UNIVERSAL
LIBRARY
OU_174059
UNIVERSAL
LIBRARY

COMPARATIVE ANATOMY OF ANIMALS

AN INTRODUCTION TO THE STUDY OF THE COMPARATIVE ANATOMY OF ANIMALS

BY

GILBERT C. BOURNE, M.A., D.Sc., F.R.S., F.L.S., F.Z.S.

VOL. II.

THE COELOMATE METAZOA



ELEVENTH IMPRESSION

LONDON

G. BELL AND SONS, LTD.

1929

Printed in Great Britain by The Riverside Press Limited
Edinburgh

PREFACE

THE publication of this volume has been long delayed, owing to my having been on military duty throughout the year 1900. As in the first volume, I have been guided in my selection of types of animal organisation by the requirements of students reading for the preliminary and intermediate science examinations in the Universities of Great Britain.

A considerable space has been allotted to the leading features of the embryology of the various types, since, as I believe, a just appreciation of the problems of Comparative Anatomy cannot be attained without the study of embryonic as well as adult structures.

The second volume has been finished under more favourable circumstances than the first, and I hope that it will be found to be free from any serious errors.

I have to express my obligations to Mr O. H. Latter, M A, of Charterhouse School, who has kindly read through the proof sheets of this volume and assisted me with many valuable criticisms and suggestions, and to Mr J. W. Jenkinson, M A, of Exeter College, Oxford, who has helped me in many ways, particularly in placing at my disposal his wide and exact knowledge of the placentation of the Mammalia.

GILBERT C. BOURNE.

OXFORD, *February* 1902.

CONTENTS

Chapter XVI.

The Platyhelmia; Distomum hepaticum; External Feature Alimentary Tract; Excretory System; Reproductive System; Nervous System; Histology; Parasitism; Development; The Miracidium Larva; Sporocyst; Redia; Cercaria; Alternation of Generations; Cœlom 1-16

Chapter XVII.

The Common Earthworm; Lumbricus herculeus; External Features; Metamerism; Alimentary Tract; Cœlom; Excretory System; Nervous System; Blood-vascular System; Histology 17-32

Chapter XVIII.

The Earthworm; Reproductive Organs; The Ova; Segmentation and Formation of Blastula; Gastrulation; Mesoblast Bands; Mesoblastic Somites; Neuroblasts and Nephroblasts; Formation of Nephridia 33-44

Chapter XIX.

The Annelida; Archiannelida; Polygordius; The Trochosphere Larva; The Chætopoda; Polychæta; Hirudinea; Echuroidea; Metameric Segmentation 45-52

Chapter XX.

The Mollusca: Anodonta cygnea; The Shell; Muscular Impressions; Mantle; Mantle Cavity; Foot; Visceral Hump; Alimentary Tract; Gills; Blood-vascular System; Pericardial Cavity; Excretory Organs; Nervous System; Reproductive System; The Glochidium Larva; Dreissensia polymorpha; Veliger Larvæ; Migrations of Lamellibranchs . . 53-68

Chapter XXI.

The Gastropoda; Helix pomatia and Helix aspersa; The Shell; The External Features; The Pulmonary Cavity; The

PAGE

Excretory Organ ; The Blood-vascular System ; The Odontophore ; The Nervous System ; Euthyneurous and Streptoneurous Gastropoda ; The Eyes ; The Otocysts ; The Reproductive Organs ; Development of Gastropoda ; The Veliger Larva ; Larval Torsion 69-89

CHAPTER XXII.

The Arthropoda ; Crustacea ; Apus cancriformis ; External Characters ; Appendages ; Mouth Parts ; Antennæ ; Alimentary Tract ; Blood-vascular System ; Excretory Organs ; Nervous System ; Syncerebrum ; Rarity of Males ; Parthenogenesis ; Ovary and Testis ; Nauplius Larva ; Metanauplius ; Ecdyses ; Development of Larva into Adult . . . 90-111

CHAPTER XXIII.

The Crayfish, Astacus fluviatilis ; Cephalothorax and Abdomen ; Appendages ; Abdominal Limbs ; Thoracic Limbs ; Maxillipedes ; Second Maxilla compared with Limbs of Apus ; Antennæ ; Alimentary Tract ; Gastric Mill ; Blood-vascular System ; Gills ; Excretory Organs ; Nervous System ; Leydig's Organs ; Eyes of Arthropods ; Ova and Spermatozoa ; Segmentation of the Ovum ; Gastrulation and Formation of the Embryo ; Development of the Organs ; The Young Crayfish 112-148

CHAPTER XXIV.

The Insecta, Periplaneta orientalis and Periplaneta americana ; The Head and Mouth Parts ; The Thorax and Limbs ; The Wings ; The Abdomen ; Alimentary Canal ; Malpighian Tubes ; Blood-vascular System ; Fat-Body ; Respiratory Organs ; Tracheæ ; Nervous System ; Reproductive Organs ; Egg Cases ; Segmentation and Development of the Ovum ; Amnion and Serosa ; Mesoblastic Somites ; Embryonic Appendages ; The Young Cockroach ; Metamorphosis in other Insects ; Comparison of Arthropoda with Chætopoda . 149-171

CHAPTER XXV.

The Cephalochorda, Amphioxus lanceolatus ; Myotomes ; Fins ; Mouth, Anus, and Atriopore ; Atrium ; Gonads ; Alimentary Canal ; Pharynx ; Gill-Slits ; Notochord ; Cœlom ; Blood-vascular System ; Excretory System ; Nervous System ; Neuropore ; Segmentation of the Ovum and Formation of Blastula ; Gastrulation ; Development of Nervous System ; Mesoblastic Somites ; Head Cavities ; Larval Amphioxus ; Atrial Folds ; Myocœle ; Splanchnocœle ; Sclerotome ; Primitive Structure of Amphioxus ; Chordata and Allied Forms 172-202

PAGE

CHAPTER XXVI.

The Elasmobranch Fishes; British Dog-fishes, Rays and Skates; External Features of Scyllium canicula; Skin, Denticles, and Teeth; Myotomes; Skeleton; Axial Skeleton, Vertebral Column, and Cranium; Jaws; Branchial Skeleton; Pectoral Fins and Pelvic Fins; Dorsal and Ventral Fins; Cœlom; Head Cavities; Alimentary Canal; Spiracles and Gill-slits; Extra-Branchial Cartilages; Heart; Afferent and Efferent Branchial Arteries; Dorsal Aorta and its Branches; Venous System; Renal-Portal System; Hepatic Portal System; Pronephros, Mesonephros, and Metanephros; Reproductive Organs; Wolffian and Mullerian Ducts; Brain; Cranial Nerves; Occipital Nerves; Sympathetic Nerves; Olfactory Organs; Eyes; Auditory Organs; Primitive Characters of Dogfish 203-246

CHAPTER XXVII.

The Development of the Frog; the Tadpole and its Metamorphosis; Closure of the Blastopore; Internal Changes during Closure of the Blastopore; Rotation of the Egg; Neural Folds; Neurenteric Canal; Formation of Mesoblast; Notochord; Mesoblastic Somites; Liver, Pancreas and Cloacal Bladder; Gill-Slits; External Gills; Lungs; Myotomes; Genital Ridges; Development of Vertebræ; Development of Skull; Formation of Heart and Pericardium; Development of Venous and Arterial Systems; Pronephros and Mesonephros; Segmental Duct and Oviducts; Development of Brain; Olfactory Organs; Auditory Organs Eye; Ontogeny and Phylogeny . 247-283

CHAPTER XXVIII.

The Mammalia; Hair; Sweat Glands; Mammary Glands; External Ear; Perinæum; Hard Palate; Teeth; Alimentary Canal; Vertebral Column; Skull; Auditory Ossicles; Sternum; Shoulder Girdle and Pelvic Girdle; Limbs; Diaphragm; Heart; Arterial Arches; Venous System; Red Corpuscles; Brain; Auditory Organ; Cochlea; Urogenital System; Placentation; Blastocyst; Trophoblast; Trager; Formation of Embryo; Amnion; Allantois; Allantoidean Placenta; Omphaloidean Placenta; Decidua 284-307

CONCLUSION 308-311

INDEX 313-321

LIST OF ILLUSTRATIONS

			PAGE
Fig.	1.	Digestive, nervous, generative, and excretory systems of the Liver-fluke	4
,,	2.	Stages in the life-history of Distomum hepaticum	11
,,	3.	Lumbricus herculeus	18
,,	4.	Dissections showing the organs contained in the first sixteen somites of Lumbricus herculeus	22
,,	5.	Diagrams showing the structure of the nephridium of the Earthworm	25
,,	6.	Diagrams illustrating the arrangement of the blood-vessels in Lumbricus herculeus	29
,,	7.	A tranverse section through the intestinal region of Lumbricus herculeus	31
,,	8.	Segmentation and early stages of development of Lumbricus	37
,,	9.	Later stages of the development of Lumbricus	41
,,	10.	Drawings of larval stages and adult of Polygordius and of the anterior end of Nereis rubicunda	47
,,	11.	A view of Anodonta cygnea after removal of the left valve	56
,,	12.	Diagrams of the anatomy of Anodonta cygnea	58
,,	13.	Diagrammatic transverse sections through Anodonta cygnea	60
,,	14.	Diagrams of a gill filament of Mytilus edulis and of a vertical section through Anodonta cygnea	62
,,	15.	Glochidium larva of Anodonta	66
,,	16.	Helix aspersa, the shell and entire animal removed from the shell	71
,,	17.	Dissection of Helix aspersa	75
,,	18.	Nervous systems of Helix aspersa, Limnæa, and Paludina vivipara	78
,,	19.	Eye and Radular teeth of Helix	80
,,	20.	Diagrams illustrating the development of a Gastropod	85
,,	21.	Side view of Apus cancriformis	93
,,	22.	Appendages of Apus cancriformis	97

PAGE

Fig. 23. Transverse section, shell gland, and nervous system of Apus cancriformis 103
,, 24. Metanauplius and later developmental stages of Apus cancriformis 109
,, 25. Ventral views of male and female crayfish . . 116
,, 26. Appendages of the crayfish 118
,, 27. Appendages of the crayfish 121
,, 28. Longitudinal section of crayfish 125
,, 29. Gastric mill of crayfish 127
,, 30. Branchial chamber of crayfish 130
,, 31. Central nervous system of crayfish . . . 135
,, 32. Eyes of Apus and Palæmonetes 138
,, 33. Developing ova of Astacus 141
,, 34. Stages in the development of Astacus . . . 143
,, 35. Section of advanced embryo of Astacus . . . 147
,, 36. Head of Periplaneta orientalis 151
,, 37. Mouth parts and limb of Periplaneta orientalis . . 153
,, 38. Dorsal views of female and male Periplaneta orientalis . 155
,, 39. The tracheal, digestive and nervous systems of the Cockroach 159
,, 40. The generative organs of the Cockroach . . . 163
,, 41. Stages in the development of the insect's egg . . 167
,, 42. Amphioxus lanceolatus, views of the entire animal, the velum, and left wall of the pharynx . . . 174
,, 43. Transverse sections of Amphioxus . . . 180
,, 44. Plastic diagram illustrating the anatomy of the pharyngeal region of Amphioxus 183
,, 45. Nerve cord, circulatory system and branchial bars of Amphioxus 185
,, 46. Excretory tubules of Amphioxus 186
,, 47. Early stages in the development of Amphioxus . . 191
,, 48. Later stages in the development of Amphioxus . . 193
,, 49. Transverse sections of embryos of Amphioxus of different ages 195
,, 50. Two views of young larvæ of Amphioxus . . 198
,, 51. Dissections of Scyllium canicula showing the alimentary tract and chief venous sinuses 206
,, 52. The skull, visceral skeleton, vertebral column, pectoral and dorsal fins of Scyllium canicula . . . 212
,, 53. A gill partition and denticles of Scyllium canicula . 221
,, 54. Dissection of the throat of Scyllium canicula showing the afferent branchial arteries 223

PAGE

Fig. 55. Dissection of the roof of the pharynx of Scyllium canicula, showing the efferent branchial arteries . . 226
,, 56. Urogenital systems of male and female of Scyllium canicula 231
,, 57. Dissection showing the brain, spinal cord, cranial, occipital and anterior spinal nerves of Scyllium canicula 237
,, 58. A series of views of the lower pole of the Frog's ovum . 251
,, 59. Sagittal sections through developing ova of the Frog . 253
,, 60. Three views of different developmental stages of the Frog 257
,, 61. Two transverse sections through a young embryo of the Frog 259
,, 62. Transverse section through an older embryo . . 261
,, 63. Longitudinal section through an embryo of the Frog . 263
,, 64. Two horizontal sections through the head and anterior part of the body of Tadpoles of different ages . . 265
,, 65. A Tadpole of the Frog at the time of hatching . . 267
,, 66. The cranial and visceral cartilages of the Tadpole . 269
,, 67. Transverse sections showing the development of the Frog's heart 271
,, 68. Diagrams of the arterial arches of the Tadpole and the Frog 274
,, 69. Diagrams of the excretory system of the Tadpole . 276
,, 70. Section through the eye of a Tadpole . . . 281
,, 71. Diagrammatic section through the skin of a Mammal . 285
,, 72. Tympanic membrane and auditory ossicles of the human ear 291
,, 73. Diagram illustrating the development of the arterial arches of Mammals 295
,, 74. Diagrams of the urogenital system of Mammals . . 299
,, 75. Diagrams illustrating the development of the blastocyst and formation of the placenta in Mammals . . 303
,, 76. Diagrammatic transverse section of a pregnant uterus illustrating an early stage of placentation . . 305
,, 77. Diagrammatic transverse section of a pregnant uterus illustrating the later phase of placentation . . 306

COMPARATIVE ANATOMY

CHAPTER XVI

THE PLATYHELMIA—DISTOMUM HEPATICUM

It has been shown that in the Cœlenterata, of which Hydra and Obelia were chosen as examples, there are only two primary layers, ectoderm and endoderm; that the chief axis of the body is represented by a line drawn through the mouth to the opposite end of the body, the organs being disposed radially with regard to that axis; and that there is only one cavity in the body, the gastrovascular cavity, which subserves the functions of digestion and circulation.

In the phylum *Platyhelmia* we have to deal with animals in which a third layer, the **mesoderm** or **mesoblast**, is interposed between ectoderm and endoderm, and the bulk of the organs, including the muscular and reproductive systems, are wholly derived from this middle layer. Further than this, the body is generally elongated to a greater or less extent and flattened from above downwards. There is thus an upper or dorsal surface, a lower or ventral surface, and right and left sides. Most Platyhelmia move in a definite direction, and thus an anterior or head end, and a posterior or tail end, may be distinguished. The principal axis of the body is antero-posterior, and the chief organs of the body are disposed more or less symmetrically in pairs on either side of this axis, so that the animals may be described as **bilaterally symmetrical**. That is to say, if any one of them is divided into two halves by an antero-posterior cut, the right half will correspond exactly with the left half.

Although in the Platyhelmia there is no obvious cavity or cœlom, in which the gut and other organs lie, the cavity of the gut serves only for digestive functions, and cannot be regarded as a gastrovascular cavity like that of the Cœlenterata. On the other hand, there is no specialised circulatory or blood-vascular system, and in default of this

tne gut is commonly branched so that its ramifications bring the products of digestion to all parts of the body.

The Platyhelmia are divided into three classes, the **Turbellaria** or flat-worms, the **Trematoda** or flukes, and the **Cestoda** or tape-worms. The Turbellaria are delicate, soft-bodied, flattened worms, shaped something like a leaf. Some are marine, some terrestrial, and some live in fresh water. *Dendrocœlum lacteum*, a greyish-white species, is very common in pools and ditches in many parts of England, and the marine forms, which are often beautifully coloured with bands and stripes, are common in rock pools between tide marks. The Cestoda or tape-worms are generally elongated, and composed of numerous segments or **proglottides** attached to an anterior head armed with suckers and hooks. But some forms, such as *Amphilina* and *Caryophyllæus* are unsegmented, and show no external distinction between head and body. With one doubtful exception, the sexually mature Cestoda are parasitic in the alimentary canal of vertebrated animals. The Trematoda are parasitic animals, usually of flattened, leaf-like form, which in shape and organisation closely resemble the Turbellaria.

One of the best known of the Trematodes is the liver-fluke, **Distomum hepaticum**, which in the sexually mature state inhabits the bile-ducts of the sheep and other herbivorous animals, and gives rise to the disease known as the liver-rot. It is occasionally found in man. The mature liver-fluke is flattened and leaf-shaped, with a blunt triangular projection at its broader end. Numbers of them may be obtained by slitting open the bile-ducts of the liver of an infected sheep.

The mouth is situated at the extreme anterior end of the animal, on the tip of the triangular projection mentioned above. It is an oval aperture, lying in the middle of a cup-shaped muscular organ known as the **anterior sucker**. The posterior or **ventral sucker** is situated in the mid-ventral line, just behind the junction of the triangular anterior projection with the rest of the body. It has the form of a cup with thick muscular walls, and serves only as a means of attachment, having no aperture leading into the interior of the body.

Nearly mid-way between the mouth and the posterior sucker, but nearer to the posterior sucker than to the mouth, is

the **generative opening**, an orifice in the mid-ventral line. Distomum is a hermaphrodite or monœcious animal, and the male and female ducts open conjointly at the generative orifice. At the extreme posterior end of the animal there is a small pore by which the main canal of the excretory system opens to the exterior, and on the dorsal surface there is a small aperture in the middle line at about one-third of the length of the animal from the anterior end: this is the opening of the so-called **Laurer-Stieda canal**, of which the function is not fully known. The whole surface of the body is covered with small rod-like scales, which project backwards, and are embedded in as many little pockets of the external layer or cuticle. Their structure will be described further on.

The mouth opens into a nearly globular muscular pharynx, which is continued posteriorly into a short œsophagus. In front of the ventral sucker the alimentary canal divides into right and left branches, which run on either side of the middle line to the posterior end of the body, and give off on their outer borders a number of branched offsets or diverticula, which extend right up to the margins of the body (fig. 1, *A*). There is no anus.

The **excretory system** can only be seen clearly in specimens which have been injected with some colouring matter through the excretory pore. It consists of a main duct relatively of considerable size, which runs forward in the middle line from the excretory pore for about three-quarters of the length of the animal, and then breaks up into three or four branches (fig. 1, *C*). Usually there are four such branches, a dorsal and a ventral on each side, but the arrangement is not constant. Throughout their courses the main duct and its branches give off numerous side branches, which divide repeatedly, their ramifications anastomosing freely with one another, and forming a network which extends to every part of the body. The ultimate ramifications are continued into very fine tubules, with thin transparent walls, and these, after a more or less convoluted course, end in little transparent vesicles known as **flame-cells**. A flame-cell has thin elastic walls, in which fibrillæ crossing one another in several directions may be traced. Internally the flame-cell and the part of the canal nearest to it bears a few very long isolated cilia, which are constantly in motion, and produce a flickering

movement like that of a flame; hence the name flame-cell. One of these structures, when examined with a high power of the microscope, has a stellate appearance, due to the presence of numerous radiating processes which are said to be exceedingly fine capillary tubes passing from one vesicle to another, and not, as was once thought, protoplasmic processes. The actual number of flame-cells has not been accurately

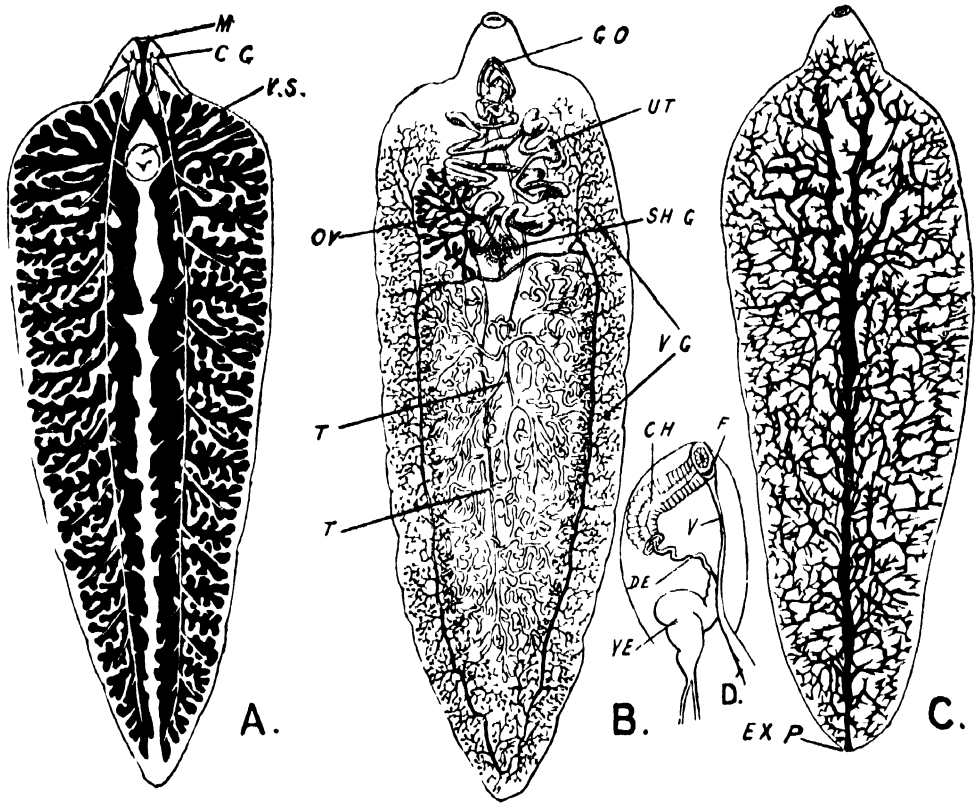


Fig. 1

A. The digestive and nervous systems of a mature liver-fluke. The branched alimentary canal is represented in black. *C.G*, cerebral ganglion; *M*, mouth; *V.S*, ventral sucker. *B*. The generative, and *C* the excretory, systems of the same animal. *Ex.p*, excretory pore; *G.O*, genital aperture; *Ov*, ovary; *Sh.g*, shell-gland; *T.T*, the ramified testis; *Ut*, uterus; *V.G*, vitelline glands. *D*. Enlarged view of the genital aperture and the organs connected with it. *Ve*. vesicula seminalis; *V*, vagina; *De*, ductus ejaculatorius, *Ch*, cirrhus; *F*, female aperture. (After Sommer.)

determined for *Distomum hepaticum*, but they appear to be fairly regularly and symmetrically distributed along each side of the body. In *D. volvens* thirty-nine flame-cells have been counted on one side of the body. The generative organs are very complex, and occupy a large part of the animal's body (fig. 1, *B*).

The male organs consist of a pair of much-branched testes,

occupying the middle third of the body. The branches of each testis are gathered into a duct, the **vas deferens**, and the two vasa deferentia run forward on either side of the middle line as far as the ventral sucker, where they unite and form a relatively large pear-shaped sac known as the **vesicula seminalis.** From the vesicula a fine somewhat convoluted tube, known as the **ductus ejaculatorius**, runs forward to enter a stout muscular organ of cylindrical shape known as the **penis** or **cirrhus**, which in its turn opens at the generative pore. Normally the penis is invaginated, and lies in a cavity just in front of the ventral sucker called the **cirrhus-sac**, but it can be evaginated and protruded from the generative aperture, in which case, as it is turned inside out, the ductus ejaculatorius is carried up the middle of it, and opens at its terminal end. (Fig. 1, *D.*)

The female organs comprise an ovary with its duct, and certain accessory glands. The **ovary**, like the testis, is a branched tubular organ, but, unlike the testis, it is unpaired. It lies usually on the right side of the body in front of the right testis and rather behind the ventral sucker. The branches of the ovary unite to form a short narrow **oviduct**, which runs towards the middle line and fuses with the **vitelline duct.** The last named is formed by the union of two transverse ducts, which convey the albuminous secretion of the **vitelline glands**, situated along the entire length of the right and left margins of the body. The vitelline glands themselves have the form of very numerous small rounded vesicles scattered over a definite area on the right and left sides of the body. Each vesicle has a duct which unites with the ducts of adjacent vesicles to form larger ducts, and these in turn unite to form on each side of the body an anterior and a posterior longitudinal collecting duct. The last named unite to form the transverse duct already mentioned, and the transverse ducts join in the middle line to form the common vitelline duct, which runs forward for a short distance before it unites with the ovarian duct. The common vitelline duct is swollen at its origin to form the so-called vitelline reservoir. The ovarian and vitelline ducts are surrounded at their point of union by a seemingly compact globular glandular mass, the **shell-gland**, which is really composed of an aggregate of minute unicellular glands.

From the shell-gland the conjoined ovarian and vitelline duct is continued forwards as a wide tube which is thrown into many convolutions, and pursues a tortuous course to the generative aperture, where it opens by a small crescentic pore to the left side of the male opening. This tortuous tube is called the **uterus**, and it nearly always contains eggs, being sometimes greatly distended by their presence. The egg has an ellipsoid chitinous shell, within which is a single ovicell surrounded by a number of vitelline cells, serving as nutriment for the developing embryo. The ovicells are developed in the ovary, and each one, on entering the conjoined ovarian and vitelline duct, receives a coating of vitelline cells derived from the vitelline glands, and is immediately encased in a firm chitinous shell secreted by the shell-gland.

The **Laurer-Stieda canal** is a short tube leading from the point of union of the ovarian and vitelline ducts to a pore placed on the mid-dorsal surface. Its function is not fully known, but as it often contains spermatozoa, it is most probable that it serves as a copulatory duct, admitting the spermatozoa to the ova as they pass down the oviduct.

The nervous system consists of a nerve-collar surrounding the pharynx, having a single median ganglionic enlargement on the ventral side of the pharynx, and a pair of lateral ganglionic enlargements, one on either side of the pharynx. Nerves are given off from these ganglia to the anterior region of the body, and from each lateral ganglion a large lateral nerve-cord runs backwards, passing beneath the bifurcation of the alimentary tract of its own side and reaching to the hinder end of the body. Nerves are given off from the lateral cords at tolerably regular intervals. (Fig. 1, *A*.)

All the organs which have been enumerated are embedded in a peculiar form of tissue generally known as the **parenchyma**, which, except for casual lacunar spaces, fills up all the interstices between them. According to the most recent accounts the parenchyma consists of a reticulum of branched cells, the meshes of which are occupied by large clear oval cells with relatively large nuclei situated close against the cell-walls. The parenchyma is traversed by muscle fibres which pass diagonally from the dorsal to the ventral wall of the body.

External to the parenchyma is a composite sheet of

epithelial and muscular tissue in which the following layers may be distinguished:—(1) Externally a thick cuticle, homogeneous in its outer and superficial but vertically striated in its deeper portion. This cuticle swells up in water, and in it are imbedded the chitinoid scales already mentioned. The scales, though they appear to project from the surface of the animal, are really contained in as many pocket-like cavities of the cuticle, and their projecting ends are covered over by a thin layer of the homogeneous cuticular tissue. The scales vary in length from ·036 to ·057 mm. and are solid structures, but easily broken up into a mass of minute fragments; (2) the ectoderm proper, consisting of a thin sheet of protoplasm below the cuticle continuous with the attenuated outer ends of a number of flask-shaped nucleated cells, the irregularly shaped swollen inner ends of which lie below the muscular layers immediately to be described. The protoplasmic layer and the flask-shaped cells taken together represent an ectoderm, of which the component cells have sunk down into and are imbedded in the underlying muscular layers; (3) an outer layer of circular muscle fibres; (4) an inner layer of longitudinal muscle fibres; (5) an inner layer of diagonal muscle fibres traversing a parenchyma composed of branching cells, among which are numerous scattered bladder-shaped cells. The muscular layers are more strongly developed in the anterior than in the posterior half of the body, the diagonal muscles being found only in the anterior half, whilst the circular muscles diminish notably in size towards the posterior end. On the other hand, the longitudinal muscles are best developed in the hinder end of the body. The oral and ventral suckers are provided with special muscular coats and also with special protractor and retractor muscle bands. The individual muscle fibres in *Distomum hepaticum* are from ·06 to ·09 mm. long and about ·003 mm. in diameter. A fully formed muscle fibre consists wholly of refractive contractile substance without a trace of nucleus or protoplasm, but in developing fibres there is a mass of granular protoplasm containing a nucleus lying on one side of the fibre at about the middle of its length, recalling the condition found in the muscular fibres of Obelia.

The alimentary tract of Distomum is lined by a single layer of more or less columnar epithelial cells, which, taken together, constitute the endoderm. The muscular layers, the

parenchyma, the excretory system, and generative organs belong to the mesoderm.

It is evident from the above description that the structure of Distomum shows a considerable advance on that of a cœlenterate polype, and that the greater complexity of structure is associated with the existence of the middle cellular layer or mesoderm which is not present in the Cœlenterata.

The adult liver-fluke, as has been said, inhabits the bile ducts of the sheep, and is therefore called an **endoparasite**. Not all the Trematoda are endoparasites. A considerable number of them cling to the external surfaces of animals, and are therefore called **ectoparasites**. The eggs of ectoparasitic Trematoda are generally laid on the place inhabited by the parent and develop directly into the adult form, without the embryo undergoing a metamorphosis or becoming parasitic in or upon another host.* Such forms are known as **monogenetic**. But in the endoparasitic Trematodes the ovum gives rise to a larval form which enters a new host, undergoes a metamorphosis, produces one or more generations different from the parent form, and eventually these generations escape from the second host (usually known as the intermediate host), and under favourable circumstances find their way back to a host of the same species that was inhabited by their parent. Such forms are described as **digenetic**.

Distomum hepaticum is a very good example of a digenetic Trematode. The eggs, as has been described, acquire chitinous shells secreted by the shell-gland, and pass into the uterus, where they undergo the first stages of segmentation. An individual egg is a minute oval body measuring about ·13 mm. in length by ·08 mm. in diameter. One end is rather more rounded than the other, and a serrated line running round it marks off a small lid or operculum, by means of which the embryo eventually escapes. From the uterus the eggs are discharged into the bile ducts of the infected sheep, where they may be found in large numbers, sometimes forming a stiff brown mass, completely blocking up the smaller ducts. A single fluke produces a very large number of eggs; it has been computed that each individual may produce half-a-million,

* The animal upon or in which a parasite lives is usually described as its "host."

and as many as two hundred flukes having been found in the liver of a single sheep, the total number of eggs passed out of the animal would amount to a hundred millions.

So long as the eggs remain in the body of the sheep they do not undergo any further development, but they are carried by the bile into the intestine, and pass to the exterior with the droppings. Then, under favourable conditions, they develop further. The conditions necessary for development are moisture and a certain degree of heat, a temperature of about 75° Fahr. being the most favourable. The eggs will not develop if kept at the normal temperature of the mammalian body, and they develop but slowly at a temperature of 60° Fahr. At lower temperatures they undergo no change at all, and it follows that they will not develop in winter time, but only in warm weather in the summer months.

The proper conditions of moisture and warmth being supplied, segmentation proceeds, and gives rise to a ciliated embryo of the form shown in fig. 2 (2). During segmentation the growing embryo is nourished by the vitelline cells contained in the egg case, and when fully formed it lies curled up in the shell, but presently forces off the operculum and emerges into the water as the larval form.

This larva, sometimes called a **miracidium**, is conical in shape, and covered all over with cilia, by means of which it swims actively through the water. In swimming, its broader end is directed forward, and this anterior extremity is furnished with a median projection which may be protruded as a conical spike, or retracted so as to form a central knob or papilla. The external skin of the larva is formed of five closely fitting rings of large hexagonal cells, whose relations are clearly shown in the figure. The most anterior ring comprises four, more rarely five cells, which are thicker and more rounded than the others. The second ring is formed of five or six more flattened cells, the third and fourth rings of four cells each, and the last row of only two cells. All these cells are richly ciliated.

