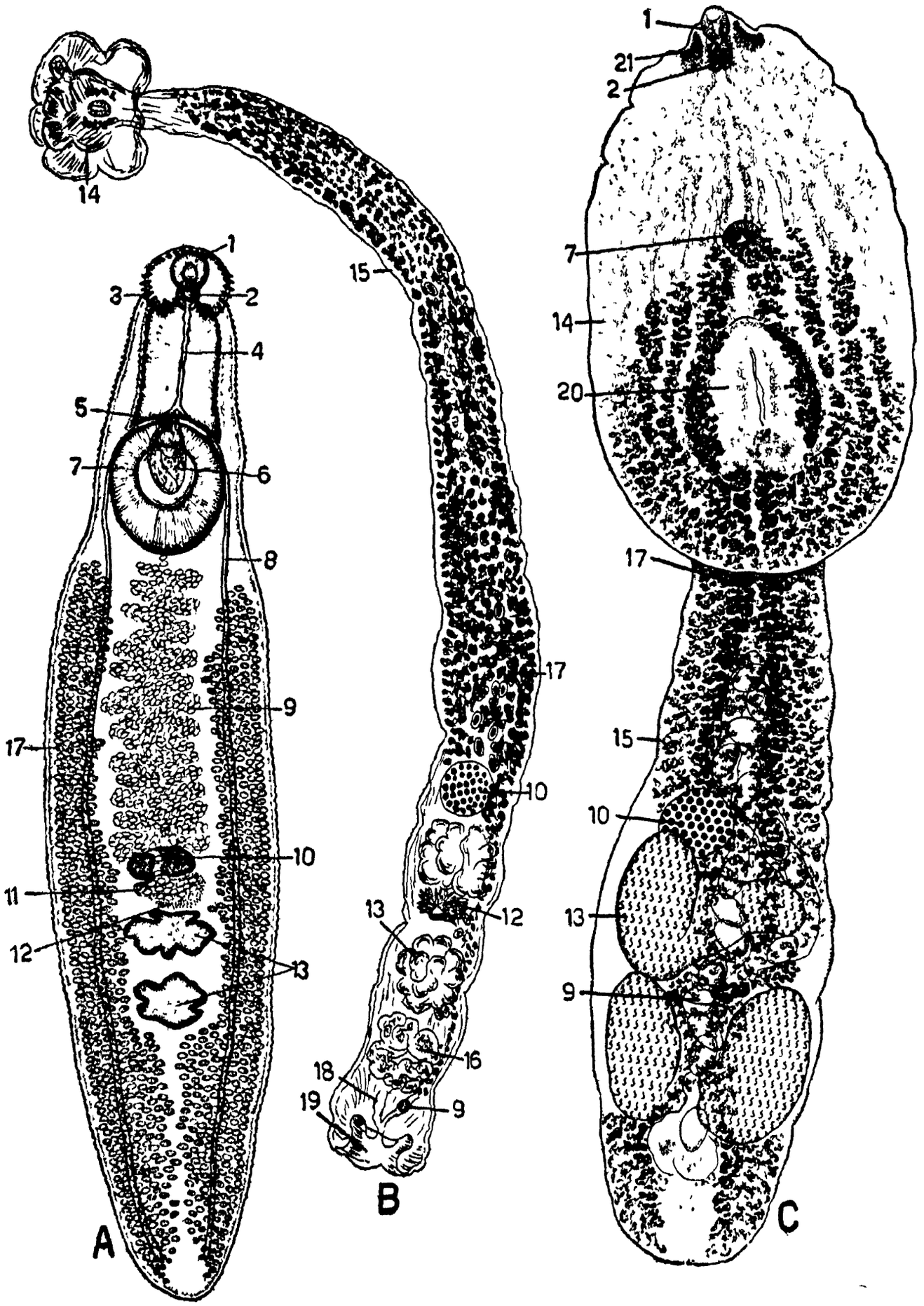

FIG. 119.—Echinostomatidae, Strigeidae. *A*. An echinostome fluke from the pigeon intestine (*after Yamaguti*, 1935). *B* Strigeid *Ophiosoma*, intestine of the bittern *C* *Diplostomum*, gull intestine. (*B*, *C*, *after Dubois*, 1938) 1, oral sucker; 2, pharynx; 3, collar of spines; 4, esophagus; 5, gonopore, 6, cirrus sac, 7, acetabulum; 8, intestine, 9, uterus; 10, ovary; 11, ootype; 12, Mehlis's glands; 13, testes, 14, forebody; 15, hindbody; 16, seminal vesicle; 17, yolk glands; 18, sperm duct; 19, genital antrum; 20, holdfast; 21, pseudosuckers.

119*C*) in ducks, other anseriform birds, and various other birds; *Posthodiplostomum*, *Apharyngostrigea*, *Cardiocephalus*, and *Tylodelphys* in gulls, terns, grebes, wading birds, etc.; and *Uvulifer* in kingfishers.

The strigeid life cycle was first worked out by Lutz (1920), and cycles have since been described for *Cotylurus* by Szidat (1924), Mathias (1925), Hughes (1929), Van Haitsma (1931), Olivier and Cort (1942); for *Diplostomum* by Hughes and Berkhout (1928) and Van Haitsma (1931); for *Apharyngostrigea* by Scheuring and Everbusch (1926) and Azim (1935); for *Uvulifer* by the Hunters (1934); for *Posthodiplostomum* by Hunter (1936) and Ferguson (1936); for *Pharyngostomum* by Wallace (1939); for *Cyathocotyle* by Yamaguti (1940b); and for *Apatemon* by Stunkard, Willey, and Rabinowitz (1941).[1] The miracidia, distinguished by 21 epidermal cells in tiers of 6, 6, 6, 3, and two pairs of flame bulbs, develop after the capsules are laid and penetrate snails, mostly lymnaeids, in which there occur two generations of sporocysts. The development of the sporocysts has been described by Cort and Olivier (1941) who find that daughter sporocysts and cercariae develop from multinucleate germ masses broken off from preexisting germ masses. The cercariae, of which many studies have been published (e.g., Cort and Brooks, 1928), are of characteristic appearance, being pharyngate furcocercous cercariae (Fig. 120*C*). These penetrate various aquatic animals, chiefly snails and fish, but also leeches, tadpoles, frogs, salamanders, and snakes, where they metamorphose into metacercariae, with or without encystment.

The metacercariae of the Strigeidae are of peculiar appearance, and several different types have been recognized. These metacercariae may be naked or encysted in a gelatinous cyst of parasite origin, or the outer part of the cyst may be furnished by the host. In the last case, the host part of the cyst is often permeated with black pigment, whence the name "black grub" often applied to these cysts by fishermen. All strigeid metacercariae have oral sucker, acetabulum, holdfast, and reserve bladder system. In the *tetracotyle* type (Faust, 1918e; Hughes, 1928, 1929a, 1929b, Fig. 121*A*), the body is pyriform, with or without a small hindbody, with well-developed pseudosuckers, and with the reserve bladder in the form of large spaces (Fig. 122*A*). The *diplostomulum* type (Hughes and Berkhout, 1928; Hughes and Holl, 1928; Hughes, 1929b, 1929e) has a foliaceous concave forebody, a small conical hindbody, pseudosuckers, and a reserve bladder of anastomosing tubules, and lacks a cyst wall of parasitic origin (Fig. 120*E*). *Tylodelphys* metacercariae are a variety of

[1] The generic names here employed follow Dubois (1938); in the articles cited various other names are used. The synonymy of the strigeids is in fact frightfully confused and the same species appears in the literature under many different names with also different names for its cercarial and metacercarial stages. The synonymy is thoroughly considered in Dubois's monograph.