Beneath the ciliated cells is a granular layer containing nuclei, but cell outlines can hardly be distinguished in it. This layer is probably homologous with the external layer or ectoderm of the adult fluke. It contains a circular and a longitudinal layer of muscle fibres, and also a sense organ in the form of a double eyespot, and a pair of excretory organs or **nephridia**.

The eyespot consists of two crescentic cells containing pigment, placed with their convex sides turned towards each other, and their anterior horns in contact. The concavity of each cell is filled with a refractive material which serves as a lens. The double eyespot is situated on what may be called the dorsal side of the body, just behind the anterior ring of ciliated cells. The nephridia are in the form of a pair of flame-cells placed one on either side of the middle of the body.

The centre of the body is occupied by a mass of large rounded cells, which, because of their subsequent history, are called germinal cells. There is no gut and no endoderm, unless a rounded granular mass lying just behind the anterior papilla is to be regarded as representative of such.

The miracidium larva is exceedingly active, and swims restlessly about, testing all objects which it comes in contact with, and leaving them if they are not suitable to its purposes. But if it comes in contact with a certain fresh-water snail, *Limnæa truncatula*, it at once begins to bore its way into its tissues. The larva presses its anterior end against the tissues of the snail, protrudes its papilla, and forcing it like a gimlet into the tissues, it spins round and round by means of its cilia until it works its way into the body of its new host. It is a remarkable fact that the larva of *D. hepaticum* selects the particular species of snail, *Limnæa truncatula*, in preference to any other; and if no members of this species are to be found, its activity gradually diminishes, and eventually it dies. The limit of the free existence of a miracidium is about eight hours. When the larva has forced itself into the snail's body, it undergoes a metamorphosis, provided that it has made its way into a suitable region. The firm, muscular "foot" of the snail is inimical to further development, and although larvæ may make their way into it, they do not long survive. But in softer regions, such as the pulmonary chamber, they are changed into a sac-like form known as the **sporocyst.** The outer coat of ciliated cells is thrown off, the eyes separate from one another and lose their crescentic form, and the organism becomes a mere sac. During these changes, which in warm summer weather take about a fortnight, the sporocyst grows considerably in size; at first it was only about ·07 mm. in length, but eventually it attains a length of ·5—·7 mm.

The sporocyst has an external cuticle, and beneath this an external circular and an internal longitudinal layer of muscle

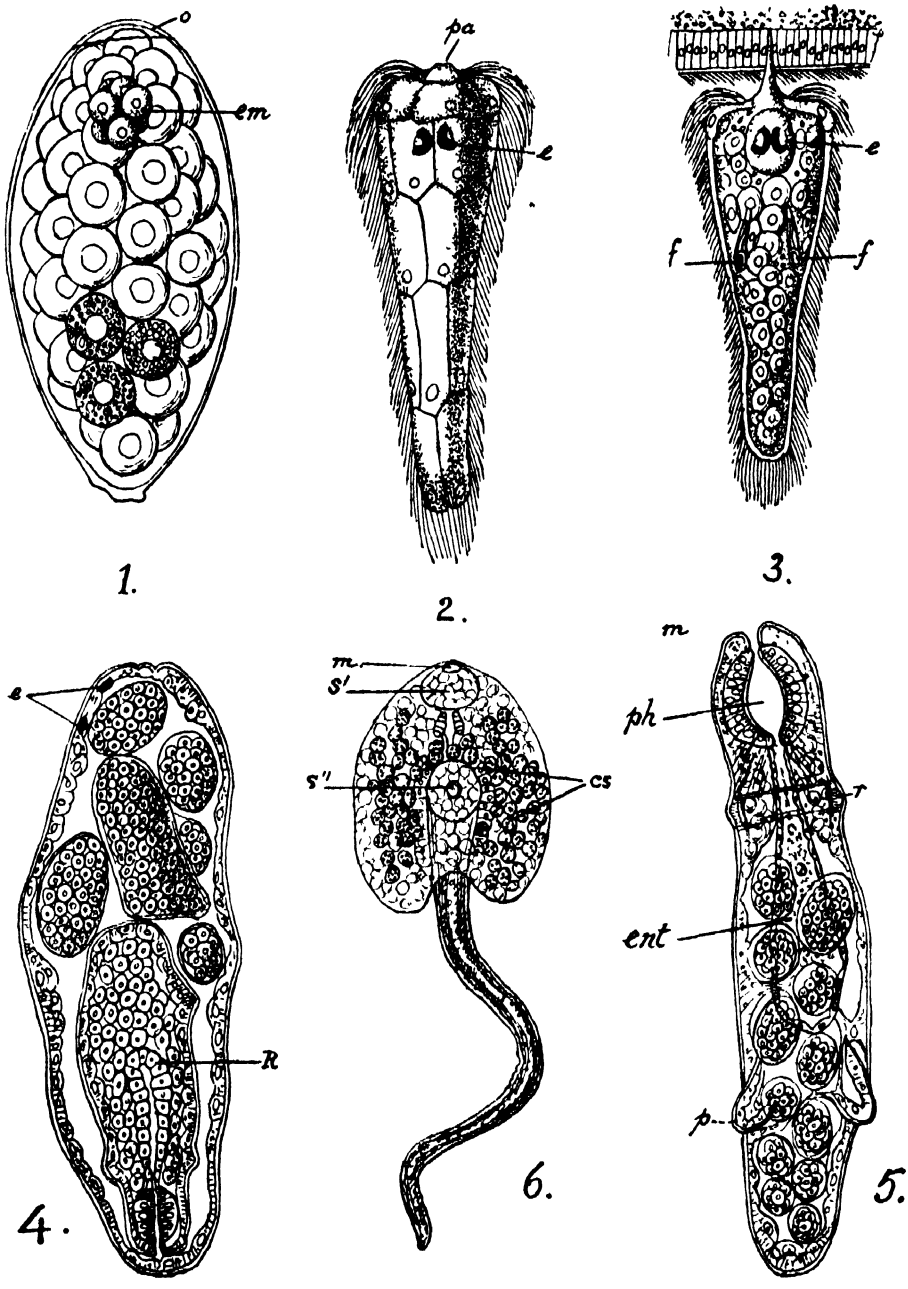


Fig. 2

Stages in the life-history of *Distomum hepaticum*. 1 An egg filled with large vitelline cells, in which the segmenting ovum, *em*, is embedded; *o*, operculum. 2. Miracidium larva, showing the large ciliated cells, the eyespot *e*, and the anterior papilla, *pa*. 3. A miracidium boring its way into the tissues of a *Limnæa*; *f-f*, flame cells. 4. A sporocyst containing one fully developed and several developing rediæ. The degenerate eyes are shown at *e*. 5. A redia containing several daughter rediæ in various stages of development; *m*, mouth; *ph*, pharynx; *ent*, enteron; *r*, muscular collar; *p*, posterior processes. 6. A cercaria; *m*, mouth; *s'*, anterior, and *s''*, posterior suckers; *cs*, cystogenous cells. (After Thomas.)

fibres. The eyes and anterior papilla persist, and the nephridial flame-cells increase in number to about half-a-dozen on either side. Immediately within the longitudinal layer of muscles is an epithelium lining the cavity of the sporocyst, and forming the greater part of the thickness of its body-wall. The interior of the cavity is filled by a number of very clear rounded cells, some of which are the germinal cells of the larva; others are derived from the epithelium lining the cavity. Occasionally a sporocyst will divide into two by transverse fission. The germinal cells in the sporocyst undergo division and form spherical masses or blastulæ, which pass through a gastrula stage, and eventually develop into a second kind of larva known as a **redia**.

A redia has an elongated cylindrical body with an anterior mouth leading into a muscular pharynx, and a short sac-like digestive tube or **enteron**. A little way below the level of the pharynx, the body is thickened to form an annular ridge or collar, in which muscular fibres are strongly developed. At a distance from the posterior end equal to about one-fourth the entire length of the body are two blunt conical processes, situated close together on one side. The structure of the body-wall of a redia is much the same as that of a sporocyst, but there are no eyes, and the excretory system is better developed, consisting of two groups of flame-cells on either side, an anterior group just behind the collar, and a posterior group near the blunt conical processes or feet. The anterior region of the body in front of the collar is filled up with muscle fibres and parenchymatous tissue, but posteriorly there is a large body cavity, the walls of which are lined by an epithelium, like that of a sporocyst. A few muscular strands traverse the body cavity. The wall of the enteron is formed by a single layer of clear nucleated cells supported by a basement membrane. When a redia has attained a length of about ·25 mm., it begins to move about actively, and presently it ruptures the wall of the sporocyst and passes into the tissues of the snail. Many rediæ are produced by a single sporocyst, and they may be seen in all stages of development within the body of the latter.

The free rediæ force their way by muscular contractions through the body of the snail, and enter various organs, particularly the liver. In so doing, they destroy the tissues,

and swallow them as food, causing the death of the snail in a shorter or longer time. During its migrations a redia increases in size till it attains a length of 1 to 1·5 mm.

The epithelium lining the body-cavity gives rise to germinal cells, which pass into the cavity and undergo a development similar to that of the germinal cells of a sporocyst. The first generation of rediæ usually gives birth to daughter rediæ, and these in turn may give rise to grand-daughter rediæ, and so on for several generations, the young rediæ escaping from the parent by a special aperture or birth-opening, situated at one side of the body, a little behind the collar. Eventually the rediæ cease to produce daughter rediæ, and give birth to another form known as the **cercaria.***

A cercaria is developed from a germinal cell, in much the same manner as a redia. When fully grown, it has the shape and structure shown in fig. 2 (6), consisting of flattened heart-shaped body with an exceedingly contractile tail, more than double as long as the body. Anteriorly there is an oral sucker, and some way behind there is a ventral sucker placed in the middle of the lower surface of the body. In the centre of the oral sucker there is a mouth, and posterior to the sucker there is a muscular pharynx leading into a short narrow œsophagus which bifurcates just in front of the ventral sucker to form a pair of simple tubular intestinal limbs, one reaching down on either side of the ventral sucker nearly to the hind end of the body. The limbs of the intestine are at first solid, being formed of single rows of thick discoid cells. The cercaria is also provided with an excretory system, having a terminal contractile vesicle, collecting ducts, and flame-cells; but the details of this and other organs are difficult to make out, because of the presence of a number of large nucleated cells crowded with coarse refractive granules which form two irregular masses, one along each side of the body. These are the **cystogenous** cells; their function is to secrete the protective case or cyst with which the animal presently surrounds itself.

As soon as a cercaria has attained a length of some ·28 mm. it escapes through the birth-opening of the parent redia, and by the help of its suckers and contractile tail wriggles out

* It is probable that temperature is the determining cause whether a redia shall produce daughter rediæ or cercariæ. In summer the rediæ are found full of daughter rediæ, in autumn of cercariæ.

of the tissues of its host, and for a short time leads a free existence, swimming in the water or wriggling among wet grass and leaves. Soon, however, it ceases to move about, comes to rest on the leaf of a water-plant or a blade of grass, shakes off its tail, and proceeds to encyst. In this operation the cystogenous cells secrete an abundant slimy material which hardens immediately, and in a few minutes the animal is covered over by a white hard case, and firmly fastened to the leaf or grass on which it lies. The cercaria lives for some time in the encysted condition, until the plant to which it is attached is eaten by a sheep or other herbivorous animal. Then, on reaching the stomach, its cyst wall is dissolved by the action of the gastric juice, and the cercaria makes its way into the bile ducts, where it grows rapidly; its intestine becomes hollow and branched, its generative organs are developed, and in about six weeks time it becomes a sexually mature fluke.

The life-history of *Distomum hepaticum* affords a very good example of true alternation of generations and of adaptation in connection with a parasitic habit of life.

It was pointed out (vol. i. p. 281) that the so-called alternation of generations in Obelia is not a true alternation, because the asexually produced individuals are not developed from germ cells, but originate, as do the members of plants, by a process of vegetative multiplication. In Distomum, however, the case is clearly different. The sexual generation is, of course, the mature fluke, living in the bile ducts of the sheep. From its eggs are formed miracidia, which, on finding their way into the appropriate new host, develop by a process of simple growth into the first asexual generation—the sporocyst. The germinal cells of the sporocyst, many of which, at least, are derived from the germinal epithelium lining its body-cavity, behave and develop like true ova, but they do not require fertilisation. The sporocyst, then, is a **parthenogenetic** form, and its unfertilised ova give rise to the second asexual generation of rediæ. The germinal cells of a redia originate and develop in just the same manner as those of the sporocyst, so the redia is also parthenogenetic. After a larger or smaller number of generations of rediæ, the young flukes, called cercariæ, are produced parthenogenetically by the rediæ, and under appropriate conditions they grow directly into the sexual form. Thus, if we use the sign = to denote generation, whether sexual or asexual (par-

thenogenetic), and the sign – to denote the simple growth of a larva into a mature form, we may express the alternation of generations of Distomum as follows :—

Fluke . . .	Sexual generation in sheep
‖	
Miracidium .	Free swimming larva
|	
Sporocyst . . .	1st type of asexual generation in snail
‖	
Redia . .	2nd type of asexual generation in snail
‖	
(Rediæ)n. . . .	Successive generations of 2nd type
‖	
Cercaria . . .	Young sexual generation
|	
Fluke . . .	Mature sexual generation

This complicated life-history is obviously connected with the parasitic habit of the animal. Living in the bile ducts of a sheep, and eventually causing the sickness and death of its host, it is necessary for the propagation of the species that Distomum should be from time to time transferred to a new host, and this transference from the liver of one herbivorous animal to another is not easy of accomplishment. Hence we find that, in the first place, the mature fluke produces an inordinate number of eggs, some few of which are sure to develop under conditions favourable to survival. The miracidium hatched out from the egg is a larva structurally adapted to seek out and enter an intermediate host, and it is interesting to observe that this intermediate host, *Limnæa truncatula*, is precisely the one whose habits ensure the widest possible dispersal of the asexual generations. Although its habit may generally be described as aquatic, *L. truncatula* is more ready to leave the water than other species of water snails with which it is associated, and it commonly makes considerable journeys through damp grass. It may even be dried up, and recover its vitality when wetted. During floods *L. truncatula* may be carried in great numbers over low-lying lands, and when the waters have subsided numerous specimens are to be found scattered over the meadows or living in the ditches at their sides. Thus, when the rediæ living in infected snails give rise to cercariæ, the last named frequently escape in situations where they are likely to be picked up by sheep pasturing on the grass on which they are encysted. It need hardly be said that the chances against the

product of any single egg arriving at the condition of a mature fluke are enormous, but where so many eggs are produced, and where the larvæ which survive multiply themselves so rapidly in the body of the snail, it is nearly certain that some few cercariæ will make their way back again into their final host—the sheep.

It may be difficult to imagine how such a complicated life-history, involving residence of different forms in an intermediate and a final host, can have been established in the course of evolution, but the difficulty is lessened by an extended study of the Trematoda, which shows that there is every gradation between direct development without alternation of generations, such as occurs in the monogenetic Trematodes, and the elaborate alternation of generations in such a typical digenetic form as the liver-fluke.

Lastly, the anatomy of the redia throws light upon a question of purely morphological interest. It has been shown that the adult fluke has no body-cavity. In the sporocyst there is a large body-cavity, but no gut, in the redia there are both body-cavity and gut, and the relations of one to the other can be satisfactorily studied. Now, what is this body-cavity? It is a large space which does not communicate with the excretory system or with any other organs, but is lined by an epithelium, which we have recognised as a germinal epithelium, because it gives rise to the germ cells from which daughter rediæ or cercariæ are developed. It is, in fact, a greatly developed generative pouch, which has its own proper opening, the birth-opening, to the exterior. The relations of this pouch to the gut and other organs are just those of the cœlom in other animals; and we shall see, in studying the earthworm and other types, that there is good reason to believe that the extensive spaces which we call **cœlom** are to be considered as having arisen from the enlargement and extension of primitive generative sacs. It will be remembered in this connection that the germ cells of the frog are developed from a part of the epithelium lining the pleuro-peritoneal cavity or cœlom (vol. i. p. 116). We may, therefore, call the body cavity of the redia, and also that of the sporocyst, a **cœlom.** In the sexual fluke we must regard the cavities of the generative organs, the ovaries, testis, and their accessory glands as the representatives of the cœlom, which, in this instance, retain their primitive characteristics.

CHAPTER XVII

THE CHÆTOPODA—THE COMMON EARTHWORM—LUMBRICUS HERCULEUS

EARTHWORMS, belonging to many different species, are very common in all parts of the world. The commonest English species, **Lumbricus herculeus**, lives in burrows in the surface soil. The mouths of the burrows are marked by the well-known worm-castings, and their upper parts are lined by leaves which the worms have dragged down into their holes. Earthworms, as Darwin has shown, are important agents in the formation of vegetable mould, and a full account of their habits will be found in his admirable memoir on the subject.* But before studying the habits of earthworms it will be desirable to gain a knowledge of the structure of these animals.

A full-grown specimen of *Lumbricus herculeus* is about seven inches long, and nearly circular in section except in the posterior region, where the body is flattened dorso-ventrally. The worm always progresses with one of its surfaces applied to the ground; this is therefore the ventral surface, the opposite side being the dorsal surface. Furthermore, it always travels with one end, the anterior end, foremost, so we can recognise anterior and posterior ends, dorsal and ventral surfaces, right and left sides. At the anterior end of the body there is no distinct head, but a small conical projection called the **prostomium**. Below and behind the prostomium, on the ventral surface, is a crescentic opening, the **mouth**, destitute of jaws and other appendages, and at the posterior extremity of the body is a circular terminal opening, the vent or **anus**. The whole body is divided by a series of transverse furrows into a number of rings, called **segments** or **somites**, and we shall see that this external segmentation of the body corresponds to a definite internal segmentation. As certain

* "The Formation of Vegetable Mould through the Action of Earthworms," by Charles Darwin. London. J. Murray, 1881.

organs of the earthworm are invariably placed in definite somites, it is of importance that the latter should be carefully

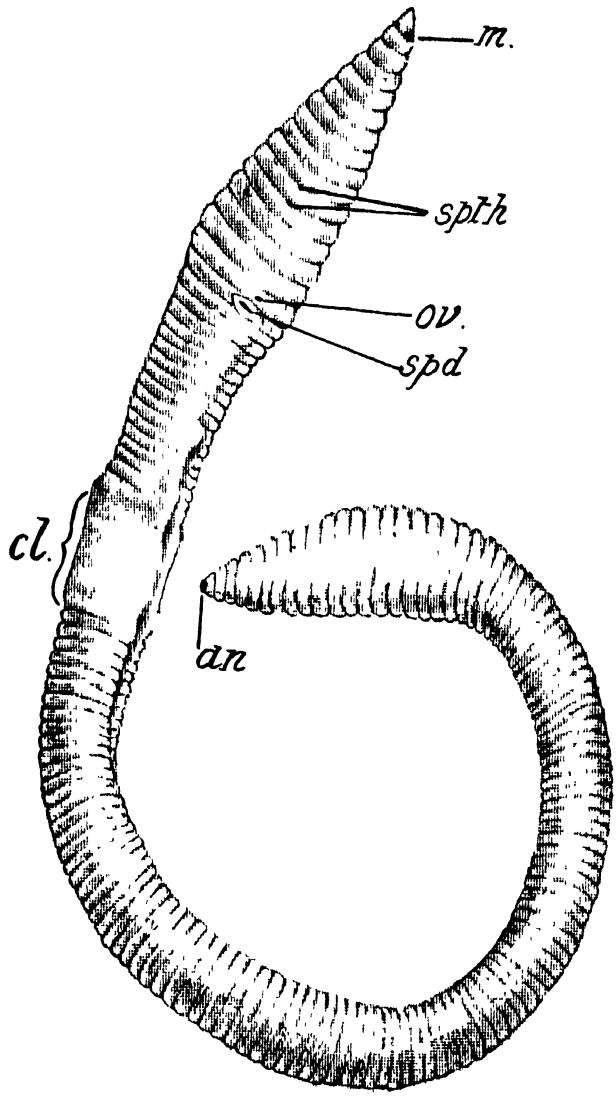


Fig. 3

Lumbricus herculeus, showing *m*, the mouth, situated on the ventral surface behind the conical prostomium; *spth*, spermathecal pores, *ov*, oviducal pore on segment 14; *spd*, spermiducal pore on segment 15; *cl*, clitellum extending over segments 32—37; *an*, anus.

counted and the positions of the more important organs and external openings accurately noted. Beginning at the anterior end of the body, it is usual to reckon the ring immediately following the prostomium and partly encircling the mouth

as the first somite. The prostomium itself, for reasons which will appear more clearly when we study the development of the earthworm, is not reckoned as a somite, but as a part anterior to the segmented body equivalent to the better developed head of other worms. It should be noticed that on the dorsal surface the prostomium is produced into a backward projection which is, as it were, dovetailed into the first somite. The most anterior somites are rather larger, and the grooves separating them are deeper than in the more posterior somites.

At a distance of about one-third of the whole length of the body from the anterior end is a thickened band of glandular tissue, nearly encircling the body, and extending from somites 32—37 inclusive. This band, known as the **clitellum**, varies in position in different species, but is always constant in position in the same species, and therefore of some importance in enabling us to recognise different kinds of earthworms. In some it forms a complete band round the body, but in *L. herculeus* it is saddle-shaped, not reaching to the ventral surface. The clitellum enables us to divide the body of the earthworm into regions. There are 31 pre-clitellar somites, 6 clitellar somites, and about 117 post-clitellar somites, the terminal one bearing the anus.

The general surface of the body is moist and smooth, and displays iridescent hues, due to the peculiar structure of a definite cuticle which uniformly covers it. But on passing a worm through the fingers it feels rough to the touch. This roughness is due to the presence of a number of bristles or **chætæ**, of which there are four pairs or **couples** in every segment except the first and last. The chætæ are easily seen with a magnifying glass, and their arrangement should be carefully noted. In each somite, with the exceptions above mentioned, there is a pair of **lateral couples** placed on the right and left sides of the body, rather nearer the dorsal than the ventral middle line, and a pair of ventro-lateral couples, placed between the lateral couples and the mid-ventral line. The chætæ are *f*-shaped chitinous rods embedded in epidermic sacs, and movable by special muscles. They are the chief organs of locomotion of the earthworm, and from them the name "Chætopoda" is given to the group to which the earthworms belong. The chætæ of the clitellar region differ from

those of the rest of the body, being finer and nearly straight, with hooked inner ends. There is also a pair of modified chætæ in somite 15.

In addition to the mouth and anus, the following external apertures must be noted:—(1) The **dorsal pores**, a series of small round apertures situated in the mid-dorsal line in the grooves separating the somites from one another. In *L. herculeus* the first dorsal pore occurs in the groove between the eighth and ninth somites, and there is one in every subsequent intersegmental groove. They open directly into the body-cavity, and their exact function is not known. (2) The **oviducal pores**, or female apertures, are minute round pores placed one on each side of somite 14. (3) The **spermiducal pores**, or male apertures, are relatively large slit-like openings with tumid lips placed one on each side of somite 15. (4) The **spermathecal pores** are two pairs of minute round openings placed in the intersegmental grooves separating somites 9--10 and 10--11 at the level of the uppermost member of the lateral couple of chætæ. (5) The **nephridiopores** are the minute openings of the excretory tubes or nephridia. There is a pair on every somite except the first three and the last, each opening being situated just in front of the uppermost member of the ventro-lateral couple of chætæ. The nephridiopores are hard to see, but they can usually be made apparent by gently squeezing the body of the worm, when small droplets of liquid exude from them.

The earthworm has no obvious organs of special sense, and no external appendages except the chætæ. Darwin's experiments show that earthworms are sensitive to light, but not to sound, though they are very sensitive to any jar or vibration, retreating at once into the depth of their burrows when the ground near them is shaken. They also appear to have some sense of smell. It will be shown later that the epidermis is provided with a great number of minute sensory organs, far too small to be recognised by the naked eye.

On opening the worm, which is best done by making a longitudinal incision in the mid-dorsal line and pinning out the walls of the body right and left, many of the more important features of its internal anatomy can be seen without further dissection. The gut is a straight tube running from the mouth to the anus, and separated from the body-wall

by a relatively considerable space, the body-cavity or **cœlom** in which other organs lie. The cœlomic space, however, is not continuous, but is broken up into a series of chambers by muscular partitions or **septa** passing right across the body. Each septum corresponds to an intersegmental groove, being inserted on the body-wall all round the line marked out by the groove, and is perforated by the gut. Thus the septa divide the interior of the body into a number of compartments which correspond exactly with the external rings, and since, as we shall see, many of the organs are repeated in each segment, and the segments lie one behind the other along the longitudinal axis of the body, the earthworm is called a **metamerically segmented** animal, and the individual segments or somites are sometimes called **metameres**. The septa, however, do not exactly correspond with the external annulation, for there are no septa between segments 1 - 2 and 2 - 3, and the septum between 3 — 4 is frequently absent, or, if present, is represented by mere muscular slips. The septum between 17—18 is also incomplete.

The gut, as has been said, pursues a straight course from the mouth to the anus, but anteriorly to segment 18 it is variously modified. The mouth leads into a short but rather wide **buccal cavity** with thin walls. Following upon this is a stout pear-shaped **pharynx**, with thick muscular walls extending as far back as the sixth or even the seventh somite when the animal is moderately extended. In reality, however, the pharynx lies entirely in front of the septum separating the fifth from the sixth segment, both this and the preceding septum being carried backwards by the posterior projection of the pharynx. Anteriorly the pharynx begins in the third segment, and it must therefore be spoken of as extending from the third to the fifth segments. The walls of the pharynx are attached to the body-wall by numerous muscular strands, which, for the most part, run diagonally backwards, the most posterior strands perforating the septa, and extending as far back as the eighth segment (fig. 4, *A*). The pharynx is succeeded by the **œsophagus**, a narrow straight tube extending to the fourteenth segment. There are three pairs of apparent pouches on the sides of the œsophagus, one pair in the eleventh and two pairs in the twelfth somite. These are usually known as the **calciferous glands**. In reality,

only the first pair are pouches communicating with the cavity of the gut: the two posterior pairs are thickenings of the

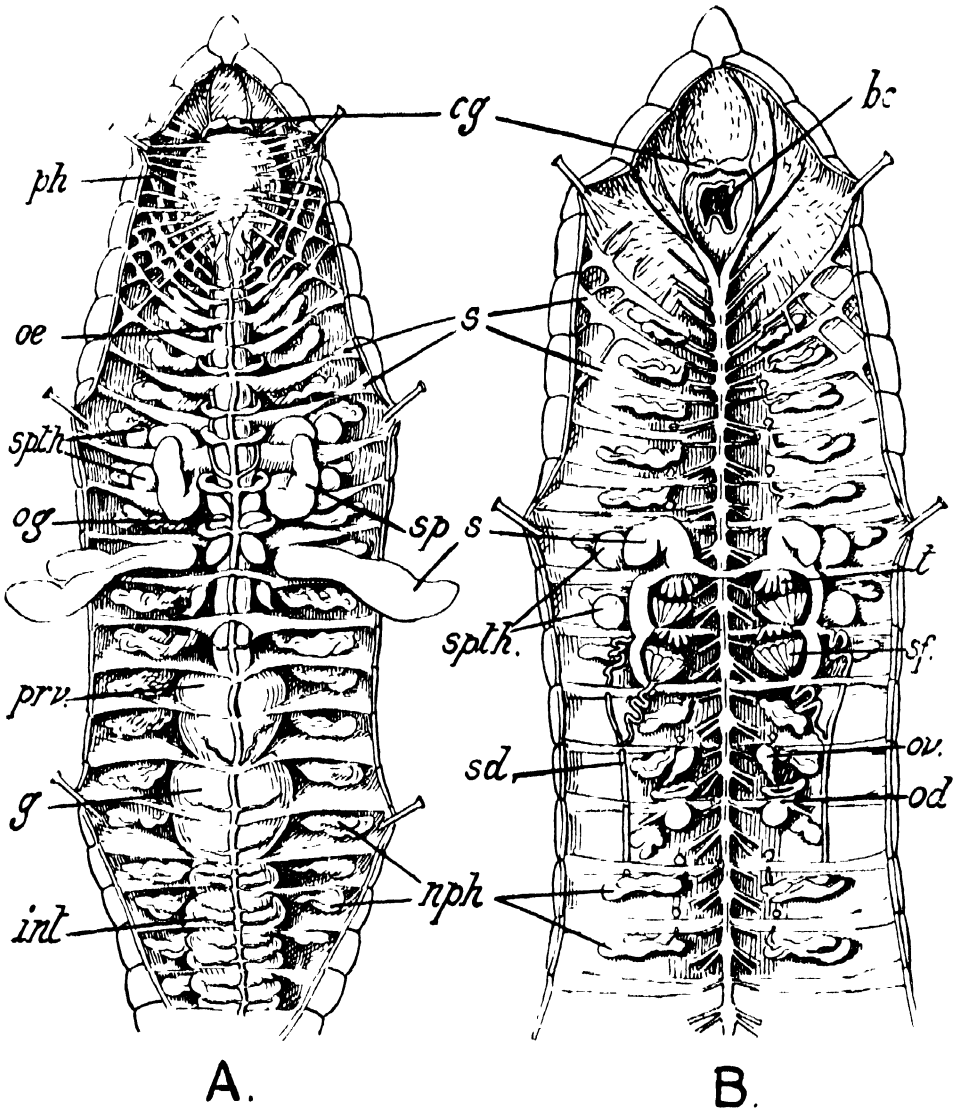


Fig. 4

Lumbricus herculeus. *A.* A view of the organs contained in the first twenty-two somites, as seen when the animal is opened by a longitudinal dorsal incision, and the body walls are pinned out without cutting the septa. The pins are placed in the 3rd, 9th, and 18th somites. *B.* View of the first sixteen somites of the same worm after removal of the alimentary tract, to show the nervous system and reproductive organs. *bc*, buccal cavity, cut across; *cg*, cerebral ganglia; *g*, gizzard; *int*, intestine; *nph*, nephridia; *od*, oviduct; *oe*, œsophagus; *ov*, ovary in somite 13; *ph*, pharynx with radiating muscular strands; *prv*, proventriculus; *s*, septa; *sd*, sperm duct; *sf*, seminal funnels; *spth*, spermathecæ in somites 9 and 10; *sp.s*, sperm sacs; *t*, testis.

œsophageal wall, which is here hollowed out by a number of cavities ending blindly behind but opening into the first

pouch in front. The partitions separating the cavities from one another are covered by large cells which secrete carbonate of lime, the secretion finding its way through the anterior pouch into the œsophagus.

The **crop** or **proventriculus** is a thin-walled dilatation of the alimentary canal in somites 15 and 16, and is succeeded by another dilatation with stout muscular walls lying between the septa separating somites 16—17 and 18—19. This muscular organ, the **gizzard**, lies therefore in somites 17 and 18, but it may project some way backwards, carrying the septa along with it. The gizzard is succeeded by a wide thin-walled sacculated tube, the **intestine**, which runs straight backwards to the anus, preserving the same characters throughout its course. The intestine is constricted where it passes through the septa, and is expanded and saccular in the intervening somites. Its external walls are covered with a layer of loosely-packed glandular cells filled with yellow granules, which are not acted upon by alcohol, alkalies, acetic, chromic, or osmic acids. These cells, which give a yellow colour to the intestine, are known as **chloragogen** cells, or sometimes, but quite erroneously, they are described as "hepatic" cells. They do not communicate with the cavity of the intestine, and their function is excretory. From about the twentieth somite backwards, the dorsal wall of the intestine is deeply infolded so as to form a longitudinal ridge projecting into the cavity of the intestine. This ridge, known as the **typhlosole**, serves to increase the digestive surface. The space between the limbs of the fold is filled with chloragogen cells, and contains blood-vessels.