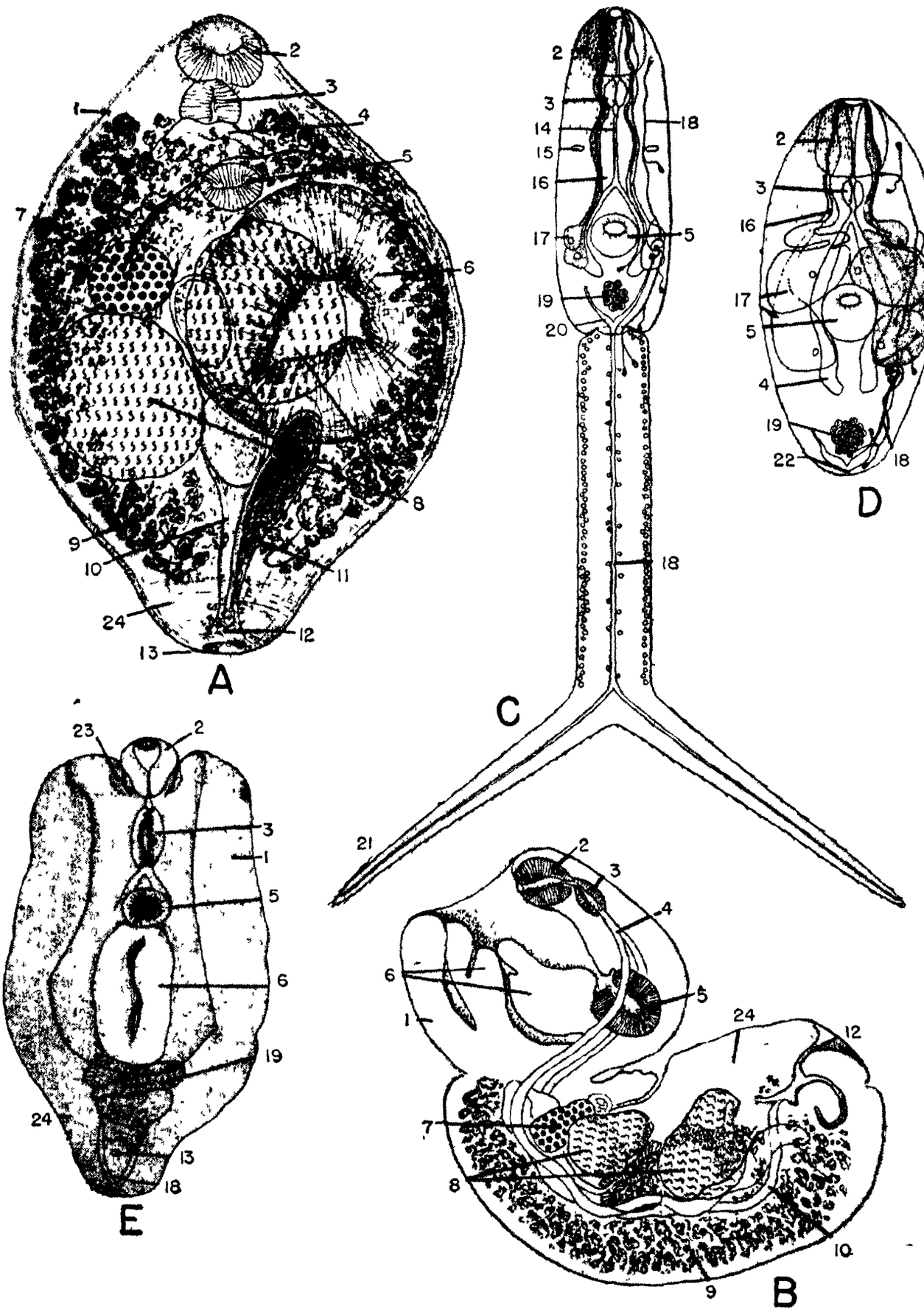

FIG. 120.—Strigeidae (continued). *A. Cyathocotyle*, duck intestine *B* Longitudinal section of *Cotylurus flabelliformis*, intestine of ducks and other water birds. (*A*, *B*, *after Dubois*, 1938.) *C–E*, larval stages of *Alaria* (*after Bosma*, 1934). *C* Cercaria, note forked tail, pharynx. *D*. Mesocercaria *E* Metacercaria of the diplostomulum type. 1, forebody; 2, oral sucker; 3, pharynx, 4, intestine, 5, acetabulum; 6, holdfast; 7, ovary; 8, testes; 9, yolk glands; 10, uterus, 11, cirrus sac; 12, genital antrum; 13, gonopore; 14, esophagus, 15, eyes; 16, ducts of penetration glands, 17, penetration glands; 18, protonephridium; 19, primordium of reproductive system; 20, definitive bladder; 21, larval nephridiopores; 22, definitive nephridiopore; 23, pseudosuckers; 24, hindbody.

diplostomulae that are more elongate with less defined pseudosuckers and hindbody. Diplostomulum and tylodelphys metacercariae often occur in the eyes of fishes, in the lens or the vitreous humor, and if sufficient numbers invade the lens, blindness ensues (La Rue, 1926). A third kind of strigeid metacercaria, termed *neascus*, was defined by Hughes (1927); this has a cup-shaped forebody, well-developed hindbody, and a reserve bladder similar to that of the diplostomulum larva but lacks pseudosuckers (Fig. 121*B*, *C*). Neascus larvae occur in *Crassiophila*, *Uvulifer*, and related forms. The *codonocephalus* metacercaria, described by Kopczynski (1907), is similar to the neascus type.

The genus *Alaria* (Fig. 80*B*) differs from all other Digenea in requiring three intermediate hosts (Bosma, 1934; Odlaug, 1940). The cercariae (Fig. 120*C*) penetrate tadpoles and frogs but do not develop very far, remaining in a stage termed *mesocercaria* (Fig. 120*D*). These, after their host has been devoured by a small mammal such as mice, rats, and raccoons, develop into metacercariae of the diplostomulum type (Fig. 120*E*) that become adult in the intestine of the definitive host, dog, cat, mink, weasel, etc. It has been shown that the mesocercaria stage cannot be omitted for the third intermediate host cannot be infected directly by the cercariae.

u. Family Brachylaimidae (= *Harmostomidae*).—This is a family of small to moderate distomes with well-developed suckers, posterior gonopore, and seminal vesicle free from the cirrus sac (Fig. 122*B*). The harmostomes occur chiefly in the intestine of birds and mammals, less often of amphibians and reptiles. The systematics of the family have been treated by Witenberg (1925) and Sinitsin (1931b). The principal genera are *Brachylaima* (= *Harmostomum*) and *Leucochloridium* (Fig. 122*B*). The remarkable sporocysts of the latter have long attracted the attention of zoologists and are regularly mentioned in zoology texts. The life cycle of the European *Leucochloridium* was worked out by Zeller (1874) and Heckert (1889), and various observations on American species confirm the account (Magath, 1920; McIntosh, 1932; Woodhead, 1935; Bennett, 1942). The capsules dropped by birds on vegetation are eaten by terrestrial and amphibious snails, chiefly *Succinea*, in which the miracidia hatch, then penetrating the snail tissues. Two generations of sporocysts ensue; the daughter sporocysts are highly branched, and branches eventually push into the snail's head and tentacles where they enlarge to swollen sacs that are brightly pigmented with green, brown, or orange bands (Fig. 122*C*) and that undergo pulsations of about 70 per minute at summer temperatures (Wesenberg-Lund, 1931). These brightly colored pulsating sacs are noticeable at a distance of several feet and presumably simulate insect larvae, thus attracting the attention of birds. The swollen snail skin ruptures at the slightest touch, releasing