The cœlomic chambers between the septa are filled by a colourless **cœlomic fluid**, which can easily be squeezed out through the dorsal pores and examined under the microscope. It consists of a plasma coagulable in alcohol and colourless corpuscles of two kinds—the one finely granular and amœboid, the other spherical and loaded with coarse granules.

In addition to the cœlomic fluid the earthworm possesses red blood, contained in closed vessels. The red colour is due to hæmoglobin, which is not, as is the case in Vertebrates, contained in the corpuscles, but is dissolved in the plasma. The blood corpuscles of the earthworm are oval and colourless. A description of the blood-vessels must

be deferred till the other organs of the body have been considered.

The excretory system of the earthworm is made up of a number of pairs of coiled ciliated tubes opening by one end into the cœlom and by the other to the exterior. Such ciliated tubes are known as **nephridia**, and as similar, though not necessarily homologous, organs enter into the composition of the excretory systems of most of the higher invertebrate and vertebrate animals, it is important that their structure and relations should be fully understood. In the common earthworm there is a pair of nephridia in every somite except the first three and the last, and as all of them are similar in structure it is not necessary to describe more than one member of a pair. The nephridia may most conveniently be studied *in situ* in the 17th and 18th somites, the gizzard and crop being pulled over to the opposite side. The main part of a nephridium consists of a tube coiled into several loops closely bound together by membrane richly supplied with blood-vessels and attached to the posterior face of a septum low down and not far from the middle line. At the point of attachment one end of the tube passes through the septum, projects a little way into the cavity of the somite in front, and opens into it by an expanded kidney-shaped funnel known as the ciliated funnel or **nephrostome**. The other end of the tube opens to the exterior by one of the minute nephridiopores which have already been described as situated just in front of the upper chæta of a ventro-lateral couple. Opening internally in one somite, and externally in the next behind it, a nephridium may conveniently be described as consisting of a pre-septal and a post-septal portion.

The pre-septal portion includes the nephrostome and a short length of a fine tube ciliated internally. The structure of the nephrostome is rather complicated. Its body is formed by a single large crescent-shaped cell known as the **central cell**. The outer margins of the central cell are beset with a number of elongated wedge-shaped **marginal cells**, each with a nucleus placed near its outer border. The marginal cells are covered on one side with fine long cilia. The marginal cells, diminished in size, pass round the horns of the crescents, and running forwards become continuous with the edges of

certain grooved cells which first run forwards then turn sharply backwards, and the groove is converted into a closed tube, which is continued backwards as the narrow ciliated tube passing through the septum. The actual opening of the nephrostome is a crescentic slit lying between the grooved cells and the inner edge of the central cell. (Fig. 5, *C*.)

The post-septal part of the nephridium consists of—(1) a

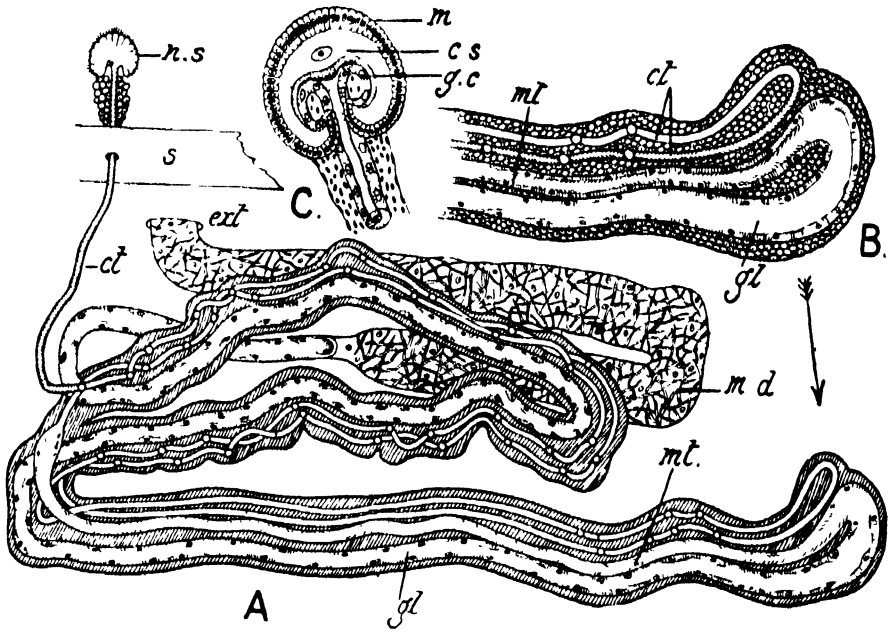


Fig. 5

A. Diagram of a nephridium of the earthworm. *n.s*, nephrostome; *s*, septum; *ct*, narrow ciliated tube; *mt*, middle tube; *gl*, wide glandular non-ciliated tube; *m.d*, muscular duct. *B*. A portion of *A* enlarged to show the passage from the middle tube to the glandular tube. *C*. A nephrostome enlarged. *m*, marginal cells; *c.s*, central cell; *g.c*, grooved cells. (After Benham.)

long narrow ciliated tube continuous with the narrow pre-septal tube. This tube is composed throughout of hollow cells joined end to end like so many drain-pipes, and is ciliated in certain parts of its course. (2) A short middle tube, brown in colour and ciliated internally throughout its extent; (3) a wide tube which is not ciliated; (4) a relatively short muscular tube or duct which opens to the exterior. The three first sections are twined round each other in the manner shown in fig. 5 to form two loops, the muscular duct forming another loop separate from the other two. Calling the

muscular loop the first loop, we find that the second loop lying nearest to it contains part of the wide tube and the greater part of the narrow tube, whilst the third loop contains part of the wide tube, part of the narrow tube, and the whole of the middle tube. All the tubes, with the possible exception of the muscular duct, are composed of hollow "drain-pipe" cells joined end to end, and the opening of the nephrostome is due to the enlargement of the lumen of the drain-pipe cells, accompanied by the thinning out and eventual disappearance of their walls on one side.

The drain-pipe cells of the middle tube and wide tube are glandular, and filled with excretory granules which are passed in to the lumen of the nephridium and so to the exterior. The opening of the nephrostome is nearly always choked with broken-down corpuscles of the cœlomic fluid, which are gradually swept by ciliary action into the nephridial tube and passed out of the body.

The nervous system consists of a pair of supra-pharyngeal ganglia lying just above the anterior end of the pharynx in the third somite. They give off large nerves to the prostomium and smaller nerves to the second and third segments. The supra-pharyngeal ganglia are connected by a pair of **circum-pharyngeal connectives** passing on either side of the pharynx, with a **sub-pharyngeal** ganglion pair lying in the fourth segment. From the sub-pharyngeal ganglion pair a **ventral nerve-cord** is continued straight backwards in the mid-ventral line to the posterior end of the body. In each somite the ventral cord swells up to form a ganglionic enlargement from which three pairs of nerves are given off, two close together in the hinder part of the somite and one pair more anteriorly. The nerves contain both afferent and efferent fibres, and pass to the musculature and integument of the body-wall. It is noteworthy that the efferent fibres originate from nerve ganglion cells situated in the ganglionic enlargements of the cord, whilst the afferent fibres originate from sense cells in the epidermis, and their inner ends branch and come into contact, but do not unite with the plexus of nerve fibrils in the cord.

Though the ventral nerve cord appears to be single it is really double, being composed of two longitudinal ganglionated cords firmly fused together. The double nature of the cord

can best be seen in transverse sections (fig. 7), when it can be seen that it is divided into right and left halves by a median vertical partition of connective tissue. The lower and lateral parts of each half are occupied in the ganglionic swellings by nerve ganglion cells, and the middle and upper parts by fine longitudinally disposed nerve-fibres. In the upper part of the cord there are three so-called **giant-fibres**, looking like three large tubes. Each consists of a central bundle of nerve-fibres enclosed in a double sheath, the bundles being direct prolongations of certain large nerve ganglion cells. In the adult worm the nerve cord lies wholly in the body-cavity, but it will be shown that in development it arises from the ectoderm in the form of two bands of cells which unite in the middle line and sink below the epidermis.

The blood-vascular system of *Lumbricus herculeus* comprises five main longitudinal trunks with their branches and communicating vessels. (1) The **dorsal** or **supra-intestinal** trunk lies just above the gut, extending from the pharynx to the hinder end of the body; anteriorly it breaks up to form a plexus of branching vessels on the walls of the pharynx. The course of the blood in the supra-intestinal vessel is from behind forwards. (2) The **sub-intestinal trunk** lies between the gut and the ventral nerve cord, being suspended from the former by a vertical fold of connective tissue. In it the blood runs from before backwards. (3) The **sub-neural trunk** lies close under the ventral nerve cord; in it the blood runs from before backwards. (4 and 5) The **lateral-neural trunks** are closely applied one to each side of the ventral nerve cord. The principal connections between and branches from these vessels are shown in the diagrams *A*, *B*, *C*, *D*, fig. 6. The supra-intestinal trunk communicates with the sub-intestinal trunk by five pairs of dilated contractile vessels, one pair in each of the segments 7—11. These enlarged vessels, called **hearts**, are conspicuous objects when the worm is opened from above. The blood running forwards in the supra-intestinal vessel is driven by the contraction of the hearts into the sub-intestinal vessel, and there flows in the reverse direction. Each heart gives off posteriorly a branch which passes to the septum behind and supplies branches to it.

The blood in the sub-intestinal vessel is carried outwards by two vessels in each somite. Of these one goes to the

body-wall and outer integument, the other to the nephridium. In the integument the blood, being brought in close contact with the air, is oxygenated, and is returned by two sets of vessels to the main trunks. One set leads straight to the sub-neural trunk, in which the blood is carried backwards to the posterior part of the body. The other set carry the blood to a special system known as the **intestino-tegumentary** system. The intestino-tegumentary vessels arise one from each side of the supra-intestinal trunk in the tenth somite, and run forwards on the sides of the œsophagus, eventually breaking up into branches on the walls of the pharynx. In each of the somites 10—6 they give off on either side a vessel carrying blood to the walls of the œsophagus, and they receive trunks carrying back blood from the integument and nephridium respectively (fig. 6, *A* and *B*).

Posteriorly to the eighteenth somite — that is to say, throughout the region of the intestine—the arrangement of the blood-vessels is different. The main trunks make the following communications, and give off the following branches in each somite:—The sub-intestinal trunk gives off a vessel on either side, which divides into two branches, one passing to the nephridium, the other to the body-wall and integument, and supplying these regions with blood. The sub-neural is connected with the supra-intestinal trunk by a pair of **commissural vessels** running in the hind wall of the septum. Each commissural vessel is joined by branches bringing back blood from the body-wall and integument, and by an efferent nephridial vessel bringing back blood from the nephridium. There is, in addition, an intestinal system consisting of two pairs of **efferent intestinal** vessels carrying blood from the supra-intestinal trunk to the walls of the intestine in every segment. The blood, after passing through capillaries in the walls of the intestine, is collected by two pairs of **afferent intestinal vessels** and carried back to a **typhlosolar** vessel running longitudinally in the fold of the typhlosole, and from this it is conducted back to the supra-intestinal trunk by three or four short vertical vessels in each somite.

The circulation of the blood in the earthworm is thus a very complicated affair, and much uncertainty still prevails on the subject. The uncertainty is increased by the fact that the arrangement of the blood-vessels, and consequently the course

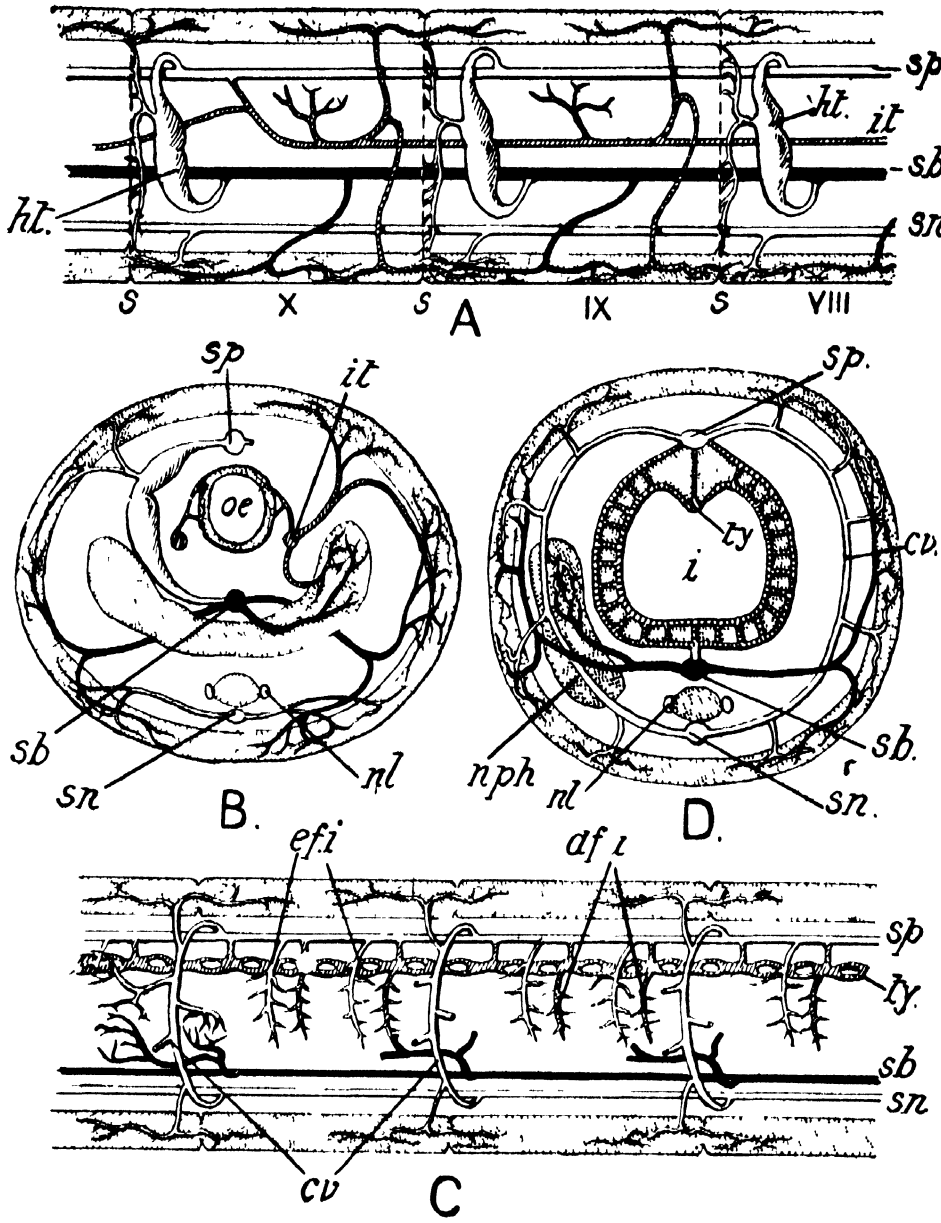


Fig. 6

A series of diagrams to illustrate the arrangement of the blood-vessels and the course of the circulation in *Lumbricus herculeus*. *A*. Longitudinal view of the vessels in somites 8, 9 and 10. *B*. The blood-vessels as seen in transverse section in the same region. *C*. Longitudinal view of the vessels in the intestinal region. *D*. Transverse section through the intestinal region. *sp*, supra-intestinal; *sb*, sub-intestinal, and *sn*, sub-neural longitudinal trunks; *nl*, lateral neural vessels; *ht*, *ht*, contractile vessels or "hearts"; *it*, intestino-tegumentary vessels; *cv*, commissural vessels; *af.i*, afferent intestinal vessels; *ef.i*, efferent intestinal vessels; *ty*, typhlosolar vessel; *i*, intestine; *œ*, œsophagus; *s*,*s*, septa. (From a drawing by Dr W. B. Benham.)

of the blood stream, differs considerably in different species of oligochæte worms, so that the statements of one author frequently seem to stand in contradiction to those of another who has worked on a different species. The account given above is probably nearly correct for *L. herculeus*. It will be observed that the blood of the sub-intestinal vessel must pass either through the body-wall or through the nephridia before it finds its way back to the supra-intestinal trunk, so that in the one case it is oxygenated, in the other case it is purged of excretory nitrogenous material. In the anterior region of the body, where there are no commissural vessels, the oxygenated blood from the body-wall is carried back to the intestino-tegumentary vessels, and then distributed to the pharynx and anterior segments.

It is beyond the scope of the present work to enter into a detailed account of the histology of the different organs of the earthworm, but the general relations of the organs and the general histology of the tissues as visible in transverse section are represented in fig. 7. Externally the body is invested by a cuticle, which may easily be stripped off a worm which has been left some time in water. It is perforated by numerous minute pores, the orifices of unicellular glands of the epidermis, and viewed from above it is seen to be traversed by two sets of fine lines or striæ, which cause the iridescent hues mentioned above. Beneath the cuticle is the epidermis formed of two layers of cells. The innermost layer consists of very small cells, the inner broad ends of which lie on a basement membrane, their outer ends being pointed and wedged in among the cells of the outer layer. The outer layer consists of gland-cells, interstitial cells, and sense cells. The gland cells are pear-shaped, the narrower end directed inwards, and the swollen outer part filled with granules. The interstitial cells are much smaller than the gland cells, and may be described as modified columnar epithelial cells. Amongst them are many rod-shaped cells, not differing much in appearance from ordinary interstitial cells, but having their inner ends produced into fine fibrils, one of which is continued into a nerve trunk as a sensory or afferent nerve fibril. In the anterior segments of the body groups of sense cells furnished with fine processes at their outer extremities are found, chiefly in proximity to the chætæ. The modified

epidermis of the clitellum is made up of several layers of glandular cells.

The sacs in which the chætæ are implanted are invagina-

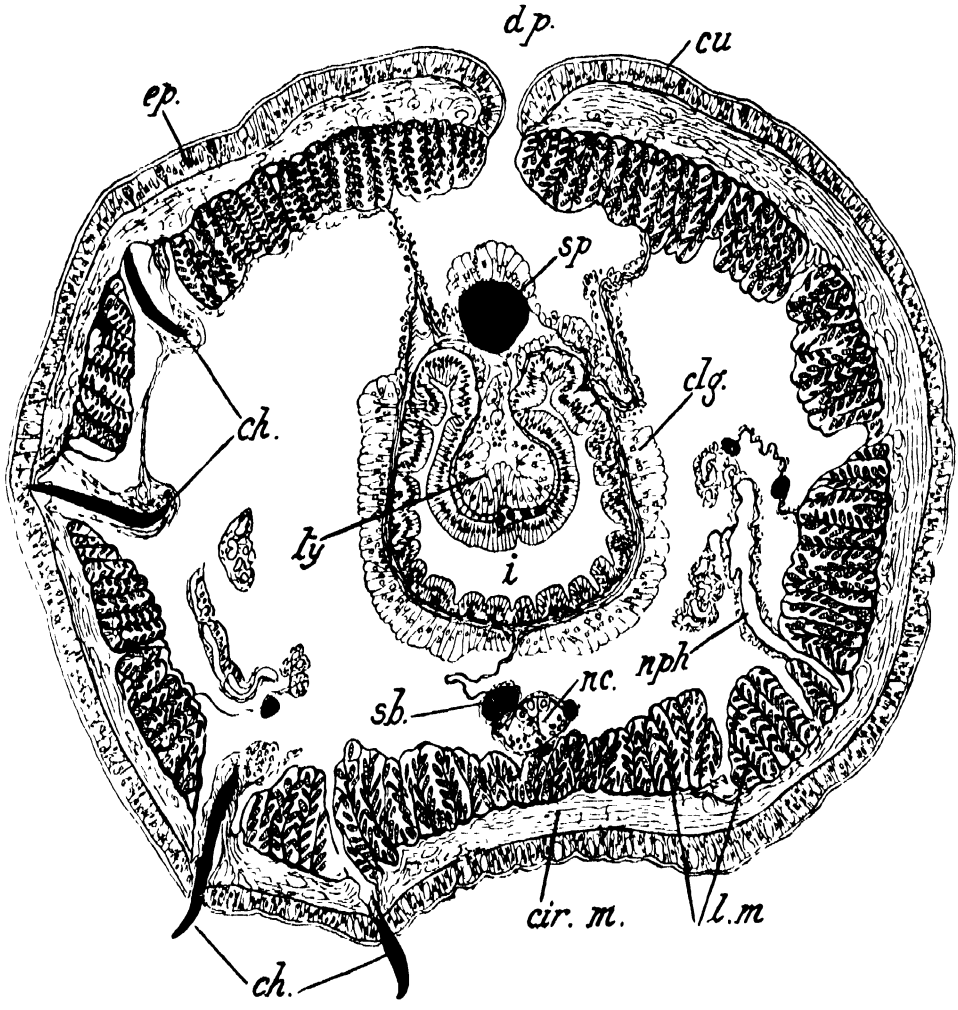


Fig. 7

A transverse section through the intestinal region of *Lumbricus herculeus* magnified. *Ch*, *ch*, chætæ; *cir. m*, layer of circular muscles; *clg*, chloragogen cells; *cu*, cuticle; *d p*, dorsal pore; *ep*, epidermis; *i*, intestine; *l.m*, longitudinal muscles; *nc*, nerve cord; *nph*, nephridium; *sb*, sub-intestinal blood-vessel, below it are the sub-neural and lateral neural vessels attached to the nerve cord, *sp*, supra-intestinal blood-vessel; *ty*, typhlosole.

tions of the epidermis. The cuticle forms a lining to the sac for a certain distance: beyond this the chæta ends in a mass of cells, each one of which can produce a new chæta to replace the old one. Beneath the epidermis is a layer of circular muscle fibres embedded in a granular nucleated substance. The individual muscle fibres are elongate, pointed at both ends, and longitudinally striated.

Internal to the circular layer is a much thicker layer of longitudinal muscles, imbedded, like those of the circular layer, in a granular substance. The muscle fibres are identical in structure with those of the circular layer and are arranged in such regular rows that the layer appears to consist of a series of radial connective tissue septa with the muscle fibres attached on either side of every septum, looking in transverse section like the barbs of a feather. The layer of longitudinal muscles is much thicker than the circular layer. Internal to the longitudinal muscles is a layer of pavement epithelium forming the lining of the cœlomic cavity.

The gut lies free in the cœlomic space and is not attached to the body-wall by vertical mesenteries, though a suspensory fold connects it in the mid-ventral line with the sub-intestinal blood-vessel. (The section drawn in fig 7 passes close to a septum, and the strands of tissue passing from the body-wall to the gut on the dorsal side are not mesenteries but folds of the septum.) The cœlomic epithelium covering the intestine is modified to form the peculiar chloragogen cells whose characters have already been noted. Similar chloragogen cells surround the supra-intestinal blood-vessel, and are continued downwards into the fold of the typhlosole. Beneath the chloragogen cells, which are, it must be remembered, cœlomic epithelium, is the muscular coat of the intestine, chiefly composed of circular muscle fibres, the scanty longitudinal fibres lying internal to the circular layer. The cavity of the intestine is lined by an epithelial layer consisting of a single layer of ciliated columnar cells. The structure of the ventral nerve cord has already been described.

CHAPTER XVIII

THE EARTHWORM—*continued*

THE earthworm is hermaphrodite (monœcious), being furnished with two pairs of testes and one pair of ovaries, together with accessory generative organs, which will now be described. The **ovaries** are a pair of small pear-shaped bodies lying in somite 13. They are attached by their broader ends to the hinder face of the septum separating the 12th from the 13th somite, and lie low down in the body-cavity not far from the ventral nerve cord. Essentially an ovary arises as a local multiplication of cells of the cœlomic epithelium. Its thicker end consists of a solid mass of cells or oogonia, and the narrower end contains ripe ova, the intermediate part being occupied by ova in different stages of maturation. The mature ovum is surrounded by a distinct follicle consisting of a single layer of flattened cells. On the bursting of the follicle, the ovum, which is a large round cell with granular cytoplasm and a very distinct nucleus and nucleolus, passes into the cavity of the somite and is thence conducted to the exterior by a special **oviduct**. There is a pair of oviducts opening into segment 13 by wide ciliated funnel-shaped mouths. Each duct passes through the septum separating segments 13 and 14, dilates on the other side of it to form a small chamber, the **receptaculum ovorum** or **ovisac**, and turns sharply outwards and downwards to open to the exterior by the oviducal pore on segment 14. The ova remain for some time in the ovisac before they pass to the exterior, and in it they undergo the final phases of maturation.

The two pairs of **testes** are small digitate organs situated in somites 10 and 11, in positions exactly corresponding with those of the ovaries. Like the ovaries, they are local thickenings of the cœlomic epithelium, but the sperm mother-cells produced from them do not develop into spermatozoa in the testes themselves, but pass into two large sacs which surround

the testes and the openings of the sperm ducts, and there undergo their further development.

The **sperm-sacs**, into which the sperm mother-cells are shed, vary considerably in form and size at different seasons of the year. When fully developed in the autumn months they are conspicuous white structures with three pairs of lateral elongated lobes projecting at the sides of the œsophagus. They must be regarded as a special portion of the cœlomic cavity which has been cut off by the growth of a horizontal partition from the septa in segments 10 and 11. Each sperm-sac may be regarded as consisting of two parts, a spacious median unpaired sac, distinguished as the sperm-reservoir, and paired lateral appendages of these, distinguished as the sperm-sacs proper.

The anterior sperm-reservoir lies in the ventral part of the 10th somite, and its four corners are produced into horns, which are the paired sperm-sacs. The antero lateral horns seem to project through the septum separating the 10th from the 9th somite, and to lie in the cavity of the latter. But really they are covered by a pocket-like fold of the septum, and therefore must be regarded as belonging to the 10th somite. Similarly, the postero-lateral horns push the wall of the septum separating the 10th from the 11th somite before them and seem to lie in the 11th somite. The posterior seminal reservoir lies in somite 11, and has only one pair of sperm-sacs connected with it; these spring from the postero lateral angles and push through the septum behind so as to project into the 12th and even into the 13th somite. The cavities of the horns or sperm-sacs proper are divided up by partitions into numerous chambers, but the cavities of the median seminal reservoirs are not thus divided.

Immediately behind the testes in each seminal reservoir is a pair of large ciliated funnels whose walls are thrown into numerous pleats like the folded filter papers used in chemical experiments. These are the openings of the sperm-ducts, and from their shape they are often called the ciliated rosettes. The sperm-duct from each ciliated rosette of the anterior pair passes through the septum dividing the 10th from the 11th somite, runs outwards and backwards as a fine convoluted tube in the ventral body-wall, and then turns backwards, runs with a straight course through the next three somites,

and opens to the exterior by the spermiducal pore on segment 15. The duct of each member of the second pair of ciliated rosettes passes through the septum dividing somites 11 and 12, and after a short convoluted course joins the duct of the anterior rosette in segment 12. It should be clearly understood that the median seminal reservoirs lie below the œsophagus, but cover in the testes, the ciliated rosettes, and the ventral nerve cord (fig. 4, *B*).

In each of the somites 9 and 10 there is a pair of accessory organs in the shape of small white spherical vesicles, opening by small intersegmental pores between segments 9 and 10 and 10 and 11. These are the **spermathecæ**, and at certain times of the year they contain large numbers of ripe spermatozoa; long filiform bodies slightly thickened at one end, and capable of active movement. The spermatozoa are formed in the sperm-sacs and seminal reservoirs from the sperm mother-cells derived from the testes. The sperm mother-cells divide in such a way as to form a peripheral layer of cells attached by their inner ends to a central generally non-nucleated mass of cytoplasm called the **cytophore**. The nucleated cells surrounding it gradually increase in length, and eventually are drawn out into long filiform structures adhering by their thickened inner ends to the cytophore. Ultimately they are detached as ripe spermatozoa, and are drawn by the cilia of the rosettes into the sperm-ducts, through which they pass to the exterior. From the sperm-ducts the spermatozoa are transferred to the spermathecæ of another worm, two worms in adjoining burrows coming together for this purpose.

The ova of the earthworms are laid in cocoons which are formed by the secretion of the glands of the clitellum. The secretion hardens on exposure to the air, forming a membranous ring which the worm slips over its head. As the ring passes the openings of the oviducts and spermathecæ it receives a number of ova and spermatozoa, and also albuminous matter secreted by certain capsulogenous glands situated on the ventral side of some of the segments anterior to the clitellum. As the cocoon is elastic, it shrinks when free of the worm, the middle part is swelled out by the ova and albumen and the two ends are reduced to tag-like projections. The cocoons are deposited in the earth. As a

rule, only one of the ova contained in a cocoon attains complete development.

The ova are spherical and laden with small clear yolk spherules and granules, which, however, are not so abundant as to prevent its being fairly transparent. The early stages of segmentation are irregular, and when seven or eight cells are formed the embryo consists of two large lower cells called **macromeres**, surmounted by a cap of five or six smaller cells called **micromeres**. As segmentation proceeds a cavity is formed between the micromeres above and the macromeres below, and the embryo becomes a hollow sphere or blastula, whose walls are composed of a single layer of cells, those at one pole being larger than those at the other, though it is not any longer possible to make a distinction between macromeres and micromeres. After the establishment of the blastula the cells composing its walls divide repeatedly by radial divisions, excepting two large cells lying close together near the equator. These do not divide, and therefore retain their primitive size, whilst the other cells of the embryo become smaller and smaller as the result of continued division. These two large cells are known as the pole-cells of the mesoblast, or **mesomeres**. Their inner ends soon project into the cavity of the blastula (blastocœle), and presently these inner ends are segmented off to form two smaller cells lying in the blastocœle, the two large parent cells retaining their position at the surface of the embryo. This process is repeated several times, so that two rows of small cells formed by successive unequal divisions of the mesomeres lie side by side in the blastocœle. During this time the mesomeres themselves gradually sink below the surface and lie at the ends of the two rows in the blastocœle. The mesomeres and the two rows of smaller cells derived from them are the **mesoblastic bands**, from which the musculature of the body-wall and gut, the cœlomic epithelium, the muscular septa, and the gonads and their ducts are eventually derived. The mesoblastic bands define the longitudinal or antero-posterior axis of the future worm. The mesomeres are placed at what will be the hinder end of the animal, the other ends of the bands, which converge and unite in the middle line, consequently represent the anterior end.

The blastula has hitherto been nearly spherical in shape.