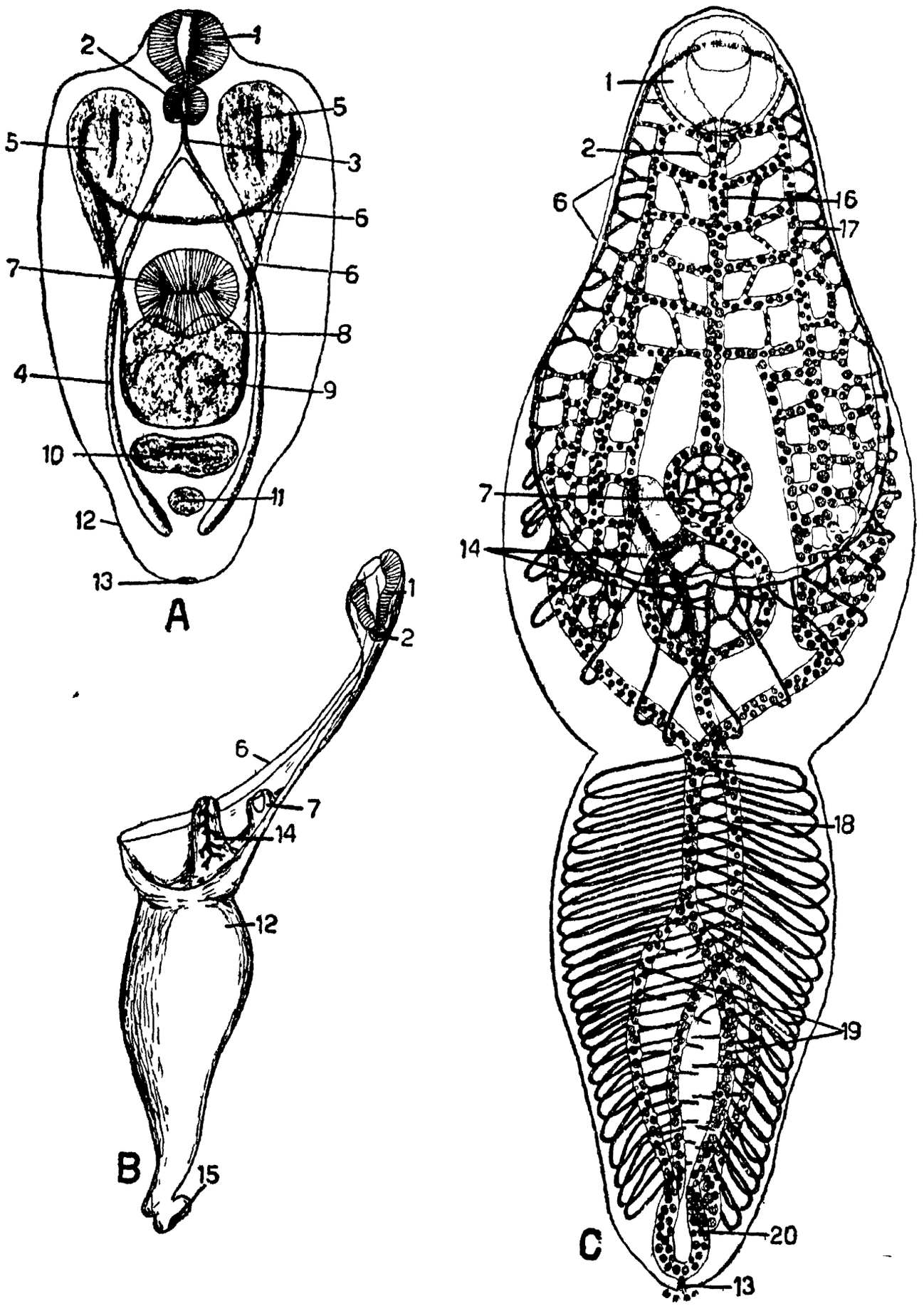

FIG. 121.—Strigeidae (continued). *A*. Tetracotyle from a garter snake (*after Hughes*, 1929). *B*. Neascus larva from the bass (*after Hughes*, 1927). *C* Same, to show vessels of the reserve bladder (*after Hughes*, 1927). 1, oral sucker, 2, pharynx, 3, esophagus, 4, intestinal crura; 5, pseudosucker; 6, edge of cup-like forebody, 7, acetabulum, 8, anterior lobes of holdfast; 9, posterior lobes of holdfast; 10, glands of holdfast, 11, primordium of reproductive system; 12, hindbody; 13, nephridiopore, 14, holdfast; 15, gonopore, 16, median dorsal vessel; 17, main lateral vessel; 18, median dorsal vessel of hindbody, 19, median ventral vessel of hindbody; 20, excretory bladder.

the colored sacs, which continue to pulsate. The sacs are filled with encysted cercariaea (Fig. 122*D*) that are infective to various passerine birds. Although Zeller saw captive birds peck the sacs from the tentacles of infected snails and swallow them, it seems more probable that in nature the sacs are released through chance contacts and are then picked up by birds (Wesenberg-Lund, Woodhead). Juvenile birds are more susceptible to infection than adults, and probably the sacs are often fed to nestlings by parent birds.

v. Family Sanguinicolidae.—This and the next two families are blood flukes, i.e., they live in the blood of vertebrates inside the blood vessels and hence are of slender shape with weak or degenerate suckers. The present family comprises the single genus *Sanguinicola* (Fig. 123*A*) which inhabits the blood of fishes of the families Cyprinidae, Siluridae, and Percidae. Three species are known from Europe (Odhner, 1911b 1924; Scheuring, 1922; Ejsmont, 1925) and one from North America (Van Cleave and Mueller, 1932). The animal is slender, pointed at both ends, about 1 mm. long, without suckers. The protrusible anterior tip contains the mouth armed with three hooks in some species and leading into a long tube provided or not with a poorly developed pharynx and terminating in a small lobed intestinal sac. The numerous testes occupy a central position, and from them the sperm duct runs to a posterior, dorsally located male pore before which it widens to a simple cirrus. From the bilobed ovary a long oviduct proceeds posteriorly and shortly after receiving the common vitelline duct widens to form an ootype. This is followed by a short vagina opening dorsally by a female pore. A uterus is lacking, and the curious triangular capsules (Fig. 123*F*) are formed and laid singly into the blood stream which carries them to the gills. Meantime the miracidium has already developed, hatches in the host blood vessels, and escapes through the gills (Scheuring, 1922; Ejsmont, 1925). It enters a snail in which sporocysts and cercariae develop. The cercariae are furcocercous without a pharynx and lophocercous (Fig. 103*C*) and were long known under the name of *Cercaria cristata.* Whether there is a second intermediate host is not known; it is supposed that the cercariae penetrate the definitive host directly.

w. Family Spirorchidae.—These are flukes of small to moderate size, either distome or monostome, found in the blood of turtles, chiefly in the heart and larger arteries. They have been extensively discussed by Stunkard (1923) and Byrd (1939). The mouth provided with an oral sucker leads by a long esophagus, for a pharynx is lacking, into the intestine that may have the usual two crura, or may be wholly or partly single. The principal genera are *Spirorchis* (Fig. 123*B*) with a central longitudinal row of several (to 10) testes; *Hapalorhynchus* with two testes; and *Vasotrema* with a single elongate spirally coiled testis. The capsules are

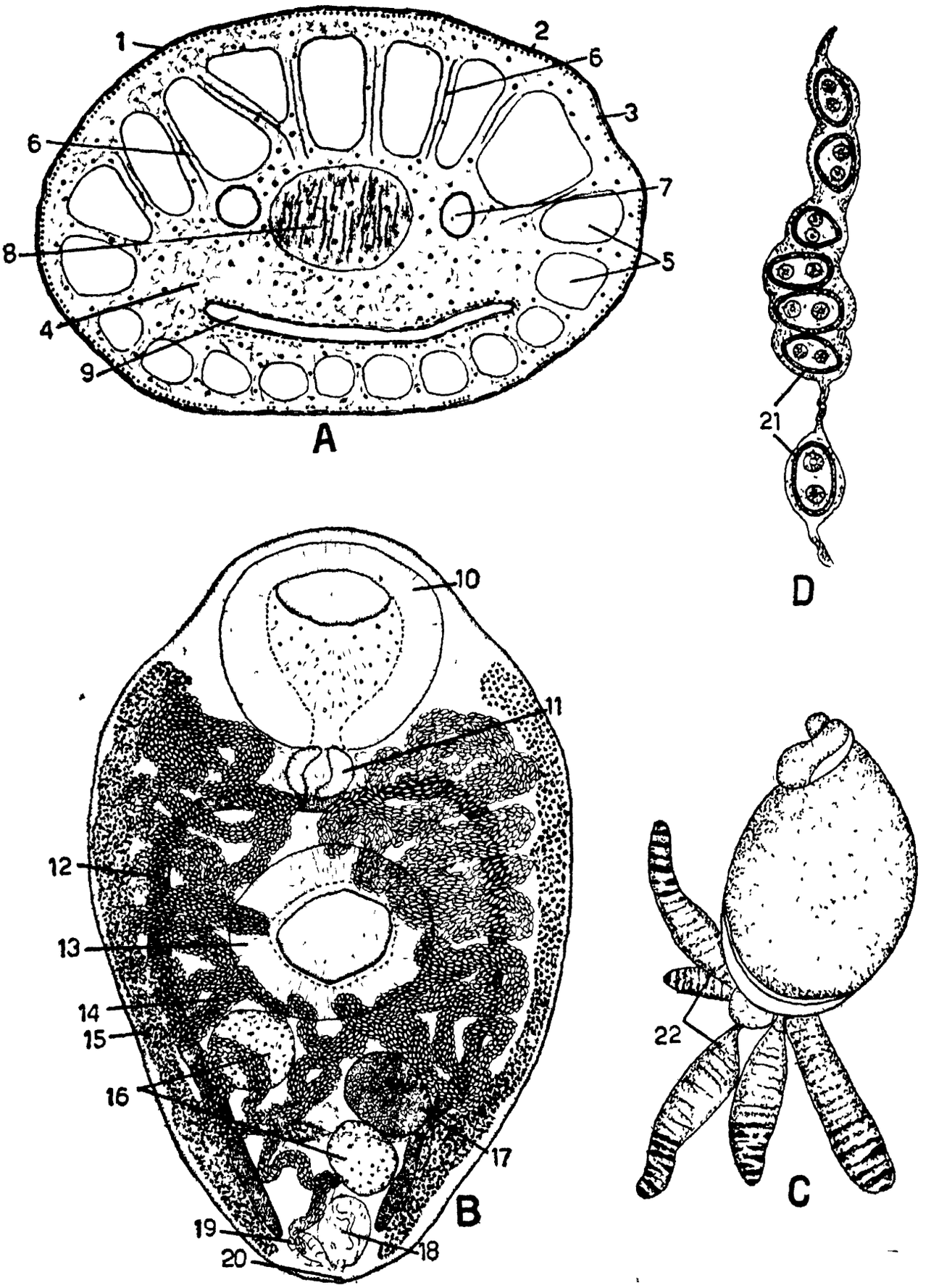

FIG. 122.—Strigeidae, Leucochloridium. *A*. Cross section of tetracotyle shown in Fig. 121*A*, at level of acetabulum, to show spaces of reserve bladder (*after Hughes*, 1929). *B*. *Leucochloridium* (*after McIntosh*, 1932). *C* Snail *Succinea* with protruding sporocyst sacs of *Leucochloridium*. *D*. Small portion of branching sporocyst of *Leucochloridium* to show encysted cercariaea. (*C*, *D*, *after Wesenberg-Lund*, 1931.) 1, cuticle; 2, circular muscle layer; 3, longitudinal muscle layer; 4, mesenchyme, 5, spaces of reserve bladder; 6, mesenchymal muscle fibers; 7, section of intestinal crura, 8, section of acetabulum; 9, cavity of forebody; 10, oral sucker, 11, pharynx; 12, intestine, 13, acetabulum; 14, uterus; 15, yolk glands; 16, testes; 17, ovary; 18, cirrus sac; 19, metraterm; 20, gonopore; 21, cercariaea; 22, sporocyst sacs.

discharged into the tissues of the host whence they find their way into the digestive tract and so to the exterior. The life cycle has been worked out by Wall (1941a, 1941b). The miracidium, provided with two pairs of flame bulbs, hatches some days after the capsules are laid and penetrates lymnaeid snails where two generations of sporocysts occur. The cercaria as in the case of other blood flukes is apharyngeal and furcocercous; it penetrates directly into the definitive host.

x. Family Schistosomatidae (= *Bilharziidae*).—These are blood flukes that inhabit the hepatic portal system and pelvic veins of birds and mammals, including man. They are notable among flukes for their sexual dimorphism. The sexes are completely separate, and neither sex retains any part of the reproductive system of the other sex. The schistosomes are of long slender form; most species are below 10 to 15 mm. in length, but *Gigantobilharzia acotylea* from birds is 140 to 165 mm. long. The male is generally broader than the female; in some schistosomes the male is shorter, in others the female is shorter, and in some both sexes are about of the same shape and length. The usual thing is for the female to be slender and thread-like (Fig. 123*D*). The ventral surface of the male is usually incurved for a length varying in different species to form the *gynecophoric canal* in which the female remains (Fig. 123*D*) more or less permanently. The body surface is often spiny or papillose, or spines may be confined to the inner surface of the suckers. Both suckers may be present close together as in *Schistosoma* (= *Bilharzia*), or the acetabulum or both suckers may be wanting. The acetabulum is often better developed in the male than in the female (Fig. 123*D*). A pharynx is wanting, and a long esophagus leads to the intestinal crura which are fused posteriorly to form a single stem for a distance variable in different species. There are several to many testes in the male (Fig. 124*B*) and a long tubular ovary, voluminous yolk glands, long oviduct, ootype, and straight uterus containing relatively few eggs, in the female (Fig. 124*A*).

The capsules, laid one or a few at a time, may or may not be provided with a projecting spine (Fig. 123*E*, 124*F*). In laying them, the female leaves the gynecophoric canal of the male and pushes herself into the smallest possible vessels where she deposits the capsules. These work their way into the intestine or in *Schistosoma haematobium* into the urinary bladder and so reach the exterior, containing by this time fully developed miracidia (Fig. 124*C*). These hatch in the presence of water into miracidia with two pairs of flame bulbs that penetrate suitable pulmonate snails in which two generations of sporocysts ensue (development of schistosome sporocysts studied by Cort and Olivier, 1943b). Very large numbers of cercariae are produced. The cercariae as in other blood flukes are of the apharyngeal furcocercous type, distinguished from the similar strigeid cercariae by the lack of a pharynx (Fig. 124*D*, *E*). They