It now becomes elongated antero-posteriorly and flattened from above downwards, so as to form an oval plate with

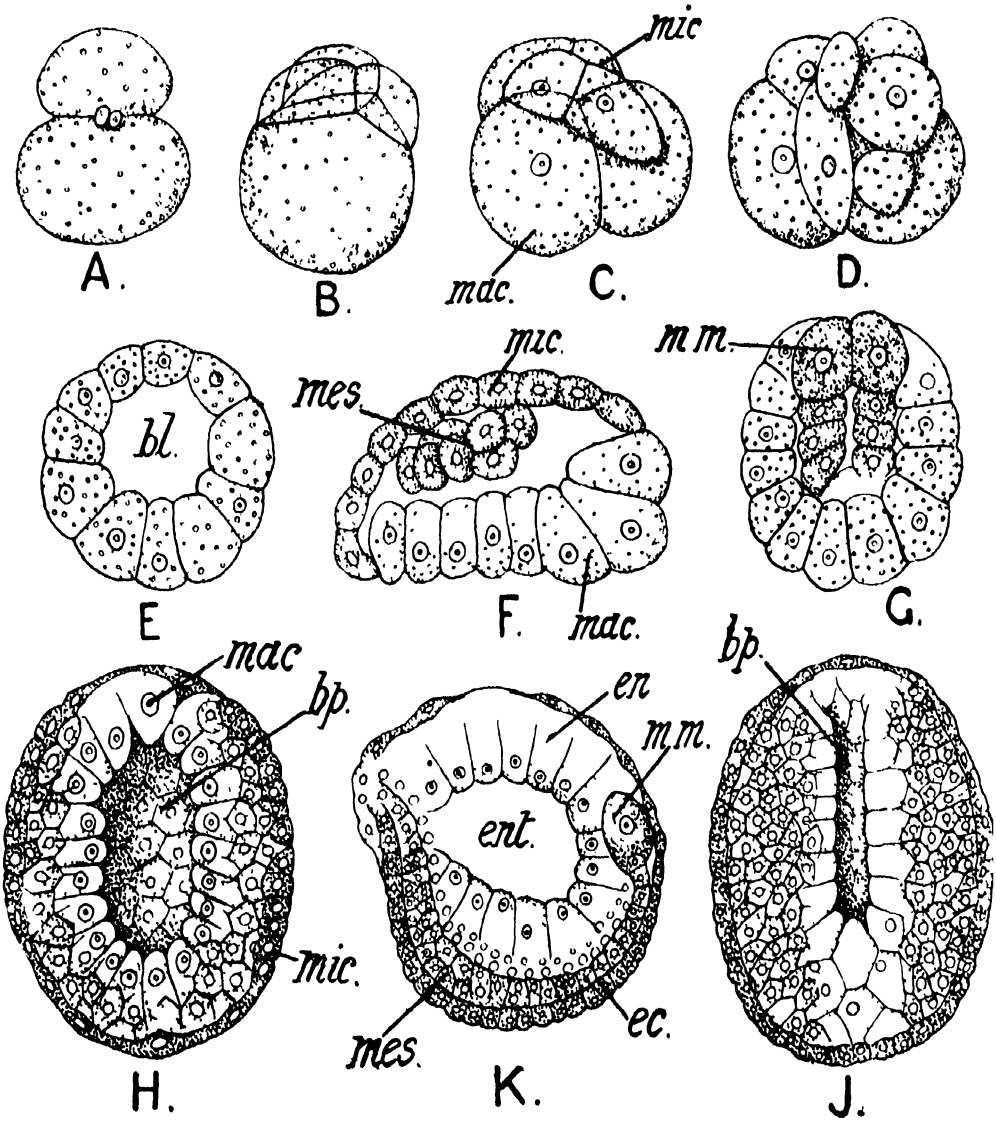


Fig. 8

Segmentation and early stages of development of *Lumbricus*, after E. B. Wilson. *A*, *B*, *C*, *D*, successive stages of segmentation. *E*. Blastula stage. *F*. Commencement of invagination; the macromeres form a flat plate on the ventral side. *G* An embryo somewhat younger than *F* viewed from above, showing the mesomeres and mesoblast rows derived from them. *H*. Gastrula stage viewed from below, showing the wide oval blastopore bounded by macromeres; at the sides the micromeres are growing over the macromeres. *J*. Later stage, showing the elongated blastopore and the further overgrowth of the macromeres by the micromeres. *K*. Optical longitudinal section through a later stage after closure of the blastopore. *bp*, blastopore; *ec*, ectoderm; *en*, endoderm; *ent*, enteron; *mac*, macromeres; *mes*, mesoblast; *mic*, micromeres; *mm*, mesomeres.

rounded edges. The cells on one side, the lower side, are larger than those on the upper side, and become tall and

columnar, forming a perfectly flat plate. The cells on the upper side become flattened and form a relatively thin roof to the still persistent, though much reduced blastocœle. The mesomeres lie side by side in the posterior end of the blastocœle; the mesoblast bands in front of them diverge from one another and pass forwards and downwards, their anterior ends being widely separated from one another at this stage.

The flattened embryo now begins to fold up along the antero-posterior axis, and at the same time the anterior and posterior ends are bent over downwards so that the lower surface formed by the large cells becomes concave. At the same time, the small cells on the upper side begin to grow over the large cells all round the edge of the plate. As the plate of large cells at the lower side becomes more and more concave through the folding over of its edges, and as the small cells grow further and further over the infolded cells of the lower layer, an embryo such as is shown in fig. 8, *H*, is produced. It is ovoid in shape, and on its lower side there is a large oval orifice leading into a cavity which is lined by the large cells which at an earlier stage formed the flat lower plate. The cavity is the **enteron** or primitive gut, and the large orifice leading into it is the **blastopore**. The lips of the blastopore are still bounded by large cells, but elsewhere the small flattened cells have grown over the large cells and form a nearly complete external investment for the embryo. As a result of the folding up of the lower plate, the blastocœle has almost wholly disappeared, but the mesomeres and the mesoblast bands derived from them lie between the large and the small cells at the sides of the embryo. The three germinal layers are now definitely established. The small outer cells are the **epiblast** (or ectoderm), the large cells lining the enteron are the **hypoblast** (or endoderm), and the pole cells with the mesoblastic bands are the **mesoblast** (or mesoderm). The process by which the hypoblast cells become folded up, so as to enclose a cavity opening to the exterior by the blastopore, is known as a process of **gastrulation.**

In the course of further growth the blastopore becomes slit-like through the continued folding in of its lateral walls, and eventually the walls meet and coalesce behind, the coalescence passing rapidly forward till only a small orifice is left

at the anterior end, which persists and forms the mouth of the adult animal.

During these changes important developments have taken place in the mesoblastic bands. At first each band consisted of a single row of cells which had been successively budded off from the mesomeres. As growth proceeds and the embryo elongates, not only are fresh cells added to each existing row by continued unequal division of the pole-cells, but the more anterior cells of each row begin to divide horizontally, so that each row becomes two or three cells deep in its anterior part. During the formation of the enteron the anterior ends also grow upwards and forwards till they meet and unite in front of the blastopore, so that the last named is completely surrounded by the mesoblast as it were with a ring. As the blastopore narrows and closes up from behind forwards, the mesoblast bands are approximated to one another, and form two nearly parallel bands, one on either side of the middle line. At the same time the epiblast overlying the mesoblast becomes thickened. The cells of this thickened area are only one layer deep, but they are columnar, and pass rather suddenly into the flattened epithelium, which elsewhere forms the outer layer of the embryo. As development proceeds these lateral bands of thickened epiblast extend forwards till they meet above and in front of the blastopore, and somewhat later they send out ventral extensions, which meet behind the blastopore and enclose it, forming thickened lips. These lips afterwards grow into the blastopore, and form an epiblastic lining to the entrance to the enteron. An epiblastic ingrowth of this kind into the mouth is called a **stomodæum**. On the formation of the stomodæum the embryo begins to engulf the albumen contained in the cocoon, and so obtains the food necessary for its further development.

The changes which follow affect the mesoblast bands and the thickened epiblast lying immediately outside them. The mesoblast cells in the anterior and middle parts of the bands continue to divide by both horizontal and vertical divisions, so that the bands become several cells deep, and more than one cell thick. At the same time, each band becomes divided from before backwards into a number of blocks, the **mesoblastic somites**. The successive somites of the right and left bands form pairs. They are solid at first, but shortly a cavity appears

in each, and they grow upwards and downwards, pushing their way between the epiblast and hypoblast. Eventually the somites of each pair meet above and below, and fuse in the mid-dorsal and mid-ventral lines. The effect of this is that in each pair of somites an inner layer of cells applied to the gut is separated from an outer layer applied to the body wall. The former may be called the **splanchnopleur**, the latter the **somatopleur**, and the two are separated by a space lying outside the enteron, which is the cœlom or body-cavity. The transverse partitions separating the successive pairs of mesoblastic somites persist and form the septa of the adult worm. The cœlom, then, is formed as a series of paired cavities hollowed out in the mesoblast, the cavities of each pair meeting and coalescing above and below. The inner layer of mesoblast cells or splanchnopleur forms the musculature of the gut and the cœlomic epithelium surrounding the gut, the outer layer or somatopleur forms the musculature of the body-wall and the cœlomic epithelium internal to it.

Coincidently with these changes, important differentiations make their appearance in the thickened epiblast lying outside the mesoblast bands. On either side of the mid-ventral line the epiblast is arranged in three or four distinct rows of cubical cells, each row ending posteriorly in a rounded cell known as the **teloblast**. At first these rows are part of the superficial epiblast, but as development proceeds they sink inwards, are overgrown by the adjacent epiblast, and come to lie between it and the mesoblast bands. As the embryo increases in length so do the rows increase by continued addition of new cells budded off from the terminal teloblast. Of the three or four rows on each side the innermost—*i.e.* the rows nearest the mid-ventral line—give rise to the ventral nerve cord, and are therefore called the **neural rows**, and their teloblasts the **neuroblasts**. The two succeeding rows on each side give rise to the nephridia and the inner row of chæta glands, hence they are called **nephric rows**, and their teloblasts **nephroblasts**. The fate of the outermost rows is rather doubtful, but probably they give rise to the outer rows of chæta glands.

As the mesoblastic somites are successively formed from before backwards, the cells of the nephric rows become converted into nephridia, one nephric cell giving rise to a nephridium on either side of each somite. The development

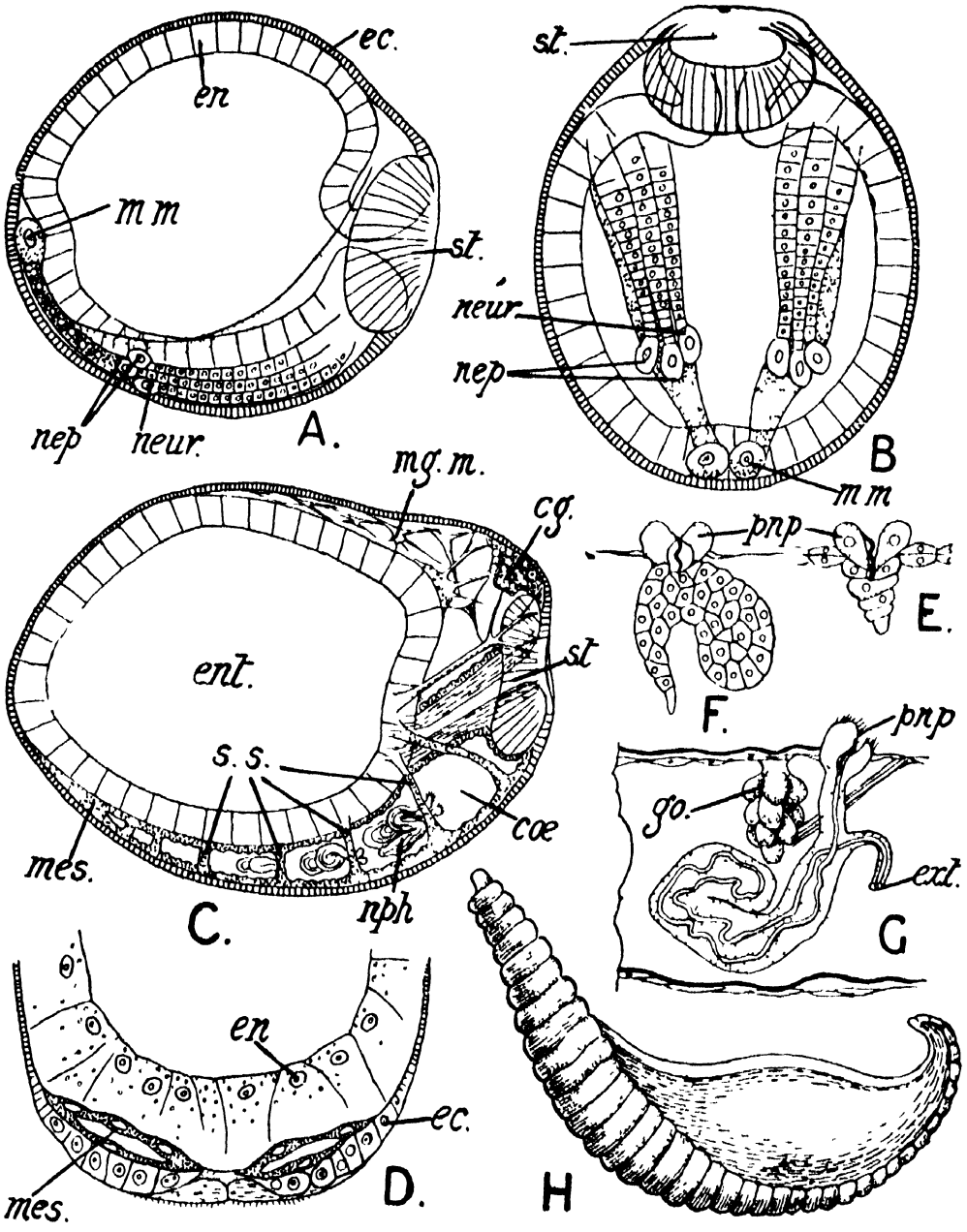


Fig. 9

A. Lateral view of an embryo of *Lumbricus fœtidus*, in which the germ bands are clearly visible. *B*. Ventral view of the same embryo. *C*. Lateral view of an older embryo. *D*. Transverse section through the ventral half of an embryo, showing the cleavage of the mesoblast. *E*. Early stage in the development of a nephridium of *Rhynchelmis*, showing the pronephridiostome with a single flagellum. *F*. A later stage in the development of a nephridium. *G*. Nephridium in the eleventh somite of a young worm. *H*. View of an older embryo of *Lumbricus*. *ec*, ectoderm; *en*, endoderm; *ent*, enteron; *ext*, external pore of nephridium; *go*, gonad; *mes*, mesoderm; *mm*, mesomeres; *nep*, nephroblasts; *neur*, neuroblasts; *nph*, nephridia; *pnp*, pronephrostome; *s.s*, septa; *st*, stomodæum. (*A* to *D* after E. B. Wilson; *F* to *G* after Vejdovsky; *H* after Kowalevsky.)

of a single nephridium may be described as follows: - An individual nephric cell increases in size, becomes detached from the nephric row and takes up a position among the cells of a septum separating two somites. It then divides into two cells, a larger lying partly imbedded in, partly projecting in front of, the septum, and a smaller projecting behind the nephridium. The large anterior cell gives rise to the nephrostome, which is at first very simple, consisting of two cells enclosing a cavity, within which is a single flagellum. The small hinder cell by repeated transverse division gives rise to a row of cells, which grows towards, and eventually becomes attached by one end to, the ventral epiblast. The cells of this row are at first solid, but eventually they become hollow, and the row, greatly increased in length and thrown into convolutions as the result of a lateral outgrowth, the details of which need not detain us, develops into the ciliated and glandular parts of the nephridial tube. The muscular section of the nephridium is formed from an invagination of the epiblast. By a further process of cell division and growth the simple embryonic nephrostome becomes converted into the complicated nephrostome of the adult. Nephridia are not formed in the first pair of somites. It appears from this that the nephridia are derived from the epiblast, and come into secondary relations with the cavities hollowed out in the mesoblastic somites.

On the other hand, the sperm-ducts and oviducts appear to be formed as outgrowths of the cœlomic epithelium. These outgrowths penetrate the body-wall and acquire openings to the exterior, the male and female generative pores. Thus, although in position and structure the generative ducts offer a strong resemblance to nephridia—they are developmentally quite distinct from them. The nephridia are epiblastic structures which grow towards the mesoblast, the gonaducts are mesoblastic structures which grow outwards towards the epiblast. Since the two sets of organs are not homologous, it is advisable to reserve the name **peritoneal funnel** exclusively for structures which, like the gonaducts, are derived from the mesoblast, and grow outwards, and acquire external openings

To return to the mesoblast bands. It has been shown that at a comparatively early stage the two bands meet and unite anteriorly dorsal to the persistent anterior part of the blastopore which becomes the mouth. Whilst the mesoblastic

somites are being formed behind the mouth, the cells of the conjoined anterior ends of the bands become branched and amœboid, and ultimately arrange themselves so as to enclose a single anterior median cavity, the prostomial or head cavity, which is traversed by branched contractile cells. This anterior cavity defines the prostomium, whose nature is therefore different to that of the paired cœlomic cavities which follow behind the mouth. Later in development the partition between the prostomial and first pair of cœlomic cavities breaks down, as also do the septa between the first, second, and third pairs of cœlomic cavities, leaving the large anterior cavity in which the buccal cavity and pharynx lie in the adult.

Fig. 9, *H*, shows an embryonic worm in a tolerably advanced stage of development. As the mesoblastic somites are formed from before backwards, the anterior part of the worm is fully segmented, the somites of either side having coalesced both ventrally and dorsally. A little further back the somites have coalesced ventrally but do not reach up to the dorsal surface, and still further back they are wholly confined to the ventral surface. Consequently, in the middle and posterior regions of the embryo, the upper surface and sides of the body consist only of the enteron covered over by a thin layer of flattened epiblast. In the further course of development the successive somites meet and fuse dorsally, and new somites are continually formed by budding from the mesomeres at the hinder end of the body. As the segmentation is completed, the embryonic cells are differentiated to form the tissues of the adult, and with the formation of the typical number of segments the worm is completed. The anus is formed late in embryonic life by an ectodermic invagination meeting and fusing with the enteron in the posterior segment.

There is every reason to believe that the earthworm is descended from fresh-water, and those in turn from marine ancestors, and, therefore, the course of development has been much modified in connection with the change from a marine to a terrestrial habit. None the less, there are many interesting lessons to be learned by the study of its development. It is most important to remember that the segmentation of the body, which is so characteristic a feature of the earthworm and all Annelid worms, is at first internal and affects only the mesoblastic bands. Only as the mesoblastic somites increase

in extent and surround the gut do the structures derived from the epiblast, the external skin, the nephridia, and the nerve cord develop in segmental connection with the somites. There is, however, one region of the body which is not segmented—namely, the prostomium with its single prostomial cavity. This region is so much reduced in earthworms that its importance is easily overlooked, but it attains greater development in many other worms, and, indeed, preponderates during larval life. In order to understand better the segmentation or metamerism of the earthworm, it will be advisable to consider shortly the structure of some of the nearest allies of the earthworms

CHAPTER XIX

THE ANNELIDA

THE metamerically segmented worms are grouped together in a phylum **Annelida**, the name having reference to the external annulation of their bodies. The phylum comprises four classes, the **Archiannelida**, the **Chætopoda**, or bristle worms, the **Hirudinea** or leeches, and the **Echiuroidea**.

As an example of the Archiannelida we may take a small marine worm called Polygordius, which is tolerably common in the sand at a few fathoms depth in the Mediterranean Sea. It is a small thread-like animal, only some three or four centimetres in length and is externally marked into segments by indistinct grooves. At its anterior end there is a distinct head-lobe or prostomium which bears a pair of tentacles. The mouth is situated on the ventral surface of the segment following the prostomium, and the anus is placed on a terminal swollen anal segment. On each side of the prostomium there is a small oval depression or pit lined with cilia, and probably functioning as a sense organ. There are no chætæ nor any other appendages besides the prostomial tentacles.

The internal anatomy follows the same plan as that of Lumbricus, but is simpler and more primitive. The nervous system consists of a ventral nerve cord connected by cords passing round the gullet with a cephalic ganglion which lies in the prostomium. (In the earthworm the cephalic or supra-pharyngeal ganglion has been shifted back to the 3rd segment.) The intestine is a simple straight tube passing from mouth to anus and separated by the cœlomic cavity from the body-wall. The cœlom is divided into compartments by septa, and the internal segmentation corresponds with the external segmentation. But whereas in the earthworm the right and left cœlomic cavities in each somite are confluent dorsally and ventrally, in Polygordius they are separated by vertical partitions, and so the gut is suspended in the cœlom

by a dorsal and a ventral mesentery. But the most important feature in Polygordius is the almost complete repetition of the organs in every segment of the body, so that the animal might be likened to a chain each link of which is exactly similar to the links in front of and behind it, with the exception of the first and last, the prostomium and anal segment.

Thus, in every somite, except the first three and the last, there is a section of the alimentary canal and the ventral nerve cord. There is a pair of cœlomic cavities, lined by a flattened cœlomic epithelium, a mass of somatic muscles consisting of longitudinal fibres (the circular layer is not developed in Polygordius), a pair of nephridia, and a pair of generative organs or gonads. When all the organs are repeated in successive segments in this manner the segmentation is said to be **homonomous.** In the earthworm, on the other hand, the segmentation is **heteronomous.** Certain of the organs are suppressed in some of the segments, and others attain to a greater degree of elaboration in some segments than in others. Thus the gut of the earthworm is considerably modified in the anterior segments and enlarged to form the pharynx, crop, gizzard, etc. The generative organs are much reduced and are confined, in normal cases, to the 10th, 11th, and 13th somites. But it is not uncommon to find rudiments of a pair of gonads in the twelfth segment, and a case has been described in which an earthworm had gonads in nine somites—viz. two pairs of testes in somites 10 and 11, and seven pairs of ovaries in segments 12 to 18 inclusive. From these and other considerations we are able to infer that the earthworm is derived from an ancestor in which all the segments were alike, as in Polygordius, and that the heteronomy exhibited by existing earthworms is due to specialisation involving the suppression of the gonads in most of the somites, and the elaboration of other organs in some few of the somites.

There are no generative ducts in Polygordius. The sexes are separate, and the generative products when ripe escape by rupture of the body wall, sexual maturity involving the death of the animal. The ova are shed into the water and there fertilised. The ovum segments and develops into a curious larval form known as the trochosphere. This larva is shaped something like a humming-top, having the form of a flattened

sphere produced into a conical projection at the lower pole. Two parallel ciliated bands encircle the equator, and between these the mouth opens on one side of the body. The mouth leads into an œsophagus, which expands into a capacious

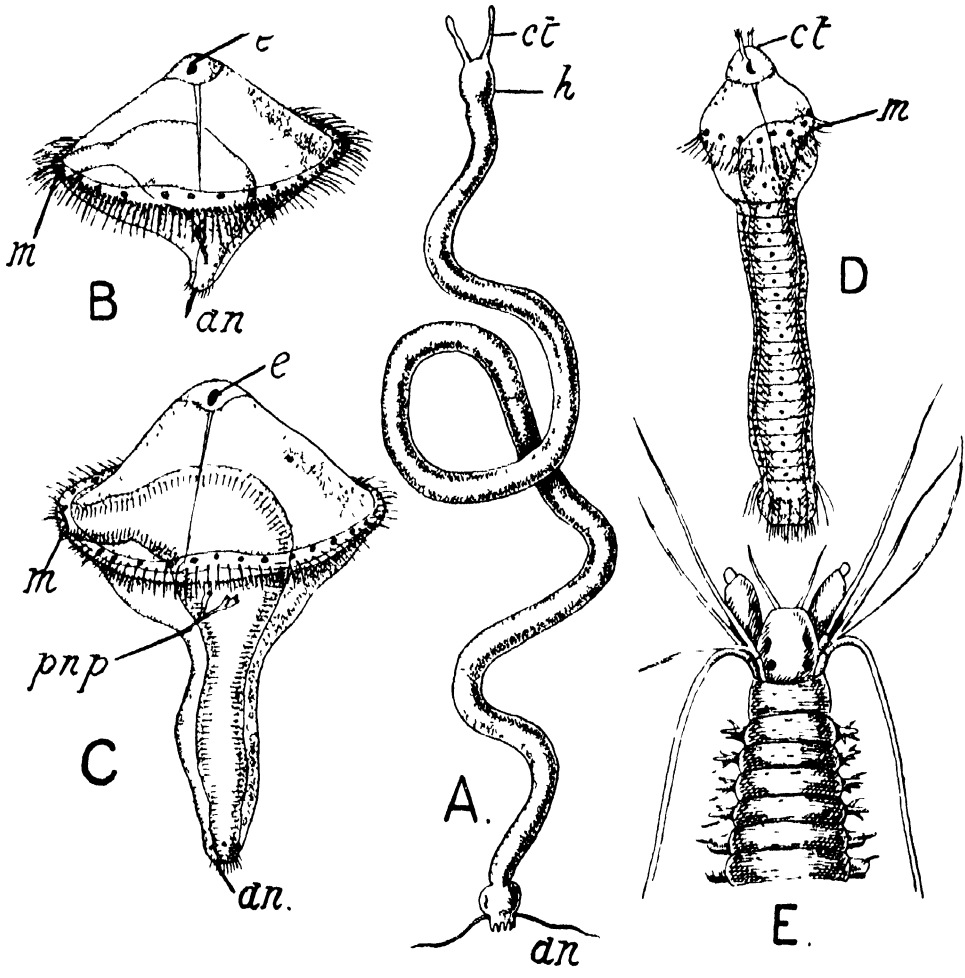


Fig. 10

A. Dorsal view of *Polygordius appendiculatus*. *ct*, cephalic tentacles; *h*, head; *an*, anus. *B* Trochosphere larva of Polygordius. *e*, eyespot, *m*, mouth, *an*, anus. *C* and *D*. Stages in the development of the trochosphere into the worm. *pnp*, pronephridium. *E* Head and anterior segments of a polychæte, *Nereis rubicunda*, showing the head, eyes, tentacles, and cirrhi, and parapodia. (*A* to *D* after Fraipont, *E* after Ehlers.)

stomach, from which a short and nearly straight intestine proceeds, opening by an anus at the extremity of the conical projection at the lower pole. There is a considerable space between the walls of the gut and the body-wall; this space is filled with fluid, contains a few scattered stellate cells, and is traversed by a few muscular fibres; but it must not be con-

fused with the cœlom of the adult worm, being in fact the persistent blastocœle formed in course of segmentation. At the upper pole there is an epidermic thickening which develops into the cerebral ganglion of the adult worm, and a pair of eyespots are developed in connection with this larval nervous plate.

On each side of the lower end of the stomach is a provisional excretory organ in the shape of a delicate tube with **flame-cells projecting into the blastocœle.** These tubes are known by the name of the head-kidneys or **pronephridia.** Lastly, there is a plate of cells lying on each side of the intestine and ending posteriorly in a pole-cell or mesomere. These are the mesoblast bands, homologous with the similarly named organs in the earthworm.

The adult worm is formed by the continued elongation of the conical projection at the lower pole of the larva. As the cone increases in length the mesoblast bands grow back into it and become segmented from before backwards, forming mesoblastic somites which become hollow and give rise to the cœlom, much in the same way as in the earthworm. But whereas in the earthworm the right and left members of each pair of cœlomic pouches fuse dorsally and ventrally, in Polygordius they remain distinct and are separated by the dorsal and ventral mesenteries described above. The cavity of the pre-oral lobe becomes the cavity of the prostomium in the adult. A glance at Fig. 10 will show how the body of the worm is evolved out of the trochosphere.

The Chætopod worms are so called because of the chætæ borne upon the segments of the body. The class Chætopoda is divided into two orders, **Polychæta** and **Oligochæta.** The last named group, of which Lumbricus is a member, have small inconspicuous chætæ unsupported by projections of the body-wall; the prostomial region is much reduced, and the gonads are few in number and restricted to certain segments. The Oligochæta are mostly terrestrial or fresh-water worms, but a few are marine.

The *Polychæta* have numerous chætæ borne upon special processes of the body-wall called **parapodia.** Usually there is a distinct head formed by the fusion of the prostomium with two or three of the following segments. The prostomium usually bears tentacles on its dorsal side and a pair of palps

on its ventral side. The buccal cavity and pharynx are often protrusible and provided with powerful chitinous jaws and plates. The body is segmented, but the internal septa often break down so that there is a continuous cœlomic space surrounding the gut. The gonads are developed from the cœlomic epithelium, and instead of being restricted in position as in the oligochæta, are more scattered over the body, occurring in the cavities of the parapodia, on the course of the oblique muscles which traverse the cœlom, on the course of the blood-vessels, on the walls of the intestine, or even on the body-wall. Nephridia generally occur in all the segments except a few of the most anterior and posterior, but are reduced in number and restricted to certain segments in some forms.

The parapodia are hollow lateral processes of the body. Usually there are no parapodia on the mouth segment (peristomium), but they are present on all the other segments except the last. The parapodia are often double, consisting of a dorsal branch called the **notopodium**, and a ventral branch called the **neuropodium**. Each bears a bunch of chætæ, among which specially large deeply embedded ones are known as **acicula**. Typically both notopodium and neuropodium bear filiform appendages called **cirrhi**; these may be modified in various ways to form branchiæ, or flattened protective scales called **elytra**. Many of the Polychæta pass through a trochosphere stage in development. The trochosphere may be more or less disguised, but in some cases it presents a remarkably close resemblance to the larva of Polygordius.

The *Hirudinea* or leeches are elongated vermiform animals with an external annulation which does not correspond with the internal segmentation. One member of the class has chætæ, but these structures are absent in all other leeches. The cœlom is curiously broken up into a number of spaces and channels, and the remainder of the body-cavity is filled with a peculiar form of tissue known as botryoidal tissue. A description of the medicinal leech is given in Marshall and Hurst's "Elementary Zoology," from which the student can learn all the important facts concerning its anatomy.

The *Echiuroidea* comprise a small group of peculiar vermiform marine animals provided with a pair of hooked chætæ. In the case of two members of the group there is a typical trochosphere larva.

Comparing the different members of the Annelids with one another, one cannot fail to be struck by the general uniformity of structure throughout the group, a uniformity which extends even to developmental details. Metameric segmentation of the body is characteristic of the phylum, and the nervous system, the cœlom and its relation to the nephridia are remarkably similar in the different classes into which it is divided. It is significant, too, that the trochosphere larva is of frequent occurrence, being absent only in those classes which, like the Oligochæta, have taken to a terrestrial or fresh-water habit of life, or, like the Hirudinea, are semi-parasitic. There are weighty reasons for believing that animal life was first developed in the sea, and then spread to fresh waters and dry land. If this belief is well founded, special interest attaches to the trochosphere larva so frequently interpolated in the life-histories of marine annelids. It is regarded by many authors as the representative of the ancestral form from which all the Annelida (and, as we shall see, other groups of animals) have sprung, its absence in terrestrial and fresh-water forms being explained by the unsuitability of the conditions of life to such a form of larval existence. How far the typical trochosphere may be representative of the actual Annelid ancestor is, of course, a question to which we are unable to give a positive answer. It must be remembered that there are many forms of polychæte trochospheres differing from one another in more or less important details, especially in the arrangement of the ciliated rings. Among so many forms it is impossible to fix with certainty upon one and say,—"This is the representative of the Annelid ancestor." Moreover, it is certain that the trochosphere, leading a free existence, and competing with numbers of its own and other kinds for the means of existence, must have been modified in the course of ages by the action of natural selection. Hence we can only say that existing trochospheres enable us to form a general idea of the ancestral form from which all the Annelida are derived, but we must not regard that form as having had an exact resemblance to any one trochosphere. But the development of the worm from the trochosphere proceeds on so nearly exactly the same lines in all cases, or, when the trochosphere form is masked or suppressed, the development offers such obvious resemblances to the course followed—*e.g.* in Polygordius—that we are able to

make definite assertions about the origin of the segmented bodies of worms, and of their most characteristic organs. Thus we always find the mesoblast formed from a pair of cells called mesomeres, which are set apart during the segmentation of the ovum, and give rise to a pair of cellular bands placed right and left of the middle line.

We can assert, as a general rule, that the metamerism of the adult worm is brought about by the segmentation of these bands, and that the cœlom arises as a series of paired pouches through the hollowing out of the segments thus produced. We can assert that the true nephridia are formed from the ectoderm, and thence grow towards and open into the cœlomic pouches, whilst peritoneal funnels functioning as generative ducts are formed as outgrowths from the cœlom towards the exterior. We can assert that the head-cavity or prostomium differs from the paired cœlomic cavities of the body proper, and is in fact the representative of the provisional body-cavity of the trochosphere larva, and therefore a part of the persistent blastocœle. We can assert that the supra-œsophageal ganglion is formed from the apical sense-organ of the trochosphere, and that the ventral cord primitively arose independently of it, as a differentiation of the ventral epiblast forming a thickening which may be called the ventral plate. And, finally, we may fairly assume that the multi-segmented Annelid was evolved from an ancestor whicl showed no more trace of segmentation than the trochosphere itself.

Having satisfied ourselves on these points, we may naturally ask: What is the significance of this metameric repetition of parts which is so prominent a feature in the development and adult anatomy of Annelid worms? What explanation can we give of this peculiar course of evolution resulting in an animal which may be described as consisting of a head-region (prostomium and mouth segment), to which a string of segments is attached? It is, of course, difficult, if not impossible, to give an exact answer to such a question, but the comparison of the adult anatomy of a number of worms enables us to make a plausible conjecture. It has been shown that in Polygordius nearly all the somites contain gonads, that in the Polychæta the generative cells, ova or spermatozoa, may originate from nearly any part of the cœlomic epithelium, and that the generative products, ova and spermatozoa, are invariably derived from that epi-

thelium. It has further been shown (p. 16) that in the redia of the liver fluke there is a body cavity surrounding the gut, and that in this case also reproductive cells are formed from the epithelium lining the cavity, which obviously functions as a generative sac or pouch. Putting all these facts together, the invariable association between body cavity and reproductive cells suggests the explanation that the body-cavity was originally nothing more than a reproductive pouch, just as it is in the redia, and the more complicated arrangements which we see in the Annelids are secondary modifications acquired in the course of evolution in correspondence with the growing needs of the organisms in which they occur.

Adopting this as the most probable explanation of the origin of the cœlom, we may further infer that metameric segmentation owes its origin to a repetitive multiplication of generative pouches. Instances of an analogous multiplication of the generative organs may be found in the Platyhelmia. In the Turbellaria the reproductive organs are multiplied, and in some cases exhibit a paired arrangement. In the Cestoda they are commonly repeated and arranged in series, and in the more elaborate forms each proglottis is a detachable reproductive segment provided with a complete set of gonads and accessory glands with their ducts. The repetition of the reproductive organs, admitting of a vast increase in the fertility of an organism, is clearly of advantage in the struggle for existence, for the more numerous the progeny the greater the chance of the survival of the species. In free-living, non-parasitic animals like chætopod worms it is evident that the conditions of existence would necessitate the development of the muscular, alimentary, nervous, and excretory systems *pari passu* with the multiplication of the generative organs. Integration would go hand-in-hand with repetition of parts.

This explanation of metameric segmentation is, of course, extremely hypothetical, but it accords better than any other with known embryological facts. The reader should be careful to distinguish the facts from the hypothesis. The former, in so far as they are records of truthful observation, will ever be a valuable part of our scientific assets, but the discovery of new facts may make the old hypothesis untenable, and give rise to new interpretations of the old facts.

CHAPTER XX

THE MOLLUSCA

THE earthworm has been taken as an example of a bilaterally symmetrical metamerically segmented cœlomate animal. The snail and the fresh-water mussel are examples of a group which is undoubtedly related to the Annelida, but differs so much from them in organisation that it requires a very extensive study to understand the relationship. The fresh-water mussel is bilaterally symmetrical, the adult snail is not, and neither are metamerically segmented. In both the cœlomic cavity is much reduced, and both possess a number of structural features peculiar to the phylum mollusca. It will be most convenient to begin with the study of the fresh-water mussel, **Anodonta cygnea**, for although this animal is deficient of some characteristic molluscan organs, it serves better than the snail to illustrate the main features of molluscan anatomy. As the anatomy of Anodonta is fully described in Marshall and Hurst's "Practical Zoology," it will not be necessary to give more than a general account of its structure.

Anodonta cygnea is a bivalve mollusc living partially imbedded in mud or sand at the bottom of fresh-water streams and ponds. It is particularly abundant in some canals, such as the Oxford and Birmingham Canal, into which it has made its way from the Thames. Though by no means an active animal, it is capable of ploughing its way slowly through the mud by means of a powerful muscular organ called the **foot**. When alive and undisturbed the two halves or **valves** of the shell are generally kept slightly apart, and the muscular ploughshare-shaped foot may be seen protruding from the blunter anterior end of the shell. When the animal is alarmed the foot is withdrawn, and the two valves are closed and held tightly together by powerful muscles, so tightly that unless the muscles are severed the valves cannot be forced apart without injury. When dead the muscles are relaxed, and the shell gapes. If a

living specimen is kept in an aquarium with sufficient sand or mud at the bottom, it will be seen to bury the anterior and blunter part of its body, leaving the posterior more pointed part sticking up in the water. If a little indigo or other colouring matter is dropped into the water near the posterior end it will be seen to be swept into the cavity of the shell by a current setting inwards just below the pointed end of the shell, and after a while it will emerge from an aperture just above this and be carried away by a current setting outwards. There is, then, a constant stream of water passing through the cavity contained in the shell, the points of entrance and exit of the current being situated close together at the hind end of the body. The current subserves nutrition as well as respiration, for the fresh-water mussel feeds entirely on minute animal and vegetable organisms contained in the water.

An empty shell should be examined before proceeding to the study of the internal structure. The shell is bivalve, consisting of two pieces called **valves**, which are equal in size, similar, and occupy the right and left sides of the animal. Each shell is irregularly ovoid in outline, the anterior end being more rounded, the posterior end more tapering. The line along which the two valves are hinged together is nearly straight, and corresponds to the dorsal surface of the animal. The exterior of each valve is of a dark olive green colour, and marked by a number of concentric lines parallel with the free margin. These represent successive stages of growth, and start from a more or less prominent projection situated close to the hinge line, and much nearer the anterior than the posterior end of the shell. The prominence is called the **umbo**, and is the oldest part of the shell. The internal surface of the shell is white and pearly. If a piece of the shell is ground down on a stone it can easily be seen to be composed of three layers—viz. an outer organic layer called the **periostracum**, formed of a substance called **conchiolin**, which projects as a dark and flexible rim all round the margin of the shell; a middle or **prismatic layer**, formed of the same substance, conchiolin, impregnated with salts of lime arranged in prisms, and an inner layer composed of mother-of-pearl or nacre, hence called the **nacreous layer.** The inner surface of each valve exhibits certain well defined depressions, which mark the attachment of the adductor and retractor muscles to be described presently. The **anterior**

adductor impression is large and oval, close to the anterior border of the shell, and nearer the dorsal than the ventral edge. Close behind it are two smaller impressions, the **anterior retractor,** above and confluent with the adductor impression, the **protractor impression** below and separate from the other two. The **posterior adductor impression** lies some way from the posterior end of the shell near the dorsal border, and immediately in front of it, and rather above it is the smaller **posterior retractor** impression. A curved line running parallel to the ventral border of the shell from the anterior to the posterior adductor impression marks the attachment of the mantle to the shell, and is called the **pallial line.**

The two valves are united along the hinge line by a strong elastic ligament, which is kept stretched when the valves are closed by the action of the adductor muscles; it is due to the elasticity of the hinge ligament that the valves gape when the adductors are relaxed. The shell can be opened by inserting the blade of a knife between the margins of the shell, cutting through the anterior and posterior adductor muscles, and afterwards dividing the hinge ligament. It will then be seen that each valve of the shell is lined by a sheet of soft muscular tissue, which hangs down like a curtain from the dorsal region of the animal. This curtain is the **mantle,** a very important and characteristic molluscan organ. On lifting up the near flap of the mantle it can be seen that it is really a fold of the dorsal wall of the animal, and that with its fellow it encloses a considerable space—the **sub-pallial space** or **mantle-cavity.** The line along which the mantle is attached to the body-wall is shown in fig. 11. It starts high up at the anterior end above the anterior adductor muscle; curving round the front of this muscle, it runs nearly straight backward for a short distance, bends sharply upwards, and then descends with a long slope to the bottom of the posterior adductor. Turning round the posterior adductor, it runs forward again towards the dorsal surface, and ends near the posterior end of the hinge line. The free margin of the mantle is thickened and muscular, its edge forming a rather prominent grooved border. The edges of both flaps are free—*i.e.* they are not joined to one another except at the extreme posterior end, where they are fused together opposite the posterior adductor muscle for about half-an-inch. The edges then separate and run forwards a little

further, as two rims bordering a narrow groove. Immediately below the point of fusion the edge of each mantle-flap is thickened and pigmented, and slightly scolloped out, and below this point again the thickened edges are slightly scolloped out and bear a fringe of small tentacles. In this manner two slit-like passages are left between the opposed edges of the mantle. The lower passage, bordered by tentacles, is the **inhalant**, the upper one is the **exhalant aperture**.

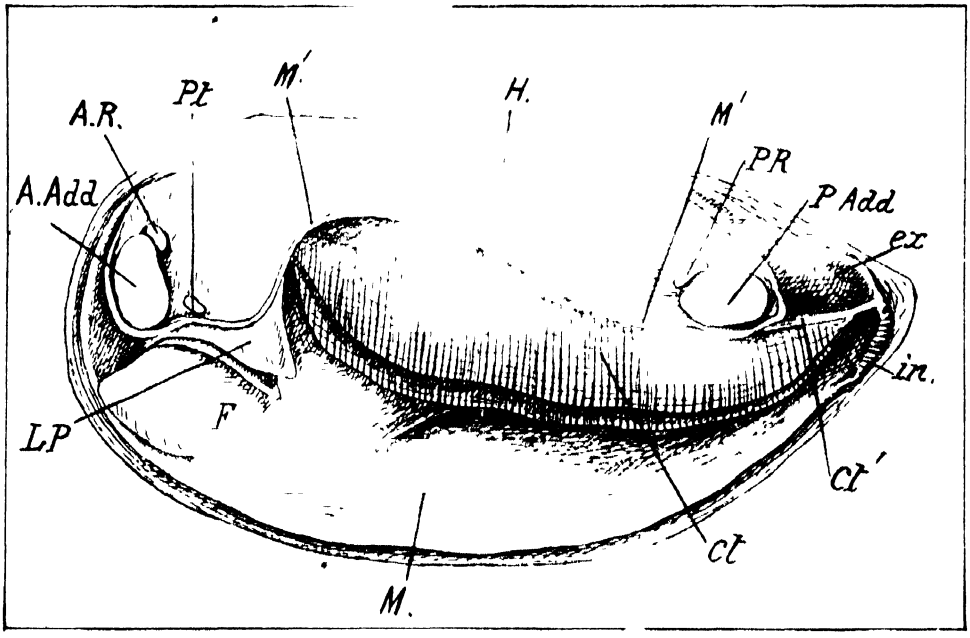


Fig. 11

Anodonta cygnea. The animal is shown lying in the right valve of the shell. The left valve and the left mantle-flap have been removed. *A.Add*, anterior adductor muscle; *A.R*, anterior retractor muscle; *Ct*, gill or ctenidium; *Ct'*, posterior extension of the ctenidia forming the septum dividing the branchial from the cloacal chamber; *ex*, exhalant orifice; *F*, foot; *H*, heart seen through the transparent pericardial wall; *in*, inhalant orifice; *L.P*, labial palps; *M*, right mantle-flap; *M'*, line of attachment of left mantle-flap which has been cut away; *P.Add*, posterior adductor muscle; *P.R*, posterior retractor muscle; *Pt*, protractor muscle of the foot.

The outer and middle layers of the shell are secreted by the epithelium of the thickened border of the mantle. The inner nacreous layer is secreted by the whole of the outer surface of the mantle. On cutting away the mantle-flap of one side, the general shape of the animal and some of its more important organs lying in the mantle-cavity are exposed. Ventrally and anteriorly is the triangular muscular **foot**, its anterior margin

passing into the body just below and behind the anterior adductor muscle. Posteriorly the foot is overlapped by the anterior ends of a pair of long flat lamellate structures shaped somewhat like pea-pods. These are the outer and inner gill-plates. On turning them up the posterior end of the foot is seen to be prolonged into an elongate muscular band which may be traced backwards to near the hinder border of the posterior adductor. There it bifurcates, and its right and left branches are attached to the valves of the shell at the spots which have been described as the impressions of the posterior retractors of the foot. The whole of the dorsal and dorso-lateral integument, excepting a prominent ridge along the mid-dorsal line, is thin and transparent, and some of the viscera can be clearly seen through its walls. In the mid-dorsal region there is a considerable space, looking dark when seen through the thin body-wall. This space is the pericardium, and it is traversed by the posterior part of the gut, the latter being wrapped round by the ventricle of the heart.

There is no head, the fresh-water mussel, in common with all bivalve or lamelli-branchiate molluscs, being destitute of any definite prostomial region. The anterior adductor muscle, which lies where the head should be, must not be regarded as representing the head region, but rather as a special muscular development of the anterior part of the mantle. The body of the mussel, then, consists of a foot below, and a shapeless dorsal region containing a large part of the viscera. This latter region we may call the **visceral hump**. The wall of the visceral hump is folded downwards on each side of the body to form the extensive mantle-flaps, which secrete the bivalve shell.

The anterior ends of the gill-plates are attached to the body-wall in the bay formed by the curved line of attachment of the mantle a little way below the umbonal region. Just in front of and below the anterior ends of the gills is a pair of triangular flaps lying below the attachment of the mantle. The apices of the triangles look downwards and backwards, their bases run downwards and forwards from the anterior ends of the gills to the angle between the upper anterior edge of the foot and the anterior adductor muscle. These flaps are called the **labial palps**. Their edges are continued anteriorly round the front edge of the foot, and pass into two similar palps on the opposite side of the body. The labial palps form the upper and lower borders

of a deep groove into which the mouth opens in the median line just below the angle formed by the foot and anterior adductor muscle. The anus lies in the mid-line posteriorly, just above and behind the posterior adductor muscle. The mouth is a simple round aperture destitute of jaws or any other masticatory apparatus. It leads into a fairly wide but rather

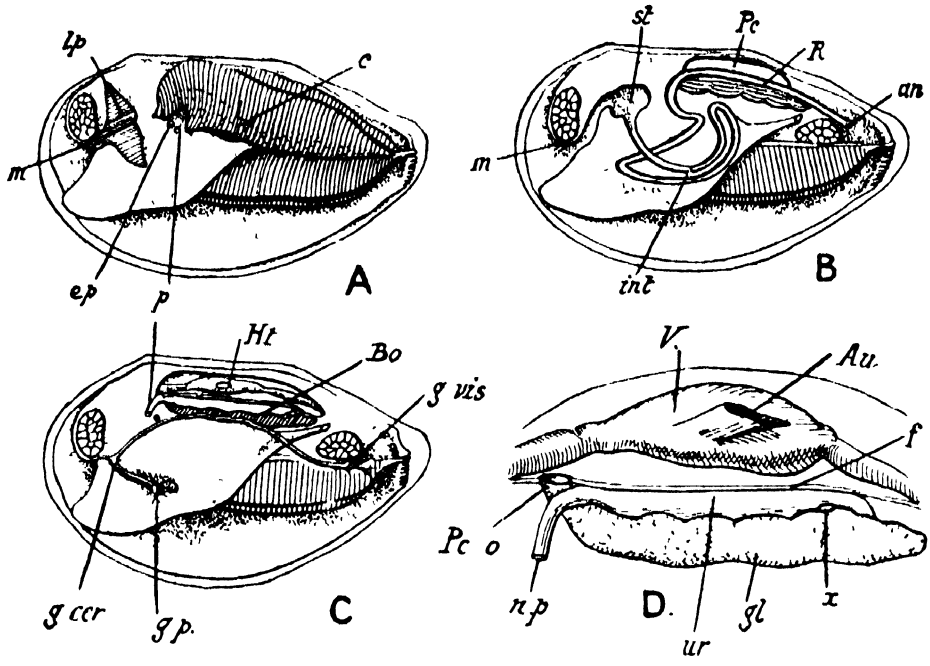


Fig. 12

Diagrams of the anatomy of *Anodonta cygnea*. *A*. The animal lying in the right valve of the shell, the left mantle-flap cut away, and the left gill turned up to show the cleft *c* between the inner gill-plate and the foot. *B*. Diagrammatic longitudinal section of the body to show the course of the alimentary canal. *C*. Dissection to show the nervous system, the position of the heart and pericardium, and the excretory organs. *D*. An enlarged view of the heart, pericardium, and excretory organ (organ of Bojanus). *an*, anus; *Au*, auricle; *Bo*, excretory organ; *c*, cleft between foot and inner gill-plate; *f*, floor of pericardium; *gl*, glandular part of excretory organ, *ep*, *np*, excretory pore; *g cer*, cerebral ganglion; *g.p*, pedal ganglion with otocyst; *g.vis*, visceral ganglion pair; *Ht*, heart; *int*, intestine; *l.p*, labial palps; *m*, mouth; *p*, genital pore (the lower reference line should point to *ep*.), *Pc*, pericardium; *Pc.o*, opening of glandular parts of excretory organ into the pericardium; *R*, rectum; *st*, stomach; *ur*, ureter or non-glandular part of the excretory organ; *V*, ventricle of heart; *x*, opening of glandular part of excretory organ into the ureter.

short œsophagus, and this enlarges to form a stomach in the upper and anterior part of the visceral mass. The intestine passes from the lower side of the stomach, is thrown into several coils in the upper or visceral part of the foot, then turns upwards, runs back in the mid-dorsal line through the

pericardial-cavity and opens at the anus (fig. 12, *B*). The stomach and coiled part of the intestine are embedded in a mass of glandular tissue, which consists largely of the numerous lobes of the large digestive glands which pour their secretion by several ducts into the stomach.

The gills of the fresh-water mussel are as much concerned with nutrition as with respiration. There is a pair of gill-plates on either side of the body. Their anterior attachments have already been noted. From thence they pass obliquely backwards and downwards beneath the posterior adductor muscle, and project beyond the posterior end of the body, their hinder ends being continued into a short horizontal septum, which is attached to the sides and edges of the mantle, and separates the inhalant from the exhalant aperture. In this manner the mantle cavity is divided into a large **branchial cavity** below, and a smaller **cloacal cavity** lying behind and above the posterior adductor muscle. The water taken in at the inhalant aperture of the mantle has to pass through the passages of the gills before it can reach the cloacal chamber and be discharged through the exhalant aperture. The gill-plates and the passages formed by them are complex structures requiring careful study. Each gill-plate is made up of a number of vertical bars, whose free surfaces are covered by a richly ciliated columnar epithelium. The bars are elongate oval in transverse section, and their inner sides are thickened and fused together at irregular intervals so as to form a plate perforated by numerous apertures. Further than this, each gill-bar is bent back at a sharp angle, the bars of the outer gill-plate being bent outwards, and those of the inner gill-plate inwards. The reflected parts of the gill-bars are fused together in the same manner as the vertical descending portions, and thus each gill-plate is made up of an outer and an inner lamella, each lamella being formed by the fusion at irregular intervals of a number of gill-bars lying side by side. The external and internal lamellæ are also connected by a number of vertical ridges parallel to the gill-bars, and containing blood-vessels. Viewed in transverse section, the four lamellæ of the two gill-plates of one side present the figure of a W, and the upper limbs of the W are attached to the mantle, body-wall, or gill-plate of the opposite sides of the body in the manner shown in the diagrams (fig 13, *A*, *B*, and *C*). The outer lamella of the outer gill-plate is attached by the whole

ength of its upper edge to the mantle just below the line of ttachment of the latter. The inner lamella of the outer gill-plate is attached throughout the whole length of its upper edge o the corresponding edge of the outer lamella of the inner gill-plate. The fused edges are somewhat thickened, and in the egion of the foot are firmly attached to the body-wall. The nner lamella of the inner gill-plate is attached in its anterior portion for a distance of about three-quarters of an inch to the body-wall. Its upper edge then becomes free, leaving a slit-

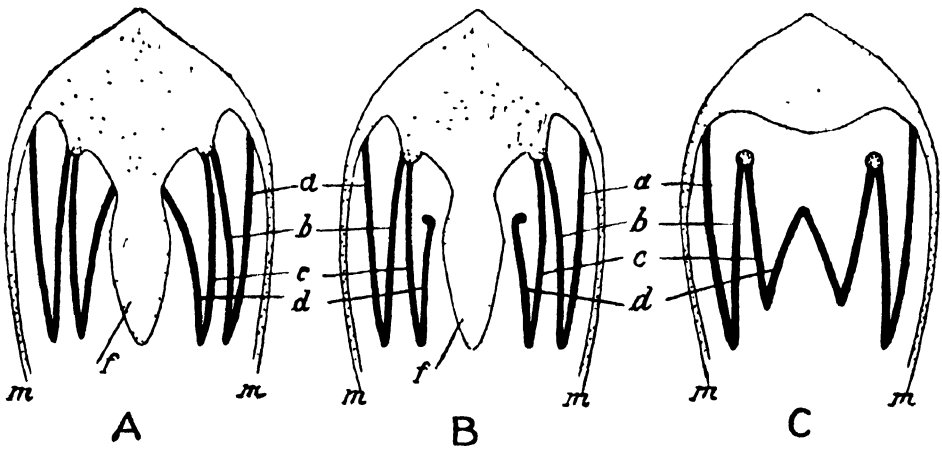


Fig. 13

Diagrammatic transverse sections through *Anodonta cygnea* to show the attachment of the gill-lamellæ to one another, to the mantle, and the foot. *A*, section through the anterior part of the foot: *B*, through the hinder part of the foot; *C*, through the region posterior to the foot. *a*, outer lamella of outer gill-plate; *b*, inner lamella of outer gill-plate: *c*, outer lamella of inner gill-plate; *d*, inner lamella of inner gill-plate; *f*, foot; *m*, mantle.

ike space between itself and the posterior moiety of the foot, nd behind the foot its upper edge is firmly fused with the cor-esponding edge of the corresponding lamella of the other side of the body. Thus, in the anterior part of the gills there are our **supra-branchial passages**, two on each side of the body, each enclosed between the outer and inner lamella of a gill-plate. In the posterior region of the foot the four passages are still present, but the inner passage of either side communicates by a slit-like aperture with the branchial chamber, owing to the detachment of the inner lamellæ of the inner gill plates from he body-wall. Behind the foot, where the gills project freely backwards into the mantle-cavity, the four branchial passages open into one another above as is shown in fig. 13, *C*, and pass

posteriorly into the cloacal chamber. A probe, passed backwards into the slit between the foot and the gills, will traverse the supra-branchial passage of one side and emerge in the cloacal chamber just beneath the posterior adductor muscle. The cilia which cover the gill-bars cause a constant stream of water to flow through the inhalant aperture into the branchial chamber. The water passes either through the pores in the gill-plates or by way of the slits between the foot and the inner lamella of the inner gill-plates into the supra branchial passages and thence into the cloacal chamber and out by the exhalant aperture. Any infusoria, diatoms, and other minute organisms contained in the water are swept by the cilia of the gills towards the labial palps. These, being richly ciliated, sweep the organisms onwards down the grooves between the upper and lower palps, and so into the mouth. The structure and disposition of the gills of Anodonta, as described above, are very complicated and difficult to understand. But in many bivalve molluscs (the common sea mussel, *Mytilus edulis*, is a good example) the structure is less complicated, and by a comparison of these and many other forms we are enabled to understand how the complexity in Anodonta has come about. The primitive gill of a mollusc has been compared to a comb with a double series of teeth, and hence has been called a **ctenidium**. It may be more aptly compared to a feather having a central axis and a number of filaments arranged along two opposite sides of the axis like the barbs of a feather. The axis is attached to the body-wall, and its other end bearing the plume projects freely backwards into the mantle-cavity. This condition is realised in a large number of living molluscs. If now, as frequently happens, the axis lies close to the body-wall, and is fused to it for the greater part of its length, the two rows of filaments will droop vertically downwards in the mantle cavity, and will represent the outer and inner gill-plates. This condition again is represented in living molluscs. Further, if the filaments become very long, are bent upwards again at an acute angle, and are connected together, they will form two flat gill-plates, each comprising an outer and an inner lamella. In the sea mussel, *Mytilus edulis*, the gills are in this condition, the filaments being loosely locked together by patches of stiff cilia so that they can be divided with great ease from one another. The descending and ascending limbs of the filaments repre-

senting the outer and inner lamellæ are also united from place to place by hollow outgrowths called **inter-lamellar junctions,**

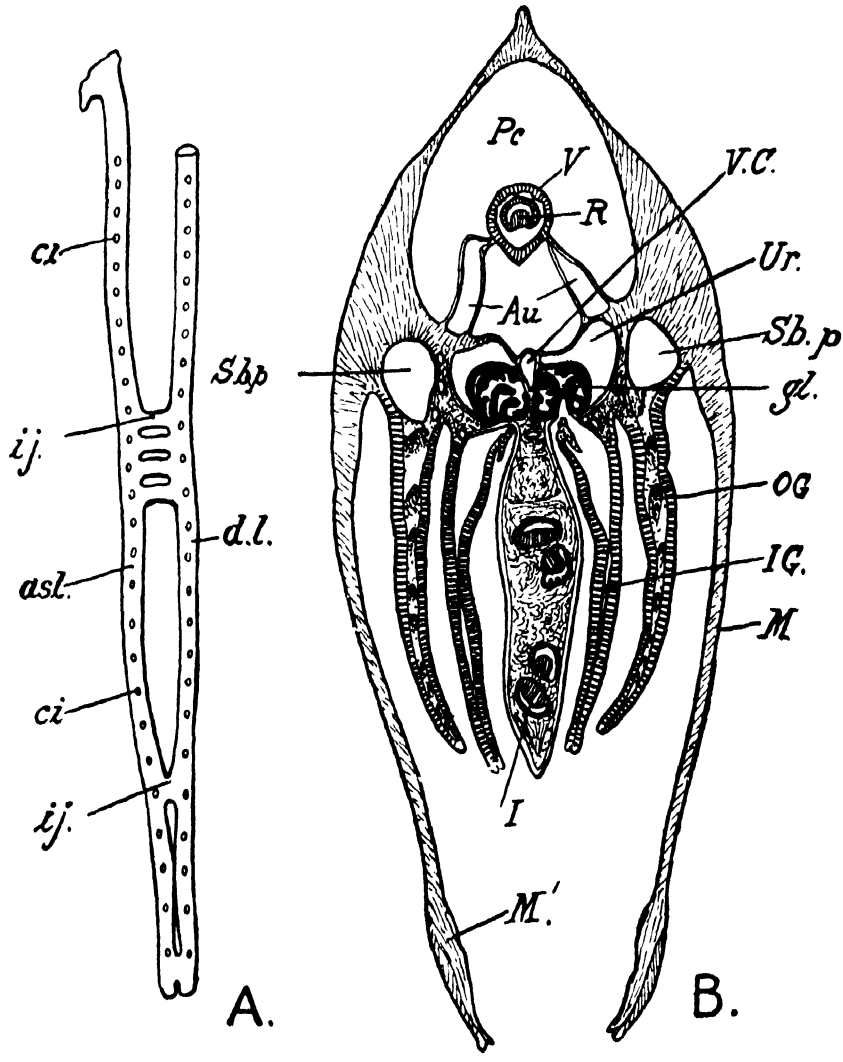


Fig. 14

A. Diagram of the hinder face of a single gill filament of *Mytilus edulis*. *dl*, descending limb of the filament; *asl*, ascending limb; *ij*, inter-lamellar junctions; *ci*, ciliated junctions. *B*. Vertical section through the body of *Anodonta cygnea* in the posterior region of the foot. *Pc*, pericardial cavity; *V*, ventricle; *Au*, auricles; *R*, rectum wrapped round by the ventricle; *VC*, vena cava below the pericardial floor; *Ur*, ureter or non-glandular part, and *gl*, glandular part of the excretory organ; *Sb.p*, supra-branchial passages; *OG*, outer gill plate; *IG*, inner gill plate; *M*, mantle; *M'*, thickened muscular border of the mantle; *I*, intestine, of which there are several coils in the foot. (*B*, original; *A* after Holman Peck.)

which clearly correspond to the vertical partitions connecting the outer and inner laminæ in Anodonta (fig. 13, *A*). By

fusion of adjacent filaments, increased development of the inter-lamellar junctions, and fusion of the upper ends of the ascending limbs (outer lamellæ of the outer gill-plates, inner lamellæ of the inner plates) with the mantle or body-wall, or gill of the opposite side, as the case may be, brings about the condition found in Anodonta.

The colourless and corpusculated blood circulates in a number of irregular lacunar spaces in the gills. From thence it is returned by numerous vessels running for the most part in the interlamellar junctions to a large pair of vessels running along the bases of the outer lamellæ of the outer gills. These efferent branchial veins carry the blood to a pair of wide, thin-walled triangular sacs, the **auricles** of the heart, and these in turn empty the blood into a median muscular ventricle of which the position has already been noted. The two auricles lie right and left of the ventricle, and traverse a considerable space, the **pericardial cavity**, in which the ventricle also lies. The ventricle is wrapped round the rectum, and gives off an anterior and a posterior arterial vessel, the branches of which carry the blood to the different parts of the body. The blood from the foot, the visceral mass and the hinder part of the body is collected into a large vessel lying in the middle line below the floor of the pericardial cavity. Thence it is conducted by **afferent branchial** vessels to the gills and from the gills back to the heart again. The blood from the mantle does not pass through the gills, but is returned direct to the efferent branchial vessels, and so to the heart. This indicates that the mantle is an auxiliary respiratory organ.

The wide pericardial cavity in which the heart and rectum lie represents the perivisceral cœlom in the adult animal. In the remainder of the visceral mass, in the foot and gills, the perivisceral cœlom has disappeared and its place is taken partly by the viscera including the large digestive glands, partly by the extension of lacunar blood-spaces running between the viscera and the muscle fibres of the foot. The pericardial cavity, however, has no connection with the generative organs, and therefore represents only a part of the cœlomic space. The remaining part is represented by the gonads, which will be described later. The cœlomic nature of the pericardial cavity is shown both by its not containing blood and by its relations to the excretory organs.

The excretory organs of Anodonta are often called the **organs of Bojanus**. They lie under the floor of the pericardial cavity and are paired, consisting on each side of a bent tube opening by one end into the pericardial cavity, by the other end into the branchial cavity. The pericardial opening of each side is a semilunar slit in the floor of the anterior end of the pericardial cavity, below and rather to the side of the rectum, just behind the point where the latter passes first through the pericardial wall. The slit leads into a wide saccular tube whose walls are thrown into a number of folds and are lined with a black glandular epithelium. This glandular part of the excretory organ runs backwards below the floor of the pericardium, and opens, a little way in front of its posterior end, by a small aperture into a wide, non-glandular tube or excretory duct, which runs forward, above and to the outer side of the glandular part, as far as the anterior end of the pericardium, where it turns sharply downwards to open by a small excretory pore between the two laminæ of the inner gill-plate, about one-eighth of an inch in front of the place where the inner lamina becomes free from the body-wall. The genital ducts open by small pores just behind the excretory pore of each side. The nervous system consists of three pairs of ganglia united by nervous cords. The most anterior pair is called the **cerebral ganglion-pair**, but it probably is a composite ganglion formed by the fusion of at least two pairs of ganglia found in other molluscs. Each cerebral ganglion lies at the hinder border of the mouth and below and in front of the protractor muscle. It is of a deep orange colour, and is connected with its fellow by a nerve running above the mouth. Nerves connecting two ganglia of the same pair are called commissures, and this is accordingly the **cerebral commissure**. Several nerves are given off from the cerebral ganglia to the anterior part of the body and to the labial palps. Nerves connecting ganglia of different pairs are called connectives, and two such nerves are given off from each cerebral ganglion. The **cerebro-pedal connectives** pass backwards and downwards to the **pedal ganglia**, which are situated close together in the foot, at about one-third of the length of the foot from the anterior edge, and just above the junction of the visceral with the muscular part of the foot. Several nerves are given off from the pedal ganglia, one of which passes back from each

ganglion to the auditory organ or **otocyst**, a small vesicle lying a little way behind the ganglion and containing a calcareous concretion or **otolith**. The **cerebro-visceral connectives** run backwards on each side through the visceral mass, traverse the lower surface of the glandular part of the excretory organ, and end in a pair of closely apposed ganglia on the under surface of the posterior adductor muscle. These **visceral-ganglia** are only covered by a layer of columnar epithelial cells, supposed to represent a patch of sensory epithelium very generally associated with the ctenidia of molluscs, and known as the **osphradium**.