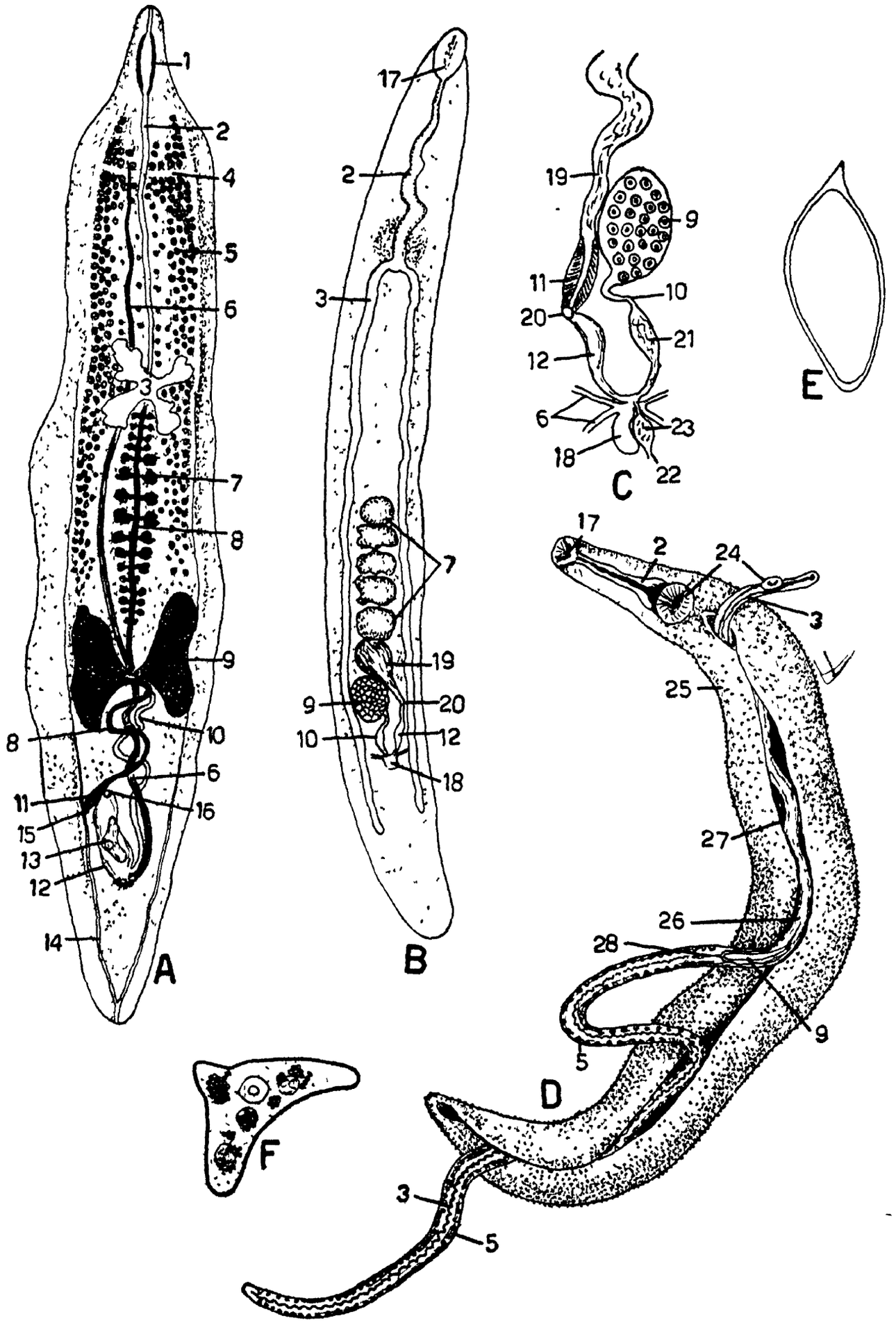

FIG. 123.—Blood flukes. *A. Sanguinicola* (*after Scheuring*, 1923). *B. Spirorchis* (*after Stunkard*, 1923). *C* Reproductive system of *Spirorchis* (*after Wall*, 1941). *D. Schistosoma haematobium*, male and female in copulation (*after Looss*, 1900). *E*. Capsule of *S. haematobium;* note terminal spine (*after Looss*, 1900). *F*. Capsule of *Sanguinicola* (*after Ejsmont*. 1925) 1, pharynx; 2, esophagus; 3, intestine; 4, nervous system; 5, yolk

penetrate directly through the skin of the definitive host or through the mucous membranes of the mouth or throat if taken in with water. They do not survive in the stomach. They make their way into small vessels where they are carried to the heart and lungs and eventually to the portal system or bladder veins. An encysted metacercarial stage is lacking; the cercariae lose their tails on penetrating the host and during their passage to the portal system gradually transform to the adult condition.

The human blood fluke, *Schistosoma* (old name, *Bilharzia*[1]), is the most important trematode parasite of man and has therefore been the object of numerous investigations. There are three human species: *S. haematobium* (Fig. 123*D*), in Africa, particularly Egypt, and southwestern Asia; *S. japonicum* in China, Japan, Formosa, and the Philippines; and *S. mansoni* (Fig. 124*A*, *B*) in Egypt and other parts of central Africa from which it has been imported, probably in the days of slavery traffic, into the West Indies and northern South America. *S. haematobium* was extensively investigated by R. T. Leiper (1915–1918), *S. japonicum* was monographed by Faust and Meleney (1924), and *S. mansoni* in Puerto Rico was investigated by Faust and Hoffman (1933–1934). These species also occur in mammals other than man and laboratory mammals can be infected with them; additional species of *Schistosoma* parasitize large mammals, as *S. spindale* in cattle, sheep, and goats, and *S. bovis* in cattle, horses, sheep, and antelopes. The human species are distinguished by structural details and also by their capsules (Figs. 123*E*, 124*C*, *F*). Infection results from wading in or drinking water containing active cercariae.

The genera of the family have been reviewed by E. Price (1929) and McLeod (1940). Most of the genera are found in birds of aquatic habits, such as gulls, ducks, grebes, and blackbirds. Some with a gynecophoric canal are *Ornithobilharzia* (Odhner, 1912) and *Schistosomatium* (Tanabe, 1923; H. F. Price, 1931; Cort, Ameel, and Olivier, 1944) and some without a definite canal are *Gigantobilharzia* (Odhner, 1910; Brackett, 1942), *Bilharziella*, and *Pseudobilharziella* (Brackett, 1942; McLeod and Little, 1942). The life cycles of these forms so far as known are similar to that of *Schistosoma*. In the Great Lakes region of North America and around lakes in various parts of the world, bathers are annoyed by a severe itch shown by Cort in 1928 to be caused by the penetration into the skin of the cercariae of bird schistosomes. The itch

[1] *Bilharzia* has priority over *Schistosoma* but *Schistosoma* has been validated by a ruling of the International Commission on Zoological Nomenclature.

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glands; 6, yolk duct; 7, testes; 8, sperm duct; 9, ovary; 10, oviduct; 11, cirrus sac; 12, ootype; 13, capsule in ootype; 14, protonephridia; 15, male gonopore; 16, female gonopore; 17, oral sucker; 18, yolk reservoir; 19, spermiducal vesicle; 20, common gonopore; 21, insemination chamber of oviduct; 22, Laurer's canal; 23, seminal receptacle; 24, acetabulum; 25, male; 26, female; 27, gynecophoric canal; 28, place of fusion of crura just behind ovary.

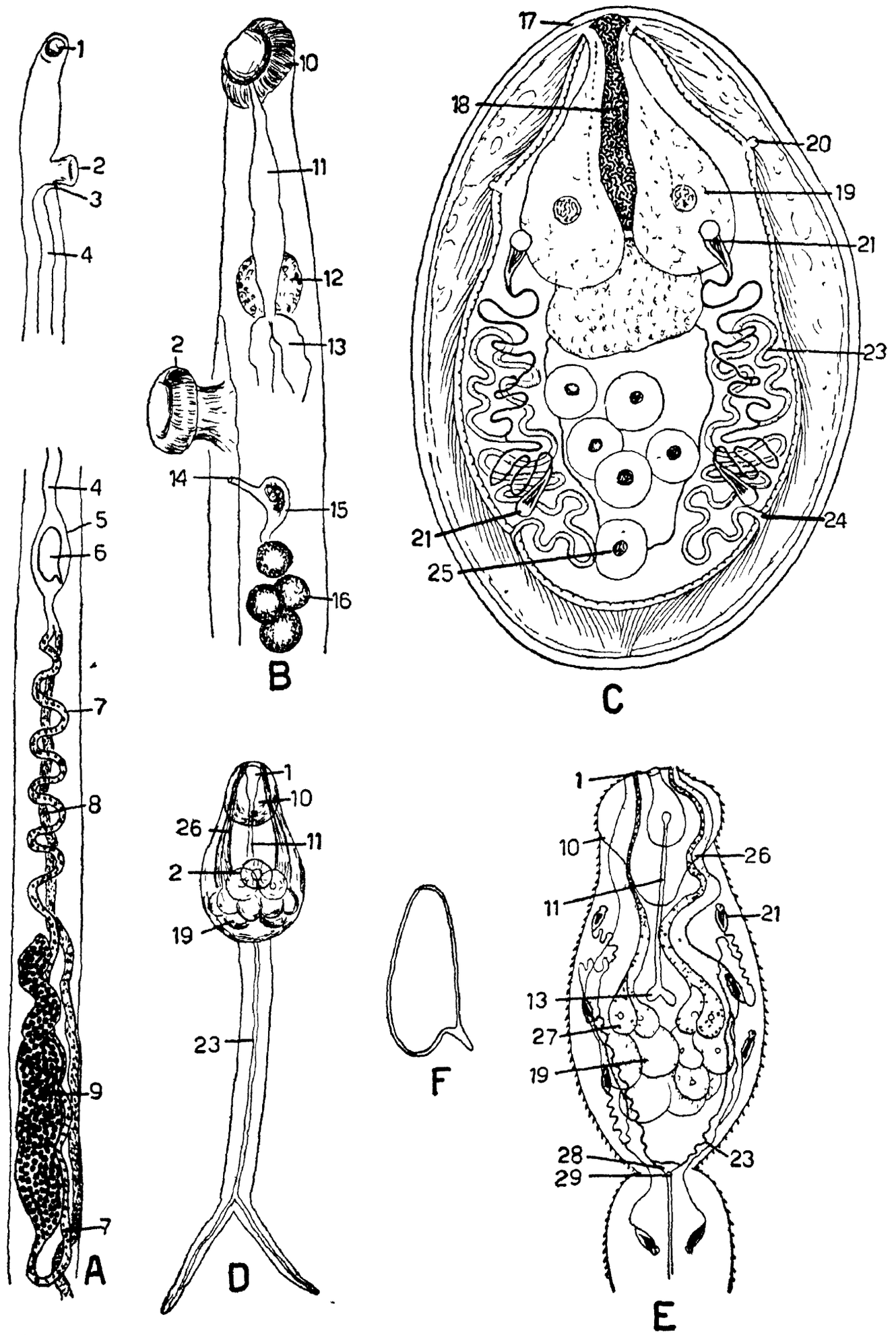

FIG. 124.—Schistosoma (continued). *A*. Female system of *Schistosoma mansoni*. *B*. Anterior part of male *S. mansoni*, to show male system. *C*. Miracidium of *S. japonicum* within the capsule (*after Cort*, 1919), note lack of spine on capsule. *D* Cercaria of *S. mansoni*. (*A*, *B*, *D*, *from slides, courtesy Dr. H. W. Stunkard.*) *E*. Anterior part of cercaria of