The sexes in Anodonta are separate. The gonads in both sexes are simple, consisting of a mass of ovarian or testicular tubes ramifying in the visceral mass. The openings of the gonads have been described; they are just below the excretory pores. The ova are swept into the cloacal chamber by the incurrent stream of water, are fertilised there, and afterwards passed into the inter-lamellar spaces of the outer gill-plate, where they undergo segmentation and go through the early stages of development. Thousands of embryos may be found in this position in the summer and autumn months, but they do not develop further, and remain in the brood-pouch formed by the inter-lamellar chamber till the following spring. They then emerge as peculiar larval forms known as **Glochidia** which are retained by the parent in the brood-pouch until some fish passes in the neighbourhood, when they are at once ejected. A Glochidium differs a great deal from an ordinary molluscan larva. It has a shell composed of a pair of triangular valves, hinged together along the base line. The apex of each triangular valve is turned inwards and forms a stout hook, the outer surface of which is covered with spines. There is only a single adductor muscle at the anterior end of the body, and immediately behind this is a gland which secretes a long sticky thread called the **byssus**. There is no foot, but the mantle lobes are large and thick, and each is furnished with four peculiar sensory organs in the form of tufts of bristles seated on as many large epidermic cells. The mouth is represented by a stomodæal invagination, and there is a small gut or enteron, but no anus. Traces of the nervous system are present, and a pair of lateral pits may possibly represent transitory sense organs. Posteriorly there is a tuft of cilia at

the edges of the mantle. The Glochidia, when a fish is in their neighbourhood, rapidly open and close their valves, and some have the luck to attach themselves to a fish by the sticky byssus thread and then fix themselves to the gills, fins, or tail by their hooked valves. They become imbedded in the integument of

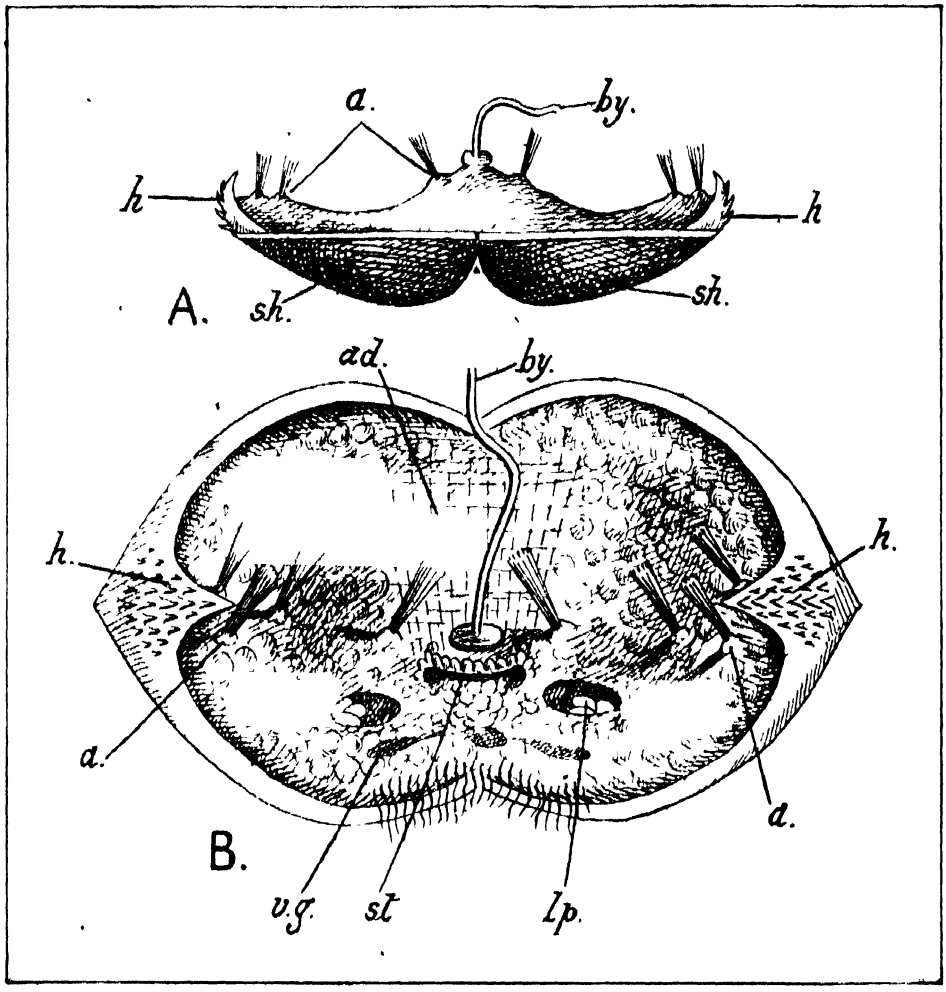


Fig. 15

Two views of the glochidium larva of *Anodonta*, after Schierholtz. *A*, from the side, *B*, from below. *a,a*, bunches of setæ, *ad*, the single adductor muscle; *by*, byssus; *h,h*, hooks on the valves of the shell: *lp*, lateral pits; *sh*, shell; *st*, stomodæal invagination; *vg*, visceral ganglion.

the fish and remain as parasites on it for several weeks, during which time they undergo further development. The foot is formed as an outgrowth behind the mouth, and the gills are developed as a series of finger-like outgrowths on each side of and somewhat behind the foot. The larval adductor

muscle atrophies and is replaced by the permanent anterior and posterior adductors, and the valves of the permanent shell are formed inside those of the larval shell. At the end of from three to twelve weeks the young Anodonta, now developed beyond the glochidium stage, quits the fish on which it has been parasitic, and continues to grow and develop for another three or four years before it attains to sexual maturity.

The temporary parasitism of the glochidium larva on fishes is an interesting example of adaptation to the conditions of existence. The slow moving Anodonta, ploughing its way through the mud and sand at the bottom of rivers, is incapable of extensive migrations, and its progeny would soon accumulate in such vast numbers in a given locality that they would be unable to subsist there if they were not provided with some means of dispersal. The glochidium, by attaching itself to the fins of fishes, is carried, it may be, to a considerable distance from its birthplace, and when it quits its host it has a better chance of colonising some fresh ground where the competition for the available food supply is less severe. Fresh-water mussels have been observed to spread rapidly into newly made canals, and their journeys in these new waters can only be accounted for by the opportunities for dispersal afforded by the temporarily parasitic habits of their larvæ.

Marine Lamellibranchs have free swimming ciliated larvæ known as **veligers.** A fresh-water mussel, *Dreissensia polymorpha*, allied to Anodonta, has a veliger larva, and its young are therefore more readily dispersed. But the minute ciliated larvæ could not swim against the stream, yet Dreissensia has been known to spread from the brackish waters at the mouth of the Rhine up as far as Mannheim, and from Mannheim up the Main into the Main and Danube Canal, and now exists in the Danube itself where it was formerly unknown. In this case, the adult fixes itself by a byssus to various objects, among others to the bottoms of boats, and thus has been carried long distances against the stream. It has been carried in the same manner up the Thames, and is abundant in the Oxford and Birmingham Canal. The two cases are instructive. Anodonta has long been an inhabitant of fresh water, and its development has been profoundly modified in connection with its habitat. Dreissensia has only recently taken to a fresh-water life, and still lives in brackish waters in estuaries. It

still retains the veliger larva characteristic of its marine relations, yet has been able, by taking advantage of the opportunities afforded by navigation, to spread itself far inland, and even to attain to waters separated from its original habitat by the whole width of a continent.

CHAPTER XXI

THE SNAIL—HELIX POMATIA AND HELIX ASPERSA

THE fresh-water mussel, whose anatomy has been described in the last chapter, is an example of a bilaterally-symmetrical, headless, lamellibranchiate mollusc. It has a median anterior mouth, a median posterior anus, a median dorsal heart enclosed in a pericardial chamber, a pair of auricles, a pair of much modified gills or ctenidia, a pair of excretory organs, a pair of gonads, and a pair of well-developed mantle lobes which secrete the right and left valves of the shell. The snail is an example of a large class of molluscs in which the primitive symmetry of the body has been to a great extent lost through distortion of the visceral mass, with the consequence that the organs of the right side of the body have disappeared. It further differs from the fresh-water mussel and all lamellibranchiata in having a distinct head-region, a complex rasping organ or **odontophore** in the buccal cavity, and a shell which is all of a piece and coiled into a spiral. These features are characteristic of the class **Gastropoda**, to which the snail belongs in common with limpets, ormers, winkles, whelks, sea-slugs, and a host of other forms. Some of the Gastropoda have shells, some have not; most of them live in the sea and breathe by gills or ctenidia, but others, like the snail, are terrestrial, have lost their ctenidia and breathe air contained in a pulmonary chamber. Some gastropods have lost the ctenidia, excretory organs and gonads of one side of the body, in others the primitive paired arrangement is retained: in fine, the class exhibits every variety of structure, and it is only by the comparison of a large number of forms that we are able to form an idea of what may be called the typical Gastropod organisation.

It is beyond the scope of this work to enter into the minute detail and comparison necessary to the complete understanding of Gastropod anatomy, but as the common snail does not

illustrate some important characters of the class, it will be necessary, from time to time, to refer to two equally common species of fresh-water snails, *Paludina vivipara* and *Limnea stagnalis*. The common garden snail, **Helix aspersa**, is found everywhere in England; the edible snail, **Helix pomatia**, is tolerably abundant in limestone districts, and is cultivated in large quantities on the Continent for culinary purposes. Both species are herbivorous, and their depredations are only too well known to gardeners. They rasp holes in the leaves and succulent plants by means of the odontophore, an organ beset with numerous minute teeth which will be described further on. The expanded snail is familiar enough to everybody. It has an oblong body, the base of which is thick and muscular and forms an elongate sole-like foot. At the anterior end is a distinct head-region, bearing two pairs of **cephalic tentacles**. The spiral shell rests on the middle of the back of the extended animal, its opening directed downwards and its apex turned to the right. The visceral hump is permanently concealed in the shell and is coiled in a spire corresponding with that of the shell, but it does not occupy the whole of its cavity, for the shell is capable of containing the whole animal when retracted.

Let us first examine the shell. It consists of from four and a half to five **whorls** increasing in size from the summit to the base. The whorls are in close contact with one another, and each lower whorl overlaps the one next above it by more than half its extent. The lines of junction between the whorls are called **sutures**. The cavity of the shell is continuous—*i.e.* it is not broken up into chambers by partitions as are the coiled shells of the cephalopodous mollusca (*Nautilus*, *Spirula* and *Ammonites*). The axis of the shell is occupied by a spirally twisted central pillar, the **columella**, which is hollow and opens below by a narrow fissure called the **umbilicus**. The opening of the shell is called the **aperture**; it is round, and its lips are even and without a notch. The outer lip of the aperture is distinguished as the **peristome**; it is thickened, and its lower end is reflected so as to partially conceal the umbilicus. The inner lip is formed by the body whorl and columella. The surface of the whorls is marked by a number of transverse ridges or growth lines and there are also several coloured lines which wind longitudinally round the spiral. At

the apex the whorls end in a small rounded extremity called the nucleus; this is the oldest part of the shell. A transverse section shows that the shell is made up of three layers, similar to those of the shell of Anodonta. In an expanded snail a thick fleshy rim may be seen projecting beyond the

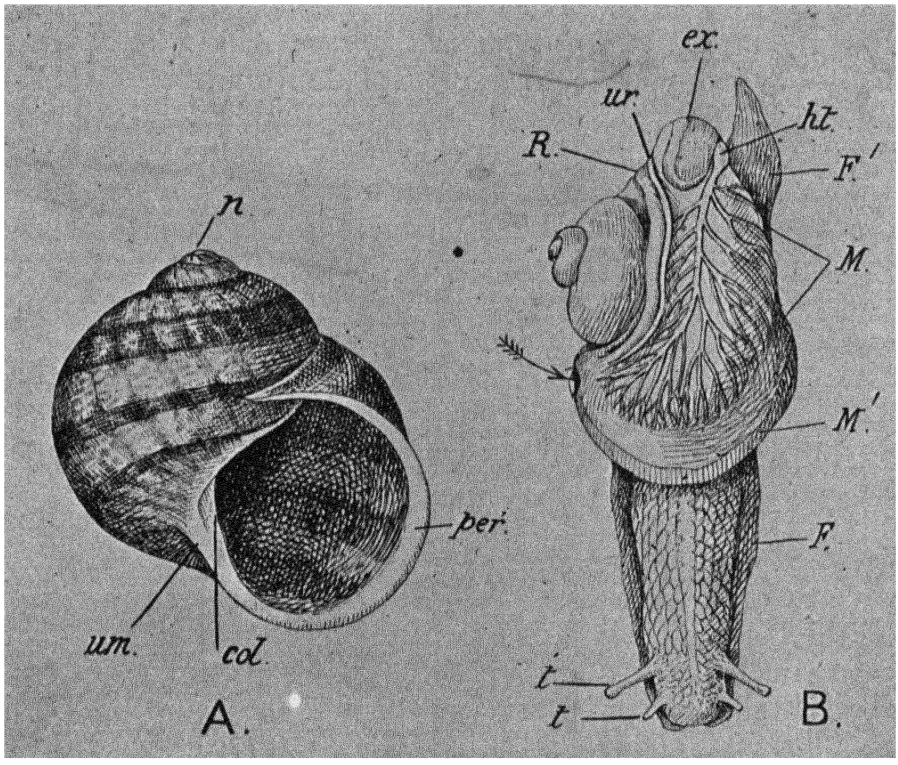


Fig. 16

A. Shell of *Helix aspersa*. *col*, columella; *um*, points to the position of the umbilicus, *n*, nucleus; *per*, peristome. *B.* Dorsal view of *Helix aspersa* after removal of the shell. *ex*, excretory organ; *F*, foot; *F'*, hinder part of foot (metapodium); *ht*, heart; *M*, mantle with blood-vessels ramifying in it; *M'*, thickened border of mantle or collar; *R*, rectum; *t*, larger or ocular tentacle; *t'*, smaller tentacle; *ur*, ureter.

aperture of the shell. This is the **collar**, which secretes the outer layer or periostracum and the middle or prismatic layer of the shell. The inner nacreous layer is formed by the integument covering the visceral hump. Thus the shell increases in size by additions to its aperture, and in thickness by additions to the nacreous layer. If the shell is held with

the apex upward and the aperture towards the observer, the aperture is on the right, and if one follows the whorls from above downwards they are coiled round to the right. Such shells are called **dextral**. Most Gastropod shells are dextral, but in some cases the spiral is reversed, and such shells are called **sinistral**.

A snail drowned in warm water will generally die expanded, and it may then be twisted out of its shell, care being taken to detach a stout band of muscle on the right side from the columella.

The external features may now be examined. The mouth opens in the middle line anteriorly on the ventral surface of the head, and is overhung by an upper lip. There are two pairs of cephalic tentacles. The anterior pair is placed low down on the sides of the head above the corners of the mouth. The posterior pair is longer, and is placed on the sides of the head above and behind the anterior pair; each bears an eye at its extremity. Both pairs of tentacles can be invaginated and withdrawn into the body by means of special muscles. A round opening on the side of the head below the right posterior tentacle is the **generative opening**; a shallow groove leads back from it along the dorsal surface. The collar is the thickened edge of the mantle, which, in Helix, is not reflected, so as to cover any part of the external surface of the shell. The thickened mantle edge is firmly fused to the body-wall all round the base of the visceral hump, except in one place on the right side, where there is a large round aperture leading into a spacious chamber, the so-called **pulmonary cavity**. In Paludina the mantle edge is not fused with the body-wall along the front and sides of the visceral hump, and consequently there is a wide passage into a cavity lying between the visceral hump and the mantle, which is evidently the mantle cavity. Paludina is aquatic, and the mantle cavity contains a gill or ctenidium, but Helix is terrestrial, has lost its ctenidium, and the mantle cavity is modified to form a pulmonary chamber suitable to aerial respiration.

The anus is a slit-like opening lying below and to the right of the large respiratory aperture, and close above it is a still smaller excretory opening. The position of the anus on the right anterior side of the body indicates clearly the distortion undergone by the upper part of the snail's body. In lamellibranchs the anus is median and posterior, but in gastropods

the visceral hump has not only been coiled into a spire, but has been rotated from left to right about an axis which may be described as dorso-ventral, through an angle of nearly 180°, so that the anus and other organs are shifted round, and organs which were primitively on the left side are actually on the animal's right, and those primitively on the right side are actually on the animal's left. But in the snail, as in most gastropods, the primitive left organs have disappeared, and those of the primitive right side are placed, as a result of the rotation of the visceral mass, on the left of the original middle line indicated by the rectum.

The pulmonary chamber is triangular in outline, and lies on the first turn of the spirally-coiled visceral hump. Its roof, formed by the mantle-flap, is thin, semi-transparent, and richly supplied with blood-vessels. Its floor is stout, muscular, and convex. By contraction of the muscles the convex floor is flattened, the body is protruded rather further out of the shell, and the cavity of the pulmonary chamber being enlarged, air rushes in through the respiratory aperture. On relaxation of the muscles the body is slightly retracted within the shell, the floor resumes its convex shape, the cavity of the pulmonary chamber is reduced, and a part of the air is forced out. The thin roof of the pulmonary chamber enables one to see the organs contained in it in their natural position. The rectum runs from the anus along the right upper side of the triangular chamber, and passes at its apex into the second whorl of the visceral mass. The excretory organ lies in the roof of the chamber to the left of the rectum, and occupies nearly the whole of the apical posterior part of the mantle. It consists of a glandular and a non-glandular portion, the former being a rather large triangular sac with folded walls lined by a glandular epithelium. Its left side lies close against the pericardium, and forms a deep bay to receive it. The non-glandular part of the excretory organ begins at its anterior end, runs back parallel to the glandular part up to the apex of the pulmonary chamber, then turns sharply forward and runs close alongside and dorsal to the rectum to open at the excretory pore just above and to the left of the anus. The glandular part of the excretory organ opens by a very small **reno-pericardial canal** into the pericardial cavity. It is obvious that the excretory organ of the snail is homologous with the organs of Bojanus of Ano-

donta, and both have the same fundamental structure as the nephridium of the earthworm, consisting of a coiled tube, divisible into a glandular and non-glandular part, and opening by one end into the cœlom (pericardial cavity in molluscs), and by the other end to the exterior. But close as the resemblance is, it is probable that the two organs are not homologous, for the excretory organs of molluscs appear to arise as outgrowths of the cœlom, whereas the nephridia of chætopods are ingrowths from the external epiblast which meet and acquire openings into the cœlom. Hence we have refrained from calling the former organs nephridia. It should be noticed that there is only one excretory organ in the snail, and that it lies to the left of the rectum. If the visceral hump were rotated in the direction of the hands of a watch so as to bring the anus back into a median and posterior position the excretory organ would lie on its right. It is, in fact, the primitive right organ, its left-hand fellow having disappeared.

A large blood-vessel runs in the wall of the mantle-cavity parallel to and not far distant from the rectum. It is formed by the union of numerous branches which ramify in the mantle, being particularly numerous in its right side. The main vessel is known as the **pulmonary vein**. It receives a considerable branch from the excretory organ, and runs into the pericardium, expanding within it to form the thin walled **auricle**. The auricle is succeeded by a pear-shaped muscular **ventricle**, from which an artery passes backwards into the visceral mass. Immediately on entering the visceral mass the artery divides into two branches, one of which ascends the spire and supplies the visceral hump with blood. The other branch turns forward and supplies the head and foot. The details of this circulatory system may be studied in Marshall and Hurst's "Practical Zoology," and will not be described here, but it is important to notice that the branches of the arteries open into a system of large and irregular lacunar spaces, from which the blood is afterwards collected by definite venous trunks, and carried to the pulmonary chamber. The anterior part of the gut and the generative organs lie in a large space of this kind, which might easily be mistaken for cœlom. It is not cœlom, however, but a greatly enlarged blood space which has encroached upon and taken the place of cœlom, the latter being represented only by the small pericardial cavity and the cavity

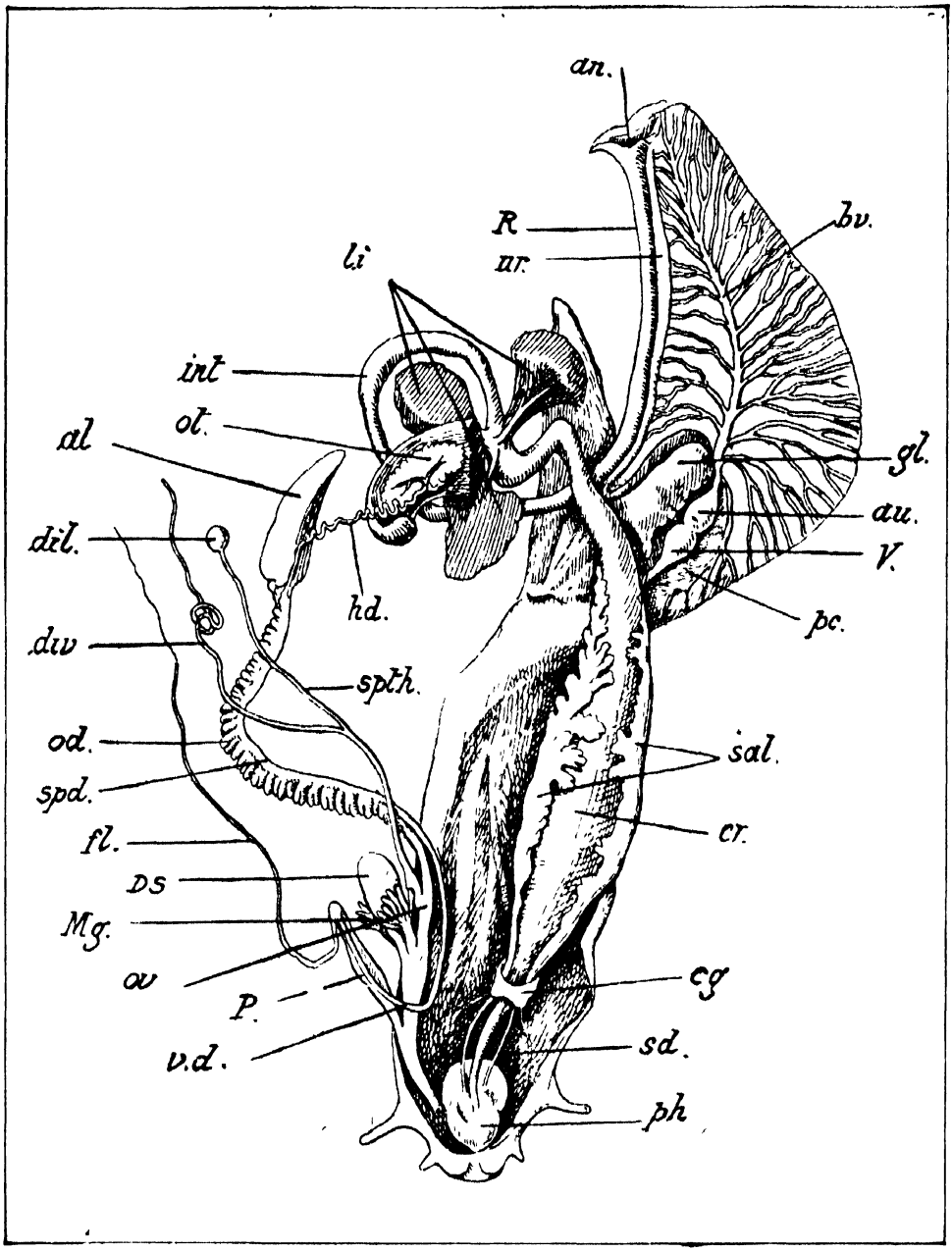


Fig. 17

A dissection of *Helix aspersa* from the dorsal surface. The roof of the mantle-cavity has been cut through near the collar and thrown back; the generative organs are displayed on the left, and the alimentary tract on the right of the figure. *al*, albumen gland; *an*, anus; *au*, auricle; *bv*, blood-vessels in mantle; *cg*, cerebral ganglion; *cr*, crop; *dil*, globular dilatation on spermatheca; *div*, diverticulum of spermatheca; *Ds*, dart sac; *gl*, glandular part of excretory organ; *hd*, hermaphrodite duct; *fl*, flagellum of penis; *int*, intestine; *li*, liver; *Mg*, mucous glands; *od*, oviducal portion of conjoined genital duct; *ov*, oviduct; *ot*, ovotestis; *P*, penis; *pc*, pericardium; *ph*, pharynx; *R*, rectum; *sal*, salivary glands; *sd*, duct of salivary gland; *spd*, spermiducal portion of conjoined genital duct; *spth*, spermatheca; *ur*, ureter; *v*, ventricle of heart; *vd*, vas deferens.

of the gonad, probably also by the glandular part of the excretory organ.

The upper whorls of the visceral hump are almost entirely occupied by the lobes of a very large pair of digestive glands, but they also contain several coils of the gut and parts of the reproductive system. The mouth opens into a rather large pharynx, the ventral wall of which bears the rasping organ or **odontophore**. The pharynx is succeeded by an œsophagus, which dilates to form a large thin-walled **crop**, its upper part lying in the first whorl of the visceral mass. The crop is succeeded by an intestine, which takes several turns in the spire, and eventually passes forward as the **rectum** and opens at the anus. The digestive gland is paired, and its ducts open into an enlarged section of the intestine often called the "stomach." The snail is also provided with a pair of **salivary** glands, large white lobed masses attached to the sides of the crop with slender ducts running forward along the sides and opening into the pharynx.

The odontophore in the floor of the pharynx is a very characteristic organ, and requires a special description. The posterior part of the floor of the pharynx is produced backwards into a hollow finger-shaped diverticulum, the cavity of which is lined by an epithelium continuous with that of the pharynx. The epithelial cells lining the ventral wall of the diverticulum secrete a chitinous band, armed on its upper surface with a number of minute rasp-like teeth arranged in transverse rows. The chitinous band is called the **radula**, and the diverticulum the **radula-sac**. In front of the radula-sac the floor of the pharynx is thickened so that it projects like a cushion into the cavity of the pharynx, and the radular ribbon is continued forwards over the surface of the cushion. In the substance of the cushion there is a piece of cartilage firmly attached to the surface on which the radula rests. This cartilage can be moved backwards and forwards by special muscles, and the whole apparatus can be moved forwards into the mouth opening and the radula made to move to and fro with a rasping action by the alternate action of the anterior and posterior muscles attached to the cartilage. The radula works against a so-called jaw, which is really a chitinous curved bar traversing the upper part of the oral aperture, with a ridged posterior surface. As the radula is worn away in front it is replaced by growth from

behind, just as a finger nail is continually replaced by growth forward from its bed. The chitinous teeth of the radula are formed from the epithelium lining the extreme hinder end of the radula sac. In the snail the radular teeth are minute, directed backwards and similar, and are regularly arranged in numerous transverse rows (fig. 18, *B*). In many gastropods the teeth of any single row differ considerably in size and shape according to their position, and one may distinguish central, lateral, and marginal teeth, but the teeth of successive rows are always similar. It would be out of place to enter upon a description of the various kinds of radular teeth found in gastropoda, but they are used as a basis of classification, and are therefore of some importance.

The nervous system of Helix is much concentrated, and its central parts form a collar which, when the animal is extended, surrounds the anterior part of the œsophagus, but when the animal is retracted the pharynx is pulled back through it. The nerve collar is covered by a thick coat of connective tissue, which must be removed before the constituent ganglia and nerve cords can be clearly seen, and even then the subœsophageal ganglia are so closely massed together that their outlines are difficult to determine. Hence it will make the description clearer if we begin with the study of the nerve system in *Limnæa stagnalis* (fig. 18, *B*). In this freshwater snail there is a large pair of **cerebral ganglia** situated above the œsophagus, and connected by a short and broad **cerebral commissure**. Nerves are given off anteriorly to the cephalic tentacles, and two nerves pass forwards on the sides of the pharynx, and there enlarge to form a pair of **buccal ganglia,** connected by a transverse commissure passing under the pharynx. Posteriorly, two pairs of stout connectives pass backwards from the cerebral ganglia. The lower and inner pair are the **cerebro-pedal connectives**, and they enter a large pair of **pedal ganglia** lying ventral to the œsophagus. The pedal ganglia are united by a **pedal commissure**, and give off stout pedal nerves to the muscles of the foot. The upper and outer pair of connectives are the **cerebro-pleurals.** They join a pair of **pleural ganglia** lying below the œsophagus, but above and to the outside of the pedal ganglia. The pleural are united to the pedal ganglia by short **pleuro-pedal connectives**, and they further give off posteriorly a pair of nerves which, after a

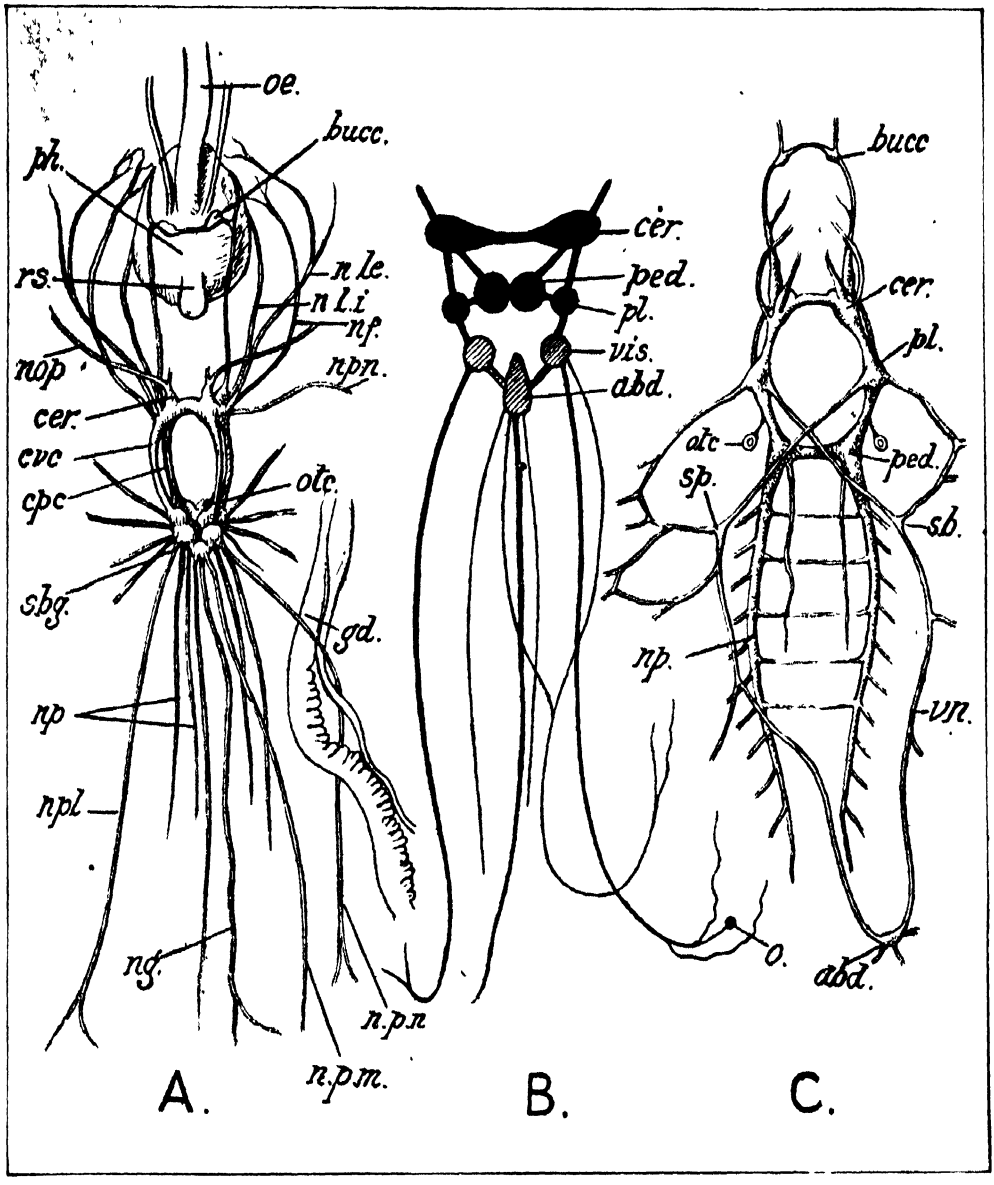


Fig. 18

A. Nervous system of *Helix aspersa*, an example of the euthyneurous condition in which the pleural, visceral, abdominal and pedal ganglia are fused to form a subœsophageal ganglion mass. *B*. Nervous system of *Limnæa*, an example of the short-looped euthyneurous condition in which the ganglia are separate (after de Lacaze Duthiers). *C*. Nervous system of *Paludina vivipara*, an example of the streptoneurous condition. *abd*, abdominal ganglion; *bucc*, buccal ganglia; *cer*, cerebral ganglia; *cpc*, cerebro-pedal connective; *cvc*, cerebro-pleural connective; *gd*, conjoined genital duct; *nf*, facial nerve; *ng*, genital nerve; *nle*, exterior labial nerve; *nli*, internal labial nerve; *nop*, optic nerve; *np*, pedal nerves; *npl*, left pallial nerve; *npm*, median pallial nerve; *npn*, penial nerve; *npr*, right pallial nerve; *o*, osphradium; *oe*, œsophagus; *otc*, otocyst; *ped*, pedal ganglion; *ph*, pharynx; *pl*, pleural ganglion; *rs*, radula-sac; *sbg*, subœsophageal ganglion mass; *sb*, sub-intestinal ganglion; *sp*, supra-intestinal ganglion; *vis*, visceral ganglion, *vn*, visceral nerve.

very short course, enter a large pair of **visceral ganglia**, and are continued beyond the visceral ganglia into a large median **abdominal ganglion**. The whole system of visceral and abdominal ganglia with the nerves connecting them and the pleural ganglia is known as the **visceral loop**. The visceral ganglion of the right side gives off a long nerve to a ganglion underlying a small patch of sensory epithelium (osphradium) in the respiratory chamber. This is the **osphradial ganglion.**

In the snail the cerebral and buccal ganglia have much the same relations as in Limnæa. The connectives passing round the œsophagus to the subœsophageal mass are double, and represent the pleural and pedal connectives. The subœsophageal mass is divided into an upper and a lower portion by an artery passing through it. The lower portion represents the closely opposed pedal ganglia from which stout nerves pass to the foot. The upper portion represents the fused pleural, visceral and abdominal ganglia. Nerves are given off from it to the viscera, and a specially stout nerve passes to the generative organs (fig. 18, *A*).

In Helix the visceral loop is obsolete, in Limnæa it is short, and the paired ganglia are symmetrically arranged. Such a disposition is called **euthyneurous** (**orthoneurous** by Continental authors). But in *Paludina* the visceral loop is long, and has been involved in the rotation of the visceral hump to such an extent that it is twisted into a figure of eight, the originally right visceral ganglion lying to the left and above the gut, the original left visceral ganglion lying to the right and below the gut (fig. 18, *C*). This disposition of the visceral nerve cords is known as **streptoneurous** (foreign authors **chiastoneurous**). The univalve gastropods are divisible into two well-marked orders according as they are streptoneurous or euthyneurous, and Paludina and Helix may be taken as examples of the two groups.

The eyes of the snail can only be studied by means of sections. They are highly developed optical organs, each consisting of a hollow vesicle or eyeball lined by an epithelium which is transparent in front, but modified in the posterior part of the vesicle to form a number of retinal cells embedded in pigment. The retinal elements are turned towards the cavity of the vesicle, and the optic nerve does not perforate the retina as in the vertebrate eye, but spreads out on the posterior surface of the eyeball. The cavity of the eyeball is occupied by

a transparent cuticular lens. The epithelium at the extremity of the larger tentacles is further modified and provided with numerous nerve end-organs, which have been proved to subserve the function of smell.

The auditory organs consist of a pair of **otocysts** embedded in the pedal ganglia. They are innervated from the cerebral ganglia, and the very fine auditory nerves pass down on either

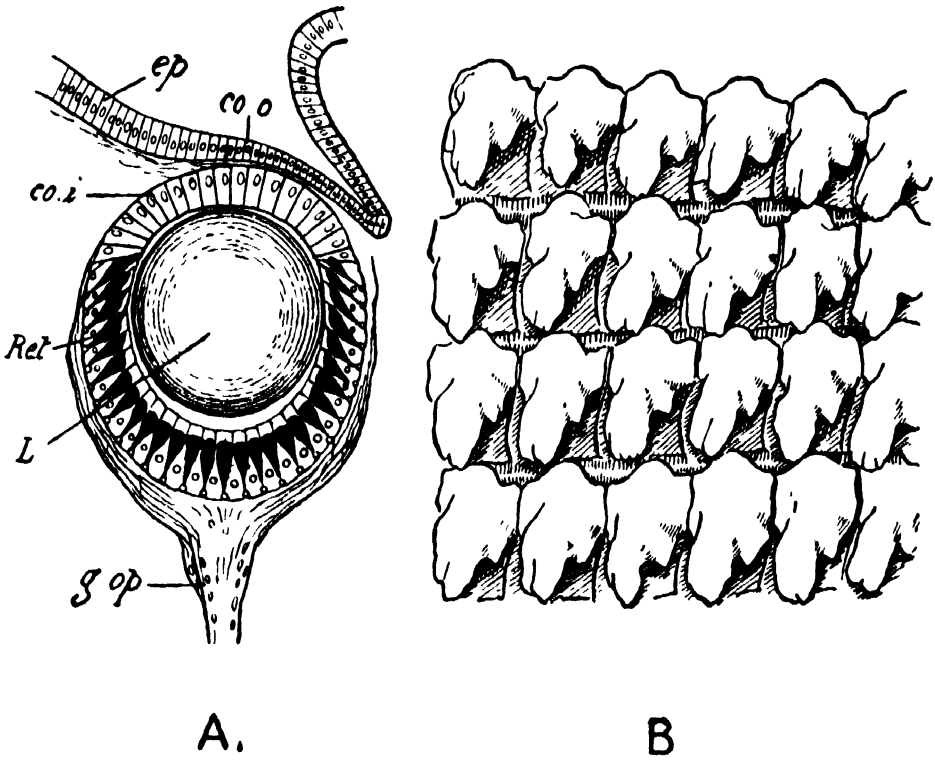


Fig. 19

A. Eye of *Helix pomatia*, after Carriere. *co.o*, outer corneal layer; *co.i*, inner corneal layer; *ep*, epithelium of tentacle; *g.op*, optic ganglion; *L*, lens; *Ret*, Retina. *B*. Radular teeth from the odontophore of *Helix aspersa*, highly magnified

side between the closely apposed cerebro-pleural and cerebro-pedal connectives. To see the otocysts, the pedal ganglia should be carefully cleared of connective tissue, and made transparent by mounting in glycerine.

The snail is hermaphrodite (monœcious) but not self-fertilising, and, as is usual in such cases, the generative organs are extremely complex. The essential organ of reproduction, the **ovotestis** (sometimes called the hermaphrodite gland), is a small yellowish body embedded in the digestive gland in

the uppermost whorl but one of the spire. It consists of a number of digitiform follicles, lined by a germinal epithelium which produces both ova and spermatozoa in each follicle. The generative ducts and accessory organs of the snail are shown in fig. 17. The ova and spermatozoa when ripe pass outwards through the **hermaphrodite duct**, a single much-convoluted tube, the distal end of which enters the substance and receives the ducts of the large conical **albumen gland**. From this point onwards the ova and spermatozoa travel by different passages, firstly along the different sides of a widish duct incompletely divided by a longitudinal partition into a sacculated oviducal and a narrower spermiducal channel. After a course of about three inches this conjoined duct divides to form a separate oviduct and sperm duct, and finally the two, after entering into relations with various accessory organs, unite again to open at the common genital pore.

The oviduct is short and thick walled, and is generally spoken of as consisting of the oviduct proper and the **vagina**, the latter being that portion of the tube which lies between the openings of the accessory female organs and the genital pore. The accessory organs are the **dart-sac**, the **mucous glands** and the **spermatheca**. The first named is a thick-walled cylindrical sac opening into the vagina. It contains a quadrangular calcareous spicule, the so-called dart or *spiculum amoris* which is used in copulation. The mucous glands open into the vagina on either side of the opening of the dart-sac. Each gland consists of a number of simple finger-like glandular tubes which unite to form the mucous duct of either side. The spermatheca is a long, slender outgrowth of the vagina lying alongside of the conjoined oviduct and sperm-duct. Its upper end is dilated into a globular vesicle, and in *Helix aspersa* it also presents an elongated diverticulum on its course.

The male accessory organs are the **penis** and **flagellum**. The former is nothing more than a muscular portion of the sperm-duct which is capable of being protruded through the genital pore and withdrawn by means of a special retractor muscle. The shape and relations of the long tubular flagellum can best be studied in the figure.

The spermatozoa before extrusion are lodged in a **spermophore**, an elongate plate of hardened mucus formed in the flagellum and rolled up to form a sort of cylinder in which the

spermatozoa are lodged. In copulation the spermo[illegible] one snail is transferred to the spermatheca of the other, w[illegible] after a while it is dissolved and the spermatozoa are stored [illegible] the terminal dilatation. As the ova pass down the vagina they are fertilised by spermatozoa injected from the spermatheca and thus cross-fertilisation is effected.

Snails deposit their eggs in the ground in masses during the summer months, and so effectually conceal the holes in which they have laid them that it is almost impossible to discover them. After the ground has been softened by a shower of rain, however, it is not uncommon to find a snail partially buried in the ground. It is then engaged in excavating a hole in which to lay its eggs, and if disturbed will quit the spot without effecting its purpose. But the place may be marked without disturbing the animal, and on the following day the eggs may be found some three or four inches below the surface. They are about the size of peas, with hard calcareous shells, and as many as sixty or eighty may be deposited in a single hole. Though the egg is large the ovum itself is minute the greater part of the contents of the egg-shell consisting of albumen, which serves as food for the embryo during development. The most important phases of development take place within the egg-shell, and the young snail is not hatched till it has assumed the characters of the adult.

Though the ova of *Helix* and its allies, the slugs, are fairly convenient objects for study, the details of their development can hardly be understood without reference to the larval forms characteristic both of marine lamellibranchs and gastropods. In these animals the young quit the egg at a very early stage in the form of a free swimming ciliated larva whose organisation is so similar to that of the trochosphere larvæ of Polygordius and polychæte worms that we cannot regard the resemblances as accidental, but as evidence that the Annelids and Molluscs have descended from a common ancestor. We may therefore omit the development of the snail in order to study the more characteristic and important life-history of a marine gastropod. The details of development, however, differ so considerably in different species that it will serve our present purpose best if we try to gain a general idea of gastropod development without confining our attention to any particular species.

The ova of those gastropods which are not abundantly furnished with food yolk are divided by two successive constrictions into four large blastomeres of nearly equal size, and these by three successive processes of unequal division give rise to twelve smaller blastomeres which lie like a cap on the upper pole of the embryo (fig. 20, *A*). The smaller cells are called **micromeres** and the larger **macromeres.** The micromeres increase by division, while the macromeres remain inactive, and the result is a hollow sphere or blastula with a tolerably large segmentation cavity or blastocœle. The roof of the blastula is formed by the micromeres, the floor by the four macromeres. The macromeres now divide and form a plate at the lower pole of the embryo, which is presently folded inwards into the blastocœle so that a two-layered embryo or gastrula is produced. During the process of gastrulation two cells derived from one of the macromeres pass into the blastocœle and lie side by side between the invaginated macromeres and the body-wall. Their position marks the hinder end of the embryo, and a comparison with the developmental history of Lumbricus shows that they agree in origin and position with the two large mesomeres which are formed at a corresponding period in that animal. They are, in fact, the primary mesoblast cells or mesomeres of the gastropod, and they give rise by repeated unequal divisions to two rows of cells, the mesoblast bands, extending forwards between the outer layer or epiblast and the inner layer or hypoblast of the two-layered embryo. During the process of gastrulation (or even during the blastula stage in the limpet), the epiblast cells situated at the equator of the embryo become larger and more columnar than their neighbours and develop tufts of large cilia. There may be one, two, or three rows of such cells forming a complete girdle round the embryo and dividing it into an upper and a lower hemisphere. In many cases an apical tuft of cilia is developed at the pole of the upper hemisphere, and there may be lateral subsidiary tufts in its neighbourhood. A similar tuft formed in the neighbourhood of the hinder end of the blastopore in the lower hemisphere is known as the anal tuft. In the first stages of gastrulation the gut opens by a wide gastrula mouth or blastopore at the lower pole of the embryo. As development proceeds, the blastopore becomes narrowed and slit-like, and is carried by the unequal growth of

the lower hemisphere round to one side, the ventral side of the future animal. In some cases—*e.g.* the limpet—the elongated blastopore closes up from behind forwards, only the anterior portion persisting as the mouth, which is then situated close under the ciliated ring on the ventral surface. In other cases the anterior part of the blastopore closes up, and the posterior end persists as the anus (Acmæa). It seems probable that in the most primitive condition the blastopore closed up in the middle, its anterior and posterior ends persisting as the mouth and anus respectively, and for the convenience of description we will assume that this is the case. The embryo now escapes from the egg-membranes and swims freely in the water by means of its ciliated band. It is obviously a trochosphere larva, with a ciliated girdle lying in front of the mouth and dividing the body into an upper or pre-oral and a lower or post-oral hemisphere. The mouth opens just below the ciliated band and leads into a gut which in actual cases generally ends blindly, but eventually establishes another connection with the exterior by an outgrowth which meets the epiblast at the posterior pole, fuses with it, and gives rise to the anus. The larva further resembles the trochosphere in possessing a pair of mesoblast bands, and in some forms the resemblance is strengthened by the appearance of a pair of provisional excretory tubules, in the form of a row of perforated cells, ciliated internally, and opening to the exterior by excretory pores situated on the ventral sides of the body just behind the velum. The position of these provisional excretory tubes, however, is different from that of the pronephridia of the Annelid trochosphere, and most authors describe them as arising from the mesoblast, whereas in Annelids they arise from ectoderm cells.

In Molluscan terminology, the upper hemisphere of the larva is called the **velum**; the pre-oral ciliated ring is the **velar ring**, and the whole larva is more usually called a veliger than a trochosphere. It is only in a few cases, such as the limpet, that a really Annelid-like trochosphere is developed. In most instances the similarity is to some extent masked by the precocious appearance of two very characteristic Molluscan organs, the **foot** and the **shell-gland**. The former is indicated by a projection in the mid-ventral line between the mouth and the anus. It therefore occupies the place of the central part of

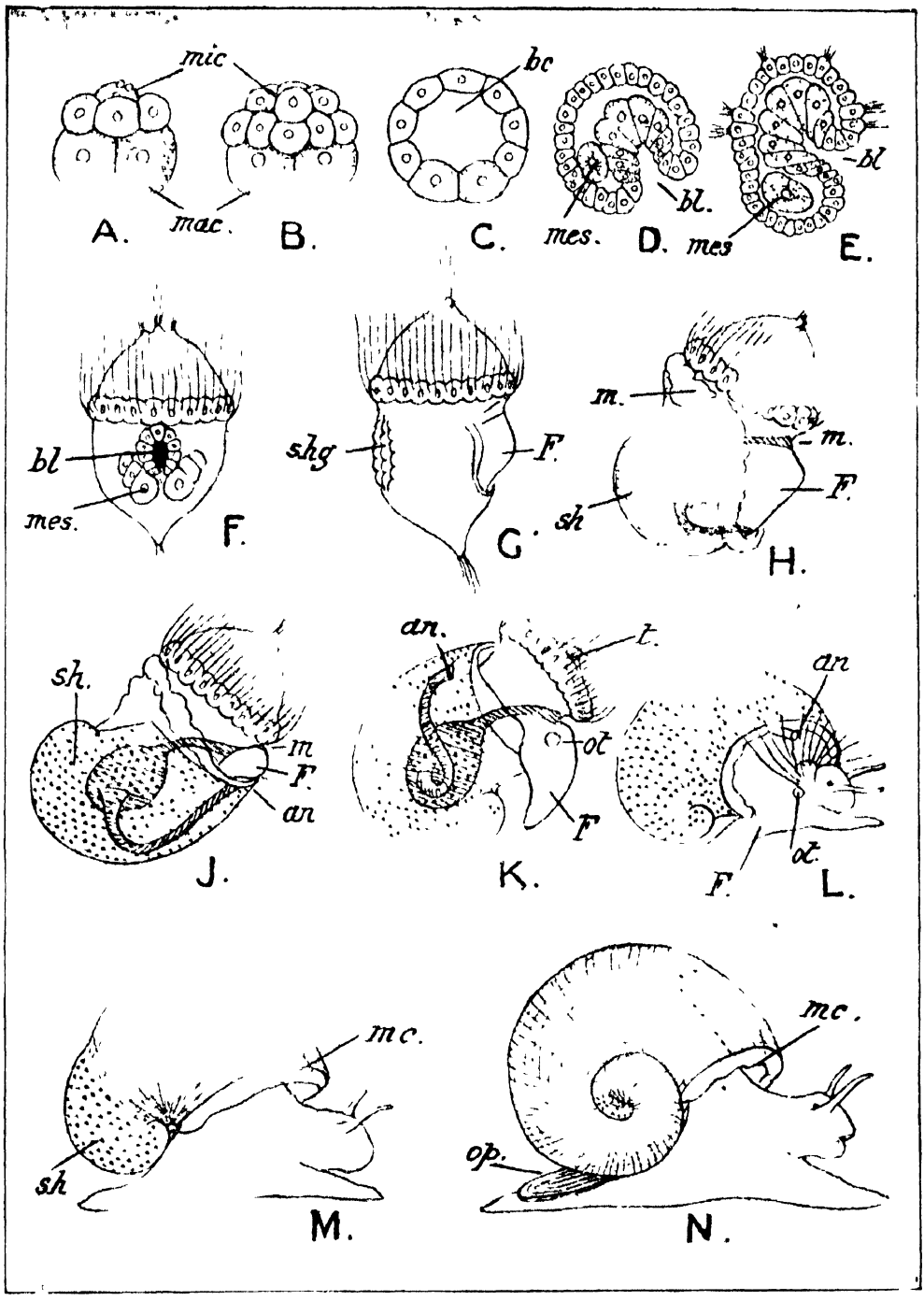


Fig. 20

A, *B*, diagrams of the segmentation of a gastropod. *mac*, macromeres; *mic*, micromeres. *C*, optical section of a blastula at the end of segmentation. *bc*, blastocœle. *D*, *E*, two stages of gastrulation. *bl*, blastopore; *mes*, mesomere. *F*, ventral view, and *G*, side view of the trochosphere of a streptoneurous gastropod. *bl*, blastopore; *F*, foot; *mes*, mesoblast bands; *shg*, shell gland. *H* and *J*, further stages showing the development of the mantle *m*, and the larval shell *sh*, and the approximation of the mouth *m*, to the anus, *an*. *K*, stage immediately after the larval torsion, showing the altered relations of mouth and anus. *t*, cephalic tentacles; *ot*, otolith; *F*, foot. *L*-*N*, final stages of development, showing the atrophy of the velum, the growth of the permanent shell, and the development of the foot and head (the larval shell is shaded with dots, the permanent shell with lines). *mc*, mantle cavity; *op*, operculum. (Figs. *G*-*N* after Boutan.)

the blastopore which has closed up. The shell-gland appears as a patch of columnar ectoderm on the dorsal surface opposite to the foot, the patch being generally invaginated to a greater or less extent.

It is, however, in the subsequent phases of growth that the Mollusc deviates most markedly from the Annelid plan of development. One may attribute a large part of the divergence to the behaviour of the mesoblast. Instead of elongating, thickening, and segmenting as in the Annelid, the mesoblast bands of the Mollusc break up into a number of amœboid cells which insinuate themselves everywhere in the space between the walls of the gut and the body wall. But two more or less distinct cell masses remain at the posterior end of the body, right and left of the anus in those cases in which the posterior part of the blastopore persists as the anus. These cell masses eventually become hollow and form a pair of vesicles, whose cavities represent the true cœlom. Usually the left vesicle degenerates while the right vesicle increases in size and gives rise to the pericardium, the excretory organ, and the reproductive organs.

Meanwhile the growth of the shell has materially altered the external aspect of the larva. The shell-gland is evaginated, and gives rise to a larval shell, which covers the dorsal surface like a cap and grows enormously in size relatively to the other parts of the body. The larval shell is generally more or less conical or helmet-shaped, and its rounded extremity curves over towards the anterior aspect of the body. The mouth of the shell is surrounded by a prominent thickening of the body-wall, representing the mantle. As a result of the excessive growth of the shell on the dorsal side, the anus, which was originally terminal, becomes pushed over to the ventral surface, and as growth proceeds it is pushed further and further forwards till eventually it lies not far behind the mouth, being separated from the latter orifice by the foot, which has not as yet undergone any considerable increase in size. As a consequence of this approximation of the mouth and anus the alimentary canal has been flexed in the manner shown in fig. 20, *H* and *J*, but the larva is still bilaterally symmetrical, and there is no sign as yet of any torsion of the visceral mass lodged in the shell.

By this time several important structures have made their

appearance. In those gastropods in which the anterior part of the blastopore persists as the mouth, an invagination of the epiblast, known as the **stomodæum**, carries the primitive mouth deeper into the body, and an outgrowth from the ventral wall of the stomodæum marks the future radula-sac. In those forms in which the anterior end of the blastopore closed up, the posterior part remaining as the anus, a similar stomodæal invagination grows inwards towards the gut, and fusing with it gives rise to the permanent mouth. The anus, if not previously present, has been formed by an outgrowth of the gut, which met and fused with an epiblastic invagination near the anal tuft of cilia. In the velum a pair of eyespots has been formed right and left of the apical tuft of cilia, and in connection with the eyespots is a pair of epiblastic thickenings representing the cerebral ganglia. A similar pair of epiblastic thickenings representing the pedal ganglia have been formed on the surface of the foot at a little distance behind the mouth, and connected with these is a pair of invaginations which will give rise to the otocysts. The pleural and visceral ganglia do not become apparent till a later stage. In the streptoneurous gastropods the larva, on attaining this stage of development, projects its foot and velum far out of the shell, and twists them round through an angle of 180°. In this movement the relative positions of foot, mouth, and velum are not altered, nor are the relations of the organs contained in the visceral mass, but the intermediate part of the body is twisted in such a manner that the anus, which previously was on the ventral side, now becomes dorsal, and the rounded extremity of the shell which previously inclined to the dorsal and anterior side is now directed posteriorly and ventrally. The change only occupies a few minutes, but the torsion is permanent, and it is by this remarkable and rapid metamorphosis that the symmetrical larva is transformed into the asymmetrical adult.* It seems probable that the primordia of the pleural and visceral ganglia and connectives, though not distinguishable, must be localised in the epiblast previous to the metamorphosis, for otherwise it would not be possible to account for their share in the torsion.

The further development of the larva into the adult form will be best understood by a study of fig. 20, *K* to *N*. The foot

* See L. Boutan. Asymétrie des Mollusques Gastropodes ; Archives de Zoologie expérimentale et générale. 3me Ser. vol. vii. 1899.

increases greatly in size, acquires a flat, sole-like surface, and is used as an organ of locomotion. The velum is reduced in size relatively to the remainder of the body; a pair of cephalic tentacles grows out of its centre, the velar ring of cilia atrophies and disappears, and the velar region is converted into the prostomial or head region of the adult. The thickened edge of the mantle secretes a permanent shell which grows out all around the border of the larval shell, and increasing rapidly in size, soon replaces the latter, but for some time the larval shell may be distinguished as a small appendage at the apex of the permanent shell. It is during this further period of growth that the shell and the visceral mass contained in it assume a spiral form. The larval shell is symmetrical, and before the torsion it is **exogastric**—*i.e.* its mouth is below and its apex or coiled end is on the anterior face of the visceral mass. After the torsion it is **endogastric**—*i.e.* its mouth is above and its coiled end on the posterior face of the visceral mass, but it is still symmetrical, and its shape has not been in any way affected by the torsion. It is clear, then, that the spiral coil of the adult shell is not directly attributable to the torsion of the body. But a glance at fig. 20, *L*, shows that when the animal begins to creep on its foot the relatively large and unwieldy shell must fall over to one side or other of the foot. It falls over to the right side, or, rather, the foot places itself obliquely to the aperture of the shell, so that the latter lies on its right side, and in consequence of this asymmetry the permanent shell in course of growth becomes spirally coiled.

In the snail and other euthyneurous gastropods there is no larval torsion, and consequently no twisting of the visceral nerves. None the less, the anus opens forwards on the right side of the body, and the visceral mass has undergone a corresponding twist, without involving the nerve centres. The manner in which this twisting of the visceral hump and spiral coiling of the shell are brought about may be gathered from an inspection of fig. 20.

The embryonic snail has no ciliated velar ring, but the region corresponding to the velum is enormously developed and distended with reserve food material. The shell-gland is, therefore, inconspicuous, and the development of the shell is retarded. At a later stage, when the nutrient organ is absorbed, the shell is formed, increases rapidly in size, and pushes forward the

anus towards the foot in the same manner as in streptoneurous gastropods. By this time the chief nerve ganglia have been developed around the œsophagus, and as yet the embryo is symmetrical, and the anus remains in the mid-ventral line. The shifting of the anus to the right side of the body is due to the development and great posterior extension of the foot, which is placed obliquely across the mouth of the shell, so that the latter falls over to the right side, and in course of growth becomes spirally coiled as explained above.

CHAPTER XXII

THE ARTHROPODA—APUS CANCRIFORMIS

We have seen that the Earthworm, a representative of the class *Annelida chætopoda*, has a segmented body following upon a minute pre-oral region called the prostomium. Each body-segment or somite is represented externally by an annulus, and bears, in nearly every case, four couples of locomotory bristles. Corresponding to the external annulations we found an internal segmentation, most perfectly expressed by the division of the body-cavity into a number of chambers separated by muscular partitions called septa. In every such chamber we found a pair of coiled and ciliated excretory tubules, the nephridia, opening into the body-cavity of one segment by ciliated funnels, and to the exterior in the segment next behind by excretory pores. These nephridia were shown to have been formed from peculiar rows of cells forming part of the ectoderm of the embryo, and to have grown from the ectoderm towards the body-cavity, acquiring an opening into the latter at a comparatively late stage of development. Further, it has been shown that the generative ducts, so similar in their general characters to the nephridia, have a different developmental history, being formed as outgrowths from the body-cavity towards the ectoderm, which they met, and eventually fused with, to form the external apertures. Further, we have seen that the "body-cavity" of the earthworm is a true *cœlom*, formed in the embryo by the hollowing out of a number of paired mesoblastic blocks or somites, and that it does not contain blood, but a colourless, corpusculated fluid quite distinct from the red corpusculated blood contained in a system of closed blood-vessels. Lastly, we have seen that, although the earthworm has no obvious sense organs, no respiratory plates or processes, no outgrowths or appendages of the body subserving locomotion, that all these things are present in those marine worms which are classed as *Polychæta*. We have now to

consider a large division of the animal kingdom, which presents many analogies with the polychæte worms—the phylum *Arthropoda*, or, as some prefer to call it, the *Gnathopoda*. The Arthropods include the spiders, scorpions, centipedes, insects, water-fleas, sand-hoppers, wood-lice, lobsters, and crabs, and also a peculiar and very interesting worm-like animal found in warm countries in very different parts of the world—at the Cape of Good Hope, in New Zealand, New Guinea, and the West Indies, and known to science as *Peripatus*.

The Arthropods exhibit a well-marked external segmentation, but internally they are not divided up into compartments as obviously as are the chætopod worms. Like the latter, they have an external chitinous cuticle, which is frequently thickened locally to form a series of hard rings or **annuli**, joined together by thinner intervening tracts of the integument, and freely movable on one another. Every such annulus may be, and some always are, provided with a pair of jointed appendages moved by internal muscles attached to the thickened external cuticle which serves as the skeleton of these limbs. It is from these hollow-jointed limbs that the name Arthropoda (ἄρθρος, a joint; πούς, a foot) is derived, and the name Gnathopoda (γνάθος, a jaw; πούς, a foot) refers to the feature, characteristic of the whole group, that a certain number of these limbs are turned forwards in the region of the mouth, and serve as functional jaws. Such "jaws" work from side to side, and must not be confounded with the jaws of polychæte worms, which similarly work from side to side, but are only local thickenings of the integument of the lips; nor with the jaws of vertebrated animals, which work up and down. Further points characteristic of Arthropods are, that all their muscles are transversely striated, that cilia are absent, or very rarely present, and that the cœlom is very much reduced, being replaced by an extensive system of blood-spaces or sinuses.

The *Crustacea* is a large class of Arthropoda, comprising the water-fleas, sand-hoppers, barnacles, wood-lice, shrimps, prawns, lobsters, crayfishes, and crabs. These are nearly all aquatic animals, and most of them are marine. Living in the water, they breathe by means of special respiratory outgrowths attached either to the limbs or body-walls and known as **gills** or **branchiæ**. The terrestrial forms have generally lost these branchiæ and have different kinds of specially constructed

respiratory apparatus, but their whole organisation betrays their descent from aquatic gill-breathing ancestors.

The water-fleas and other small crustacea nearly allied to them are placed together with the barnacles in a sub-class *Entomostraca*. As an example of this class we may take one of its largest members, *Apus cancriformis*, an animal inhabiting fresh-water pools, especially those which are dependent on the rainfall and are liable to dry up in periods of drought. Apus no longer exists in England, but it occurs in considerable numbers in France, in South Germany, Austria, Hungary, North Africa, and North America. It also occurs in Greenland and Spitzbergen, so that it has a wide distribution in the Northern Hemisphere.

The life-history of the Apodidæ was for a long time a mystery to zoologists. After a heavy rainfall they often make their appearance in large numbers in pools which have for a long time been dried up, and a search in the sun-baked mud at the bottom of such dried-up pools fails to reveal the presence of torpid specimens from which new broods could be produced when the pools are refilled. Hence they were supposed, by the older naturalists, to be spontaneously generated from the mud and slime, and their sudden and inexplicable reappearances gave no small support to the doctrine of Abiogenesis. But eventually it was discovered that the new broods were simply developed from eggs deposited in the mud by the old forms before the pools dried up, and, what is more curious, that the eggs will not develop unless they have been dried for some time.