is therefore now known as cercarial dermatitis and is, at least in part, of an allergic nature; it has been the subject of numerous studies (Cort, 1936; Talbot, 1936; McLeod, 1936, 1940; Brackett, 1941; McMullen and Brackett, 1941; McLeod and Little, 1942).

An interesting question concerns sex determination in the schistosomes. It was suspected by Cort in 1921 and demonstrated by Severinghaus (1928) and Niyamasena (1940) that all the flukes coming from one miracidium (of which there may be as many as 200,000) are of one sex. Sex is therefore determined at fertilization of the egg by a chromosomal mechanism. According to the work of Severinghaus on *S. japonicum*, using the mouse as experimental host, isolated male schistosomes develop normally but isolated females remain small and sexually undeveloped and complete their development only when given access to males.

y. Family Heronimidae.—This family comprises the single genus *Heronimus* distinguished from all other Digenea by the location of the nephridiopore (Fig. 125*B*) near the anterior end (on the dorsal surface). Another peculiarity is that the coils of the uterus traverse the body length four times. There is apparently only one species (Stunkard, 1919; Caballero, 1940), *Heronimus chelydrae*, to 15 mm. long, found in the lungs of turtles (Fig. 125).

17. Ecology of Developmental Stages.—The conditions suitable for the hatching of trematode capsules have been studied chiefly for fasciolid (Barlow, 1925; Mattes, 1926; Ross and McKay, 1929; Shaw and Simms, 1930; Krull, 1934c; Swales, 1935; Griffiths, 1939) and schistosome (Manson-Bahr and Fairley, 1920; Magath and Mathieson, 1945) flukes, forms developing in fresh water. Fresh capsules containing a mature miracidium hatch at once in a suitable medium, but those laid in the uncleaved state as in fasciolid flukes require several days or weeks up to 2 or 3 months before the miracidium is ready to hatch. Temperature is the chief factor controlling the rate of embryonic development, but great variability in hatching time may be shown by a lot of capsules kept under the same conditions. In general, fasciolid eggs do not develop at temperatures below 10°C. but remain viable at such temperatures for long periods (up to 2½ years) and can develop to infective miracidia when exposed to warm temperatures. Temperatures below freezing are fatal to later stages and to encapsulated miracidia but may not kill uncleaved eggs or early embryos if the exposure is short. Light and depth of water

S. mansoni (*after Faust and Hoffman*, 1934) to show structural details; note lack of pharynx. *F.* Capsule of *S. mansoni;* note lateral spine. 1, mouth; 2, acetabulum; 3, female gonopore; 4, uterus; 5, ootype, 6, capsule in ootype; 7, oviduct; 8, yolk duct; 9, ovary; 10, oral sucker; 11, esophagus; 12, brain; 13, intestinal crura; 14, male gonopore; 15, seminal vesicle; 16, testes; 17, capsule; 18, apical gland; 19, penetration glands; 20, lateral papillae; 21, flame bulb; 22, brain; 23, protonephridium; 24, nephridiopore; 25, propagatory cells; 26, ducts of penetration glands; 27, oxyphilic type of penetration gland; 28, definitive bladder; 29, definitive nephridiopore.

appear to be without effect upon development, but desiccation is fatal to all stages. Capsules remain viable in damp feces with a moisture content of at least 60 per cent, but less than 50 per cent is quickly fatal.

The hatching of mature miracidia is dependent on external factors. Cold and darkness inhibit hatching, which in fasciolid flukes usually occurs on bright warm mornings. Addition of fresh aerated water which must not be too acid or too alkaline favors hatching. A pH of about 7.0 to 7 5 is suitable. Lowering the salt content also favors hatching. Similar factors—aeration, change of water, lowering of salt content, moderate temperatures—also favor hatching of schistosome miracidia. In nature, the advent of rain would reproduce all these conditions and is probably the main natural stimulus to hatching. Schistosome capsules will not hatch under conditions prevailing in the human intestine—a temperature of 37°C. and a salt content of 0 9 per cent. The springing open of the operculum probably results from factors other than or in addition to the butting movements of the miracidium, such as swelling of the capsule contents through intake of water or dissolving action of miracidial secretions.

Miracidia resemble in appearance and behavior ciliate protozoans They dart about in a restless aimless fashion or may spiral in a fairly steady path or may hang to the surface film or bottom and rotate. They show great flexibility and continual peristaltic changes of form. Their general behavior suggests that they are "seeking something with feverish haste" (Barlow, 1925). They may be positive to light and negative to gravity, reactions that bring about their escape from the bottom muck in which the capsules often lie. The miracidium does not feed. The question whether miracidia find the snail host by chemotactic attraction has been answered in the negative by most observers (Swales, 1935; Mattes, 1936; Griffiths, 1939). According to their statements, miracidia test with the anterior end and attempt to bore into almost any object, including various species of unsuitable snails and other animals such as planarians. They may keep on trying to enter an unsuitable host or an unsuitable part of the snail host as the shell until they die of exhaustion. They seem to find the right host by accident, and they succeed in penetrating this host simply because their boring mechanism is adapted to succeed only with that host. Barlow (1925), on the other hand, found that the miracidium of the human intestinal fluke is attracted to snail juice and does not try to penetrate a recently killed snail.

The penetration of the snail host by the miracidium has been repeatedly witnessed and is well described by Barlow (1925). When the miracidium has by chance made contact with a suitable soft spot on the snail, the apical papilla attaches and the miracidium executes boring movements accompanied by body contractions and expansions. Flesh-dis-

solving secretions from its glands undoubtedly aid the penetration process. The miracidium gradually squeezes through the minute opening made in the host (Fig. 126), shedding its epidermis in the process. It seems that successful penetration depends not only on the activities of the mira-

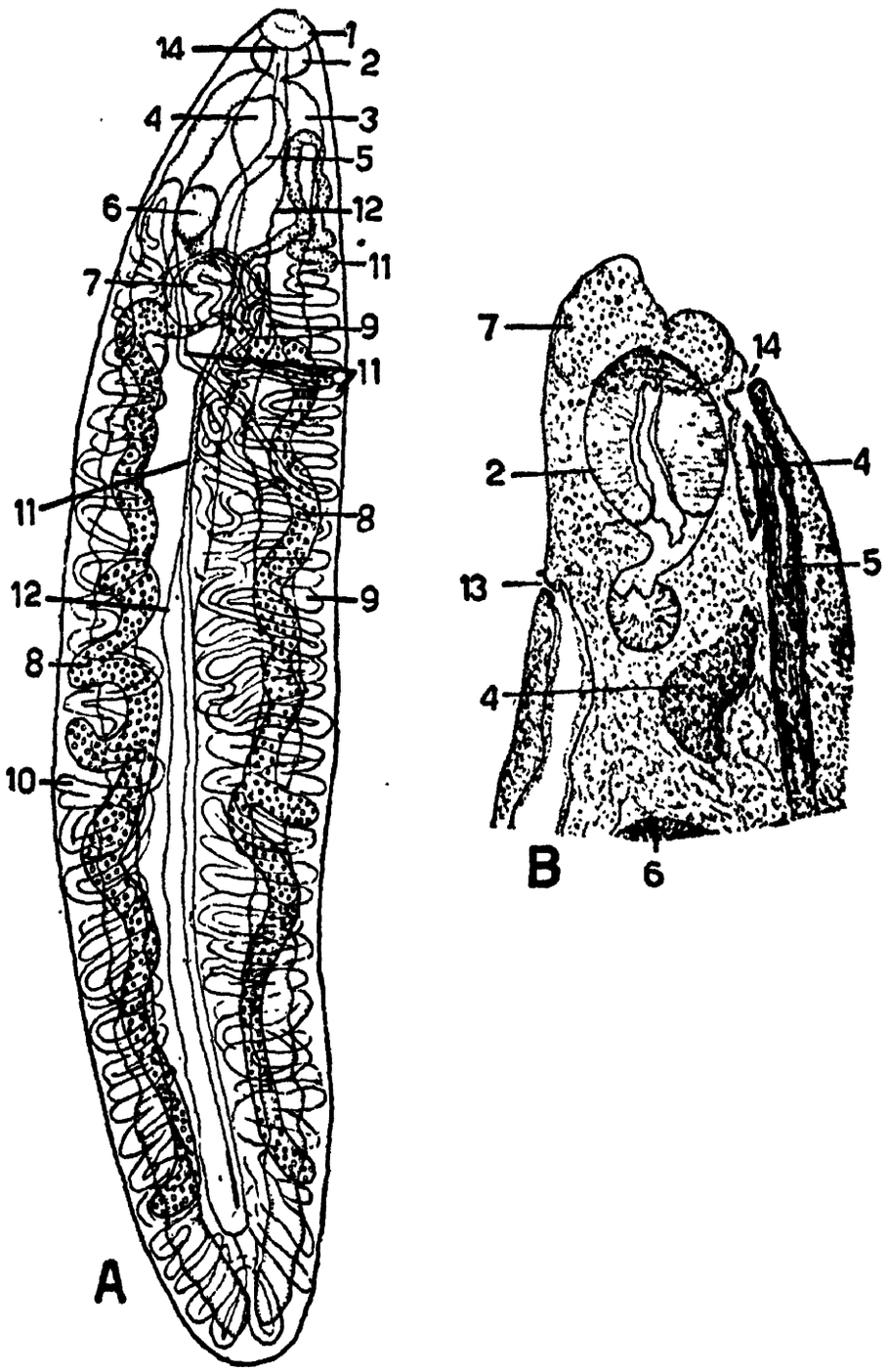

FIG. 125.—Heronimus. *A. Heronimus chelydrae.* *B.* Sagittal section of the anterior end of *Heronimus*, to show nephridiopore. (*Both after Stunkard*, 1919.) 1, oral sucker; 2, pharynx; 3, intestinal crura; 4, uterus; 5, cirrus sac; 6, ovary; 7, seminal vesicle; 8, testes; 9–12, the four successive parts of the uterus; 13, nephridiopore; 14, gonopore.

cidium but on unknown properties of the snail skin. It is generally noted that young and immature snails are more apt to be penetrated than old individuals. Although a given species of snail may serve as intermediate host for several different species of fluke (21 species in *Stagnicola*, see below), usually not more than two kinds of larval trematodes are found in any one individual snail. This indicates either that the presence

of larval trematodes in a snail inhibits penetration by other species of miracidia or that different kinds of larval trematodes are antagonistic to each other.

Nothing seems to be known of the physiology of larval trematodes in the snail host. Sporocysts and rediae may be observed moving about in the snail. They absorb nutrition through the surface and the rediae also ingest bits of snail tissue.

The emergence of cercariae from the snail host is more or less dependent on external factors. In general, warm weather favors the emission of cercariae. Cort (1922) studied the emission of one species of cercaria from the snail *Planorbis trivolvis* during one summer month and found much fluctuation in the number emitted daily by any one snail, and of course much difference between different snails depending on the number of sporocysts with which they were infected. The maximum number of cercariae issuing from one snail in a 24-hour period was about 5000. Cercariae tended to emerge at a definite time of day, but this time differed for different individual snails. Seasonal peaks, mostly one in winter and one in summer, of cercarial emergence have been noticed by several workers (Miller and Northrup, 1926; Rankin, 1939c). In general, seasonal relations of cercariae are correlated with the habits of the definitive host. Thus in a given pond cercariae infective to constantly present fish showed no seasonal fluctuation but a species having its adult state in a summer resident bird passed the winter in snails and emerged only with the advent of warm weather (McCoy, 1929b).

The behavior of cercariae has been the object of several studies (Miller, 1925–1928; Miller and McCoy, 1928–1930; Miller and Mahaffy, 1930; Rankin, 1939c; Wheeler, 1939). Some cercariae swim continuously but many swim intermittently, moving upward by lashing the tail, then pausing and sinking, then jerking upward again. The active periods are generally much shorter than the rest periods. Sudden decrease of light as by casting a shadow often evokes a marked reaction—usually an accelerated rate of swimming or renewed swimming from a rest position. But in some cercariae sudden decrease of light intensity may result in stoppage and sinking and in others any change of light intensity evokes swimming. Agitation of the water also often also starts swimming activity. Many cercariae are positive to light and negative to gravity, thus seeking surface waters, but others show the reverse reaction, remaining near the bottom. Cotylocercous cercariae do not swim but stay on the bottom creeping about like a leech or attaching by the tail sucker and swinging the body about in the water. Fork-tailed cercariae (strigeids and schistosomes) swim tail forward by lashing the tails or opening and closing them scissor-fashion (Manson-Bahr and Fairley, 1920; Szidat, 1924; Miller and Mahaffy, 1930; Brackett, 1940). They generally swim

upward and hang to the surface film by means of the spread tail forks, body down. The peculiar bucephalus cercariae swim to the surface tail foremost by alternately extending and contracting the long tails (Wunder, 1924; Bevelander, 1933; Folger and Alexander, 1938), at a rate of 55 to 70 contractions per minute at 20°C. Sudden increase of light or sudden shock evokes cessation of swimming and sinking with the tails contracted and curved inward. The reaction time of this response is shorter the greater the intensity increase or the strength of shock.

The behavior of cercariae is undoubtedly related to the nature and habits of the host on or in which they encyst. Thus the stimulating action of shadows or agitation is presumably related to the proximity of

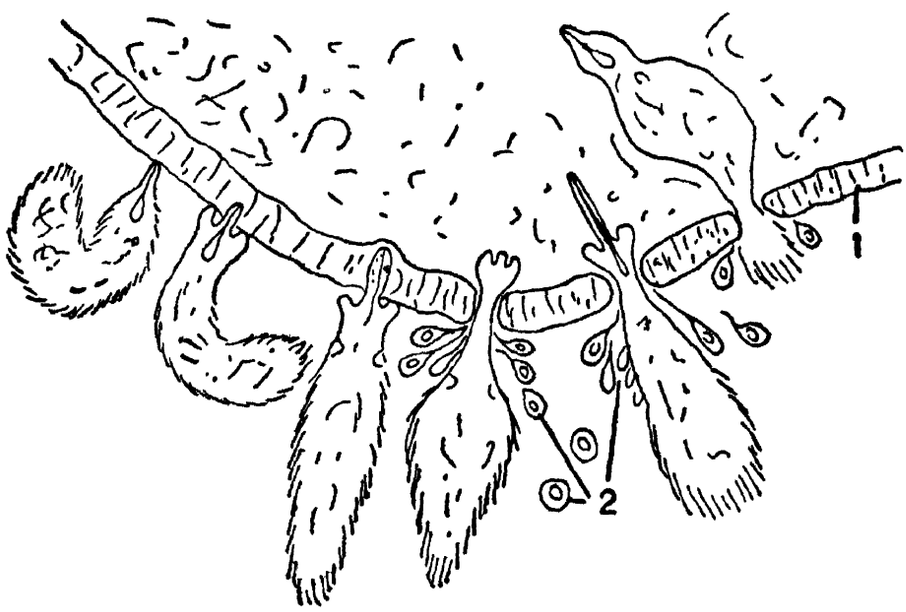

FIG. 126.—Penetration of miracidium of *Fasciolopsis buski* through the epidermis of a snail (*after Barlow*, 1925). 1, snail epidermis; 2, shed epidermis of miracidium.

a possible host such as a fish. However, cercariae do not give evidence of any chemotactic attraction to hosts (Szidat, 1924; Ferguson, 1943). They are on the other hand excessively positive to contact, pausing by and testing almost any object. They apparently swim, float, and crawl about until chance contact with a suitable host occurs, whereupon they attach and penetrate. Ferguson found that numerous cercariae would attach to a fishtail dipped for only 1 second in a heavy suspension of them. Chemical properties of the host seem to play some role after contact is established. Thus Miller and McCoy (1930) noted that cercariae would come to rest on, penetrate, and start encystment on pieces of feathers smeared with fish mucus but showed no response to control feathers. The most interesting case of chemotactic attraction is that of the eye for diplostomulum larvae of strigeids (Ferguson, 1943). These cercariae after penetrating fish at any point migrate anteriorly chiefly by way of the blood vessels and enter the eye where they encyst in the lens. They will migrate to eyes from which the lenses have been removed but do not migrate anteriorly if the entire eyes are extirpated.

Although they give no chemotactic reaction to crushed fish tissues, including the parts of the eye, the conclusion appears inescapable that they reach the eyes by some chemotactic attraction. These cercariae appear incapable of developing into diplostomulae except in vertebrate lenses; they will develop normally in isolated lenses cultivated in sterile salt solution (Ferguson, 1943c).

The penetration of cercariae into host animals is accomplished partly by such aids as the stylet and spines but primarily, so it is believed, by the flesh-dissolving action of the secretion of the penetration glands. Evidence for this view has been brought forward by Davis (1936), who noted a dissolving action on tadpole skin and muscle of an aquaeous extract of cercariae

The metacercarial cyst wall undoubtedly affords some protection against desiccation and other adverse conditions, but its chief role appears to be protection from the gastric juice of the final host. Naked cercariae and metacercariae are destroyed and digested by gastric juice but the cyst wall is generally insoluble in this fluid. Usually the cyst wall dissolves in the upper part of the intestine, releasing the metacercariae which then migrate to their typical location.

Ferguson (1940) achieved the development of the metacercariae of the avian strigeid *Posthodiplostomum minimum* to the adult condition in a sterile medium composed of Tyrode's solution (balanced salts), chicken serum, and yeast extract, but the eggs and sperm of these flukes were abnormal.

18. Host-Parasite Relations; Immune Reactions.—Discussion of the symptoms and treatment of fluke infections of man and domestic animals lies outside the province of this book and will be found in works on parasitology. Suffice it to say that heavy infections with either larval or adult trematodes are usually highly damaging to the host, resulting in retardation of growth, loss of weight, emaciation, and a general unhealthy condition, often eventuating in death. Flukes that inhabit sites such as the bile ducts, blood vessels, and lungs are generally more deleterious than those that live in the digestive tract. Heavy infections of snails with larval trematodes often result in the partial or complete destruction of favored sites of infection as the gonads or digestive gland ("liver"). Snails may respond to heavy infections by considerable increases of size (Rothschild, 1936), and this has given rise to the erroneous impression that older individuals are more susceptible to infection than younger ones. Light infections with trematodes usually fail to produce any definite symptoms.

The presence of a trematode may evoke in the host body the same kind of reaction as does a foreign body or a wound, i.e., an inflammatory reaction consisting of the aggregation of leucocytes at the site, phago-

cytosis, and production of connective tissue. A study of the reactions of fish tissues to encysting metacercariae, especially strigeid and clinostomid forms, has been made by Hunter and associates (the Hunters, 1940, 1942; Hunter and Dalton, 1939; Hunter and Hamilton, 1941). The metacercarial cysts studied consisted wholly or in part of connective tissue of host origin, often with the addition of pigmented host cells.

Trematodes may also call forth in the host body an immune reaction, that is, the host produces one or more substances known as antibodies that are chemically antagonistic to the parasite or its products. These antibodies may stunt the growth of the parasite or kill it or prevent its attachment to the host tissues or they may precipitate or neutralize parasitic products. In general, trematodes inhabiting the digestive tract do not evoke immune reactions. Such reactions are called forth by the invasion of host tissues by the parasite and hence have been studied chiefly in liver flukes, schistosomes, and the like. For a general consideration of immune reactions to worm parasites the books of Taliaferro (1929) and of Culbertson (1941) may be consulted.

It was already noted that host specificity varies greatly among flukes, i.e., some will succeed in a wide range of hosts whereas others require a specific host. Even closely related flukes may exhibit great differences in host requirements. Thus *Schistosoma japonicum* is infective not only to man but to a great variety of other mammals, including the common laboratory mammals; *S. spindale* succeeds only in ungulates; and *S. haematobium* only in man. Usually, a given fluke is able to parasitize only one kind of host or a group of taxonomically related hosts. Feeding of or other exposure to infective stages of trematodes results in infection only with a particular host or hosts. The mechanism of such protection against flukes by hosts other than the normal ones is obscure and probably differs in different cases. It is usually supposed that the fluke requires a very specific environmental complex for its development, and this is found only in the proper host (discussion in Sandground, 1929). In some cases, however, failure to establish in an unsuitable host results from the development or presence of antibodies in the host that are fatal to the developing trematodes. Thus monkeys can be infected with the cercariae of human schistosomes, but their serum contains antibodies that soon kill the invaders (Fairley and Jasudasan, 1930). Another factor preventing infection of unsuitable hosts is the inability, noted above, of miracidia and cercariae to penetrate any but the appropriate host. This failure seems to rest on a very close adaptation between the penetrating mechanism of the larval trematode and the surface characteristics of the appropriate host.

Penetration of even the proper host by miracidia or development therein is inhibited to some extent if other species of flukes are already

present. Thus many snail species serve as host to several kinds of larval trematodes but all of these are never found simultaneously in the same individual snail. The fresh-water snail *Stagnicola emarginata* harbors 21 kinds of larval trematodes (seven strigeids, six plagiorchids, two schistosomes, one echinostome, one monostome, and four others) but usually only two kinds, sometimes three or four, occur simultaneously in any one snail (Cort, McMullen, and Brackett, 1937). In other similar investigations not more than two kinds of larval flukes have been found in snail individuals that are normal hosts to several species. Very striking is the fact that the cercariae of the strigeid *Cotylurus flabelliformis* that encyst in the same snail species harboring the sporocysts are unable to penetrate snails that already contain sporocysts although metacercarial development is favored by the presence of sporocysts of other fluke species (Winfield, 1932; Cort, Brackett, *et al.*, 1945).

Animals may develop immunity to flukes to which they serve as normal hosts, as a result of repeated attacks. The best case of this kind is that of the monogenetic fluke *Benedenia* (= *Epibdella*) *mellení* which infects the skin of a large number of species of marine fish (Jahn and Kuhn, 1932; Nigrelli and Breder, 1934). Some fish species remain permanently susceptible while others develop partial or complete resistance to superinfection. The resistance may be local in that the parasites do not or are unable to attach to skin areas previously parasitized. The surface mucus of resistant fish was found to be fatal to the parasite (Nigrelli, 1935). The presence of the amphistome *Zygocotyle lunata* in the caeca of the normal duck or rat host prevents superinfection by more specimens of the same species (Willey, 1941). Man does not show any resistance to reinfection with schistosomes, but other mammals such as dogs, horses, and monkeys develop partial or complete resistance after being cured of an initial infection. A careful study of the development of resistance to *Schistosoma spindale* by goats, which are normal hosts to the parasite, was made by Fairley and Jasudasan (1930). In this case the formation of antibodies fatal to the cercariae was demonstrated, but it is not clear that the other cases mentioned of acquired resistance depend on such an immune reaction.

Age resistance to trematodes by their normal hosts also occurs, i.e., young animals are more susceptible to infection than older ones and as the animal ages, flukes already present may be ejected (*Parorchis*, Cable, 1937; heterophyids, Willey and Stunkard, 1942). Human schistosomes usually infect young persons, and adults over thirty generally do not become infected on exposure; a similar age resistance to schistosomes occurs in other mammals (Ozawa, 1930). Age resistance does not appear to depend on immune reactions but rather on changes in the host tissues that render them an unsuitable environment for the parasite.