Mature specimens of *Apus cancriformis* vary in length from 12 to 36 mm., and may be recognised by the following characters:—

The head and the greater part of the body are covered by a large **cephalic shield**, oval in shape and evenly rounded in front, but indented by a deep V-shaped notch at the hinder end. Posteriorly some eleven or twelve annuli of the elongate body project beyond the cephalic shield and end in a bi-lobed caudal piece which bears a pair of long terminal appendages, the **caudal styles**. The cephalic shield is divided by two transverse **nuchal grooves** into a smaller anterior or cephalic and a larger posterior region. The posterior part of the cephalic shield is not attached to but only overlies the body

beneath, but the anterior portion is firmly fused to and is continuous with the head and body region in front of the nuchal grooves. The posterior part of the shield is, in fact, a reduplication of the chitinous cuticle of the head, and it has an outer and an inner wall, enclosing a thin layer of tissue in which lie certain important organs called the **shell-glands.** Posteriorly to the nuchal grooves the cephalic shield slopes evenly away to the right and left of a median ridge which terminates behind in a spine projecting over the angle of the

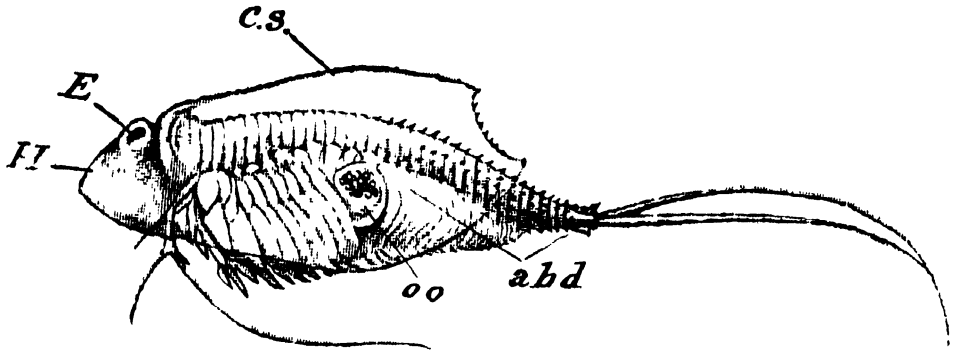


Fig. 21

Side view of *Apus cancriformis*. The free part of the cephalic shield has been drawn as if transparent, showing the thoracic and abdominal segments beneath. *H*, head; *E*, paired eyes; *c.s*, cephalic shield; *abd*, abdominal segments; *oo*, oostegopod.

posterior V-shaped excision. The margins of the excision are garnished with a number of similar spines.

The paired shell-glands lie on either side of the dorsal ridge about half-way between it and the outer margin of the shield. Each gland consists of a tube arranged in a very elongated coil. The anterior ends of the coils converge towards the middle line and touch the nuchal groove; the posterior ends diverge from one another and end some way in front of the posterior margin of the shield. The shell-glands are the functional excretory organs of the adult.

In front of the nuchal groove there is a complex of organs belonging to the head region. Conspicuous among these is a pair of crescentic compound eyes, the convexities of the crescents turned outwards, and their anterior ends closely approximated to one another. The structure of these paired eyes will be described further on, but it should be noticed here that they do not lie at the surface of the shield, but are covered over by a bi-lobed inflation of the chitinous cuticle. This

inflation is known as the **periophthalmic sac**, or water-sac, and its anterior end is prolonged into a fine canal which runs forward and opens in the middle line by a small pore a short distance in front of the eyes. Lying between the posterior lobes of the periophthalmic sac is a conspicuous white oval patch of a glandular nature. This is called the **neck gland**; it opens to the exterior by a very small pore placed near its front end. Neither the neck gland nor the pore of the periophthalmic sac must be mistaken for the median unpaired eye, often called the **nauplius eye**, which is a minute black spot situated between the anterior horns of the paired eyes.

In front of the eyes the cephalic shield slopes rather abruptly downwards, and on turning the specimen over, so as to examine the ventral surface, it will be seen that the anterior margin of the shield is thickened to form a broad flat plate lying in front of the mouth, as shown in fig. 21. The mouth itself is concealed by a large pentagonal chitinous plate, the upper lip or **labrum**, the anterior end of which is hinged to the thickened rim of the cephalic shield. The anus is terminal, lying at the end, and somewhat on the ventral side of the furcal piece.

On cutting away the free part of the cephalic shield close to its attachment at the nuchal groove the elongate vermiform body is exposed. The body proper—that is to say, the region behind the mouth, is to be regarded as made up of thirty-nine annuli or segments; the first five of these are fused with and indistinguishable from the head, and their existence can only be determined by the appendages which they bear and the nerve ganglia corresponding to them. But behind the attachment of the cephalic shield thirty-three distinct annuli can be counted in addition to the terminal or caudal segment. Each annulus is indicated externally by a hoop of chitin, the posterior edge of which overlaps the annulus next behind it. These hoops are simply chitinised thickenings of the integument, and the hinder edge of one is joined to the anterior edge of the next behind it by a soft fold of the integument which is doubled back under the overlap and so forms a flexible joint. All joints in the external armour of Arthropoda are formed in this manner, and may be compared with the ancient suits of plate armour, consisting of overlapping pieces of steel sewn on a leather jacket. The chitinous hoops are thin, transparent,

and smooth in those annuli which are covered by the cephalic shield, but are thicker and furnished with backwardly directed chitinous spines in the posterior region which projects beyond the cephalic shield. In the last four annuli the chitinous hoops are complete ventrally, and do not bear any limbs or appendages. The furcal styles borne by the last segments may or may not represent appendages belonging to the same series as those about to be described.

A glance at the ventral aspect of Apus shows that the animal is provided with a large number of limbs or appendages, which are borne on the under surfaces of all the annuli but the last four, and some appear to belong to the head region. Closer examination shows that in front of the mouth there are two pairs of minute pre-oral appendages, generally described as the first and second **antennæ**, and behind the mouth there are sixty-six pairs of appendages. Of these the first three pairs lie close together round the mouth, and, being modified for masticatory purposes, they are usually known as **foot-jaws**. The following sixty-three pairs are functional limbs, but they are not all alike, and may be divided into thoracic or pregenital, genital, and postgenital series. There are ten pairs of thoracic limbs attached to a corresponding number of annulations of the body. The single pair of genital limbs is attached to the annulus on which the generative organs open. The fifty-two pairs of postgenital limbs are borne on seventeen annuli only, the first four of these carrying five pairs of limbs, the next four ten pairs, the next four thirteen pairs, and the last five carry twenty-four pairs of limbs. The more posterior appendages are soft, foliaceous, many-lobed plates which overlie one another like the leaves of a half-opened book, but the anterior members of the thoracic series are modified and the foot-jaws and antennæ do not appear to bear any resemblance to the limbs behind them. We shall do well to take the first postgenital limb, the seventeenth of the whole series of appendages, as a type, and we will choose that of the right side.

It consists of a median axis or corm, flattened anteroposteriorly and attached by one end to the body near the mid-ventral line in such a way that one of its narrower edges looks outwards and upwards, the other inwards and downwards. The axis is invested by a chitinous cuticle, which is thinner at the junction with the body-wall, so that an imperfect joint is formed

and the whole limb can be moved by the powerful muscles which enter it and are attached to its walls (fig. 22, *XVII*). Otherwise the axis is destitute of joints. The inner and outer edges of the axis are produced into a number of lobes or **phyllites**, of which six, borne on the inner edge, are called **endites**, and three, borne on the outer edge, are called **exites**. Of the six endites, that nearest the base of the limb stands somewhat apart from the rest and is turned towards the middle line. Its surface is covered with a number of stout setæ, and it serves, in conjunction with its fellow of the opposite side of the body, to seize and conduct to the mouth any particles of food with which it may come in contact. Examination of the ventral surface shows that every one of the sixty-three pairs of post-oral limbs of Apus is provided with a similar jaw-like process or **gnathobase**, and the gnathobases of opposite sides enclose a food-groove leading forward in the mid-ventral line to the mouth. Though it has no definite joint, the gnathobase is movable by means of special muscles inserted in the axis. The four endites distal to the gnathobase are oval and leaf-like, and are beset with setae arranged in a very characteristic manner on the edges and sides, as shown in the figure. The sixth or distal endite is a good deal larger and wider than the others, and has a different arrangement of setæ. It is attached at the extremity of the axis, and extends both dorsally and ventrally from its point of attachment.

Of the three outgrowths from the outer edge of the axis, that nearest the distal end is a somewhat wide expansion, fringed with setæ, but not provided with muscles. It is distinguished as the **sub-apical lobe.** Of the two other exites the distal is the largest of all the outgrowths of the axis. Its edge is beset with stout spine-like setæ, and it is furnished with three powerful muscular slips by means of which it can be moved to and fro like a paddle. It is essentially a swimming plate, and is known as the **flabellum** or fan. The proximal exite is a rather thick oval outgrowth attached by a distinct pedicle to the axis. It is not provided with any muscular slips, and is therefore incapable of independent movement, but its internal spongy tissue appears to contain numerous blood spaces. It is probably respiratory in function, and on account of its passive movements it is known as the **bract** (Lat. *bractea*, a weather-cock). The postgenital limbs posterior to the 17th retain the

same general characters, but are progressively reduced in size till the last of the series is no larger than a single endite of the first postgenital limb.

In the rarely found males of Apus the genital limb does not

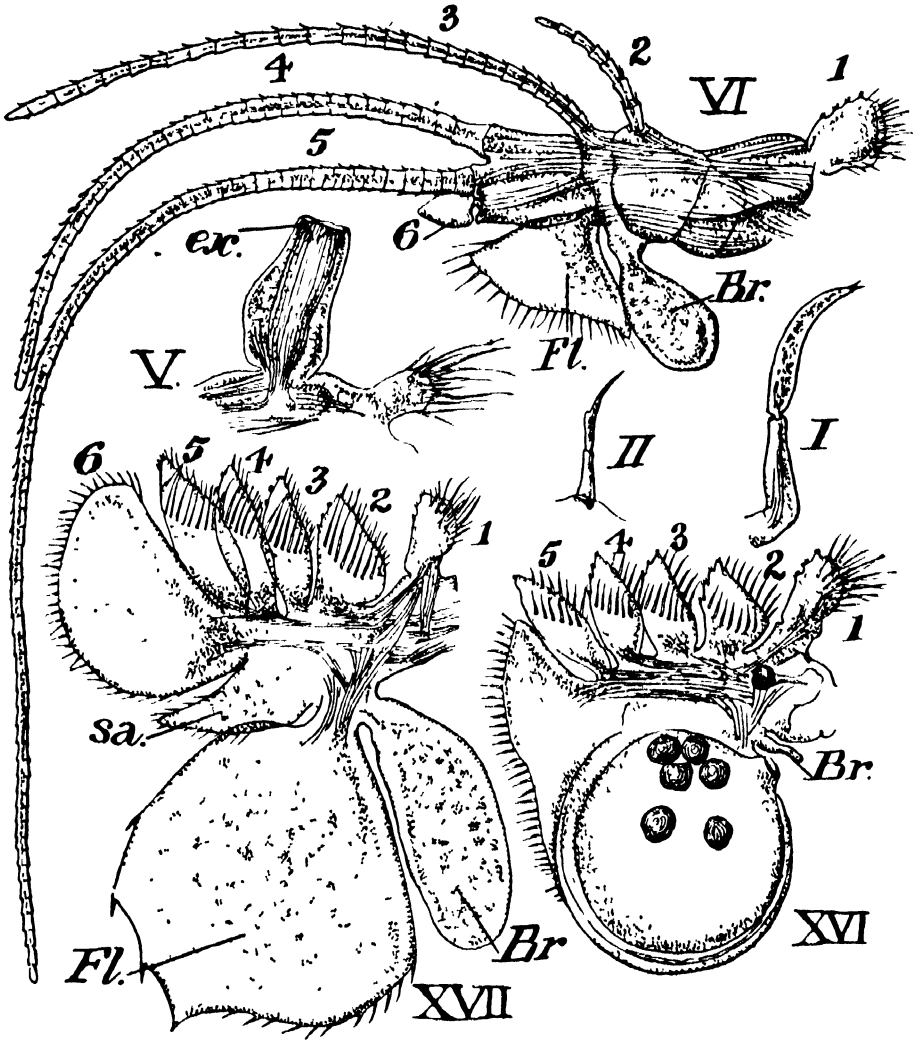


Fig. 22

Appendages of the right side of *Apus cancriformis*. *I.* The two-jointed first antenna. *II.* The second antenna, in the specimen figured it is exceptionally composed of two joints. *V.* The second maxilla, showing the excretory pore, *ex.* *VI.* The first thoracic limb. *XVI.* The oostegopod or genital limb of the female. *XVII.* The first abdominal or postgenital limb. *1*, the first endite or gnathobase; *2*, *3*, *4*, *5*, *6*, the remaining five endites; *sa*, sub-apical lobe; *Br*, bract; *Fl*, flabellum. For further description see text. Figs. *V.*, *VI.*, *XVI.*, and *XVII.* are reversed; in their natural position the endites would be below, the exites uppermost.

differ from those immediately contiguous to it, but in the female it is modified to form a receptacle for the eggs, and is

called the **oostegopod.** In it the gnathobase and four succeeding endites are normal, but the distal endite is greatly enlarged and is confluent with the sub-apical lobe. The latter structure is expanded and modified so as to form a circular shallow cup upon which the flabellum, similarly expanded into a pedunculated circular plate, fits like a lid. The edge of the flabellum posterior to its peduncle is notched to form an aperture leading into the cup. The bract is reduced to a small digitiform appendage (fig. 22, *XVI*). The posterior thoracic limbs (3-10) are very similar to the first postgenital limb, which has been taken as a type. In the more anterior members of the series the axis becomes progressively longer, the endites are carried further apart, the dorsal lobe of the sixth endite becomes more prominent, the sub-apical lobe, though still prominent, becomes reduced in size, and the flabellum is elongated in the direction of the axis. The second and first thoracic limbs present special features.

In the second limb, the axis or corm is divided by a soft fold of the cuticle into a proximal and a distal segment. The gnathobase and second endite are borne on the proximal segment, the four remaining endites and the bract and flabellum on the distal segment. The gnathobase presents no peculiar features, but the remaining endites are narrowed and elongated; the sub-apical lobe is very small, and the bract and flabellum are reduced in size relatively to the other parts. The peculiar hinge-like attachment of the sixth endite should be noticed.

The first thoracic limb is modified in a very striking manner. The axis is divided into four distinct segments. Of these, the most proximal bears the gnathobase The next segment bears the second endite, modified to form a short filamentous process, divided into rings or joints by as many annulations of the chitinous cuticle. The third segment of the corm bears the third endite, similarly modified to form a filamentous process with about forty annulations. The distal segment of the corm bears the fourth, fifth, and sixth endites. The fourth is an elongate filament, with about fifty annulations; the fifth, situated at the extremity of the axis, is very long and slender, and is divided into about eighty annulations. The sixth endite is reduced to a small boat-shaped process, the proximal end of which fits into a notch in the axis formed by the very much reduced sub-apical lobe. The bract

and flabellum are borne on the outer margin of the third segment of the axis; they are reduced in size, but do not present any other remarkable features. The whole limb, with its jointed axis and polyarthrous filamentous endites, presents many resemblances to the jointed limbs of higher crustacea, and it is interesting to observe the gradual transitional stages between it and the more posterior lobed foliaceous limbs characteristic of the order *Phyllopoda* to which Apus belongs.

The three pairs of appendages in front of the first thoracic limb are small in size, and lie close round the mouth. It will be convenient to begin with the most anterior of the three pairs — viz. the **mandibles**. These are short, stout, curved structures with thick chitinous walls. Their long axes lie nearly transversely to the body, and their inner edges, which meet below the mouth, are furnished with a number of stout conical teeth. They are moved by very powerful muscles, and are the functional masticatory organs of the animal. The mandible represents the basal part of the axis of an ordinary limb, the terminal part with the endites and exites having disappeared.

The second pair of oral appendages are called the first **maxillæ**. They are small, and each consists of two pieces fitted together in a peculiar manner. The hinder of the two pieces has the shape of a gnathobase, and probably represents that organ. The anterior piece is a half arch of chitinous substance, expanded at its distal end into a broad lobe with a setose margin. The convexity of the arch forms a smooth articular surface against which the posterior piece works. It is not clear what part of a typical appendage is represented by this anterior piece, but it is certain that the two pieces are parts of one limb, and are not two separate limbs as some authors have supposed. The third pair of oral appendages are sometimes called the maxillipedes, but it is better to call them the **second maxillæ**. They are very small and rudimentary, each member of the pair consisting of two lobes united by a low ridge. The inner lobe is provided with marginal setæ, and probably represents the gnathobase, which it resembles more nearly than any other part of a complete limb. The outer lobe is cylindrical, and devoid of setæ: it is to be regarded as the representative of the bract, but the most important thing about it is that the duct of the

shell gland passes through it, and opens at its extremity (fig. 22, *V*).

The two pairs of pre-oral appendages are known as the first and second **antennæ**. The first antennæ, though small, can be recognised without difficulty. They lie within the thickened anterior edge of the cephalic shield, a little to the outside of the angle formed between it and the mandible. Each antenna (fig. 22, *I*) consists of a proximal cylindrical segment and a somewhat larger distal blade-like segment bearing two or more setæ at its extremity. The second antennæ (fig. 22, *II*) are so minute and rudimentary that their existence has often been denied. As a matter of fact they seem to be always present—at any rate, the author has never failed to discover them in every specimen of *A. cancriformis* or the allied *Lepidurus productus* which he has examined carefully. Being evanescent organs, the second antennæ vary considerably. In most cases they are simple, unjointed filiform appendages, the extremities of which may or may not be bent like a hook. Occasionally, however, one finds a more perfect jointed appendage consisting of two segments. Such a one is shown in fig. 22. Though the two pairs of antennæ are pre-oral in position there is every reason to believe that they belong to a post-oral series of appendages, as will be shown when the nervous system and development are described.

The internal anatomy is difficult to make out in the spirit-preserved specimens which alone are available for study in England.

The mouth opens into a short œsophagus, which ascends vertically towards the region of the eyes. The œsophagus is lined by a chitinous reflection of the outer integument, and is therefore a stomodæum. In the upper part of the head the œsophagus opens into a widish triangular sac or stomach, which receives right and left the ducts of a pair of digestive glands. These ducts curve round parallel to the anterior border of the cephalic shield, and each gives off six external branches, which in turn give off a number of short ductules ending in glandular acini. The lobes of the digestive gland occupy the greater part of the cephalic region. Another pair of glands, described as salivary glands, open by small ducts into the ventral side of the stomach. The last-named organ is placed at right angles to the œsophagus, and narrows posteriorly to form a straight intestine running backwards

through the body to open at the anus. The posterior end of the intestine is lined by a chitinous reflection of the external cuticle, and is therefore known as a **proctodæum.**

The body of Apus is not divided up internally into a series of compartments corresponding with the external annulation as is that of the earthworm, and the space surrounding the gut, though capacious, is not a cœlom, but an extensive system of blood spaces or sinuses. There are, however, many indications of an internal segmentation. The heart, the musculature of the trunk and the gonads, are segmented in correspondence with the external annulation, and the nervous system is on the segmental plan, but corresponds with the series of limbs, and not with the segmentation of the body.

The heart lies in the mid-dorsal line in the thoracic region. It is a straight, muscular, thin-walled tube, divided by as many constrictions into eleven segments, but its cavity is continuous—*i.e.* is not divided into chambers by internal dissepiments. Its most anterior division lies in the first thoracic segment, and its ten succeeding divisions lie in the corresponding segments of the thorax behind the first. Posteriorly the heart tapers off and ends blindly in the eleventh thoracic segment, but anteriorly it is continued forwards as the so-called cephalic aorta, which widens out in the head region to form a large cephalic blood sinus surrounding the digestive gland. At the junction of the heart and the cephalic aorta, two wide vessels are given off right and left in the segment corresponding to the second maxilla. These vessels pass to the cephalic shield, and supply the shell gland with blood. There are no other definite blood vessels.

The heart lies in a considerable pericardial space, and is attached to the walls bounding this space by a number of segmentally arranged convergent bundles of elastic connective tissue threads, the **alæ cordis.** The pericardial space of the crustacean must not be confused with that of a mollusc. It is not a part of the cœlom, but contains blood, and the heart communicates with it by eleven pairs of valvular openings or **ostia** corresponding to the first eleven pairs of thoracic segments. The valves of the ostia are so arranged that they admit blood from the pericardial space into the heart, but prevent any flow in the reverse direction.

The intestine is surrounded by a large perivisceral blood sinus, circumscribed by a thin membranous wall: dorsally this wall forms the floor of the pericardial sinus; ventrally it is attached to the longitudinal muscles of the body-wall; laterally it is separated from the body-wall by a considerable space, which in the first eleven thoracic segments is bridged over by a series of intersegmental transverse muscular partitions, whose position and arrangement recall the muscular septa of the worm. The cavities which they include, however, contain blood, and must therefore be regarded, not as cœlom, but as a number of lateral sinuses, belonging to the general system of blood spaces, into which the apparent body cavity or **hæmocele** is divided. In the abdomen there is neither pericardial sinus nor lateral sinuses, and the perivisceral sinus is surrounded by a so-called dermal sinus running right round the body.

In addition to the blood spaces already enumerated, we may distinguish a ventral or neural sinus surrounding the nerve cord, and in each limb a ventral or efferent, and a dorsal or afferent sinus, having lateral connections respectively with the endites and exites.

When the muscles of the heart are relaxed in diastole, the elastic tension of the alæ cordis pulls its walls apart, its cavity is distended, and blood is admitted by the lateral ostia. When the heart contracts in systole, the valves of the ostia are closed, and the blood is driven forward into the cephalic aorta and the lateral vessels leading to the shell-gland. In the former case the blood flows over the organs in the cephalic region, thence flows backwards in the perivisceral sinus. The lateral and ventral walls of this sinus are fenestrated so that blood passes from it to the neural sinus and to the bases of the limbs, thence flows outwards along the ventral side of each limb, back along the dorsal side, enters the flabellum and bract, is oxygenated in the bract, and thence is returned to the body. In the thorax the blood passes in the lateral sinuses to the pericardial sinus, and so back to the heart. In the abdomen it enters the dermal sinus, and flows forward till it reaches the last of the transverse partitions, and then is directed upwards into the pericardial sinus. The blood passing to the cephalic shield by the lateral vessels circulates in a large sinus surrounding the shell-gland on either side;

its subsequent course is not accurately known, but it probably is returned to the head, and joins the stream flowing backwards through the perivisceral sinus.

The excretory organs of Apus are the shell-glands already mentioned. Each gland consists of a coiled tube divisible into the following parts:—(1) Distally a bladder-like enlarge-

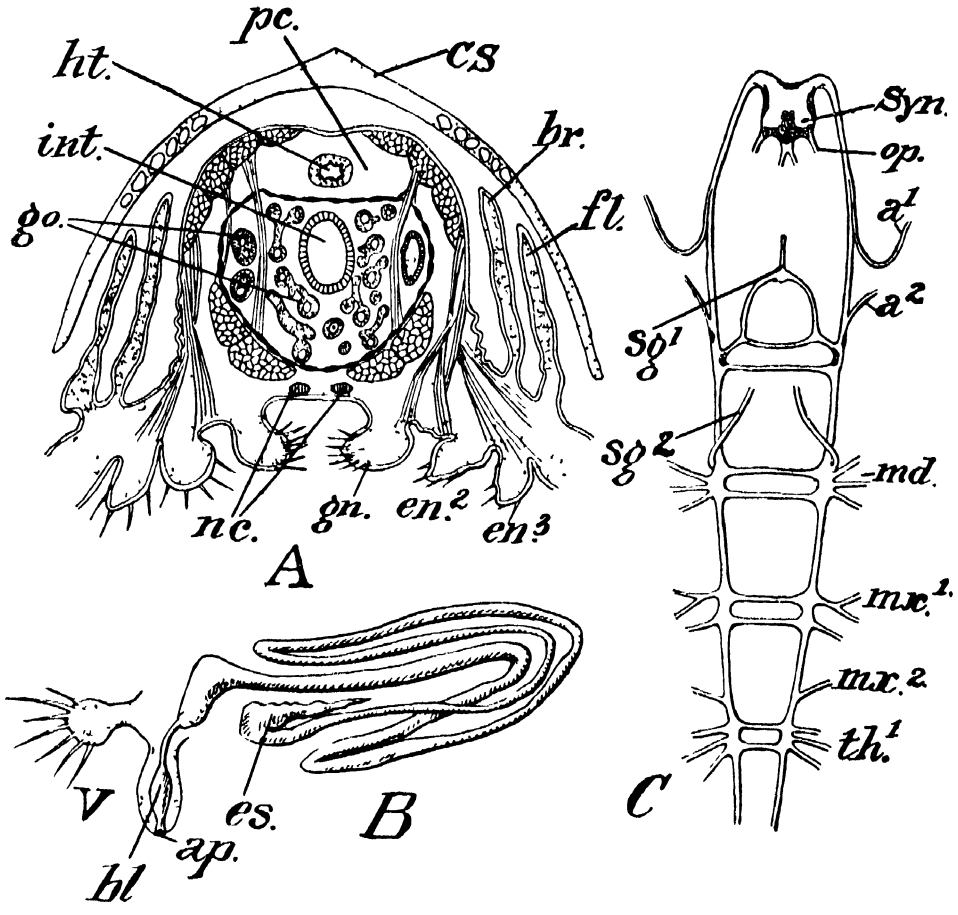


Fig. 23

A. Transverse section across the thorax of *Apus cancriformis*, semi-diagrammatic. *cs*, cephalic shield; *ht*, heart; *pc*, pericardial cavity; *int*, intestine; *go*, gonads, lying in the perivisceral sinus; *nc*, nerve cord; *br*, bract; *fl*, flabellum; *gn*, gnathobase; *en*2, *en*3, second and third endites of the limb. *B*. The shell-gland of Apus, after Bernard. *ap*, excretory aperture; *bl*, bladder; *es*, end-sac; *V*, second maxilliped. *C*. Anterior part of the nervous system of Apus, after Zaddach and Pelseneer. *Syn*, syncerebrum; *op*, optic nerve; *a*1, first antennary nerve; *a*2, second antennary nerve; *sg*1, first stomatogastric nerve; *sg*2, second stomatogastric nerve; *md*, mandibular nerve; *mx*1, first maxillary nerve; *mx*2, second maxillary nerve; *th*1, nerve to first thoracic limb.

ment lying in the bract of the second maxilla. This bladder is lined by a chitinised membrane, and is produced externally into a short canal which opens at the extremity of the

bract; internally it is produced into a fine canal which runs up to the cephalic shield, and enlarges suddenly to form (2) the urinary canal, a tube of varying diameter, coiled several times, as shown in fig. 23, *B*. The canal is lined by large, flat epithelial cells, which rest on a basement membrane, and have conspicuous nuclei. (3) The **end-sac**, a branched, irregularly-shaped structure lying between the central coils of the urinary canal. It is lined by a flat epithelium, and there is reason to suppose that it represents a part of the original cœlom. It will be seen that the larval Apus has another pair of functional excretory organs, opening at the bases of the second antennæ.

The nervous system of Apus consists of a supraœsophageal or cerebral ganglion connected by periœsophageal connectives with a ventral nerve-ganglion chain.

The supraœsophageal ganglion is a quadrangular nervous mass situated in front of the œsophagus below and rather in front of the eyes. The periœsophageal connectives uniting it with the ventral nerve chain make a bold sweep upwards as they pass round the œsophagus into the head, and the ganglion itself is tilted upwards and backwards so that its actual upper and anterior face is really the ventral side, its posterior and lower face the dorsal side. A large nerve passes from each of the two anterior corners of the ganglion to the paired eyes, and a pair of smaller nerves arising from the middle of the anterior edge is distributed to the median nauplius eye. The fibres composing these nerves spring from a large mass of pyriform nerve ganglion cells occupying the anterior moiety of the ganglion. The posterior corners of the cerebral ganglion are continued into the periœsophageal connectives which, sweeping downwards and backwards on either side of the gullet, are united behind the gullet by a pair of postœsophageal transverse commissures. These commissures spring from a distinct ganglionic swelling on either side, and the more anterior of the two sends forward on either side a branch which, uniting with its fellow of the opposite side above the gullet, forms the anterior œsophageal or stomatogastric nerve. The connectives run back to the second post-oral or mandibular ganglion pair, united by two transverse commissures and giving off the nerves supplying the mandibles. From these ganglia also arise the second œsophageal or stomatogastric nerves. The third pair

of post-oral ganglia supplies the first maxillæ, but the nerves going to the second maxillæ have no visible ganglion corresponding to them: they seem to be given off from the connectives between the third and fourth pairs. The fourth pair of post-oral ganglia supplies the first thoracic limbs, and for every succeeding pair of limbs there is a pair of ganglia united by two transverse commissures and joined to the pairs before and behind it by longitudinal connectives. There are no ganglia behind the last pair of limbs, thus the nervous system, though segmentally arranged, does not correspond with the annulations of the body but with the limbs.

Turning now to the nerves supplying the antennæ, we find that the first pair of antennary nerves is given off from the periœsophageal connectives about half-way between the cerebral and first post-oral ganglia. The fibres of the nerves can be traced forward in the periœsophageal connectives as far as the cerebral ganglion where they end in two groups of ganglion cells situated on the external posterior margins of the brain. These groups of ganglion cells are quite distinct and separate from the larger mass from which the optic nerves originate and appear to represent the ganglia of the first antennæ. There is reason to believe that the antennæ were originally post-oral appendages which have been shifted to a pre-oral position, and that their ganglia have been still further shifted forward till they have coalesced with the prestomial ganglion, the two forming the compound cerebral ganglion or **syncerebrum** of the adult Apus.

The second pair of antennæ, as we shall see, are post-oral in the larval Apus, and are shifted forward in the course of development. Their nerves spring from the periœsophageal connectives just in front of the stomatogastric or first post-oral ganglia, and originate from a little lateral group of nerve ganglion cells on either side, which undoubtedly represent the ganglia of the second antennæ. The nerves of the second maxillæ, though they seem to spring from the ventral nerve cords, are found to originate from two little groups of ganglion cells imbedded in the substance of the cords, these groups representing the rudimentary ganglia of a rudimentary pair of appendages.

It has recently been stated that some of the northern species of Apus—viz. *A. glacialis* and *A. spitzbergensis*—are hermaphrodite, but the writer has not been able to find any evidence

of hermaphroditism in *A. cancriformis*, or in the closely allied *Lepidurus productus*.* In these genera males are of rare occurrence, and whole broods have been taken from ponds consisting entirely of females. Yet the ova of these virgin females develop, so we have in Apus an instance of the phenomenon of **parthenogenesis**. Occasionally, however, males are found in abundance. Thus out of seventy-nine specimens taken by Sir John Lubbock in pools near the Somme, thirty-three were males; and similar instances have been recorded by other naturalists.

The reproductive organs, whether male or female, lie in the perivisceral blood-sinus, and have the form of a long sacculated tube extending on either side of the body from about the third to the twenty-second segment, counting from the first pair of thoracic limbs. In *Apus glacialis*, the sacculations of the ovary correspond with the annulations of the body, and the organ therefore shows traces of metameric segmentation, but this is not so clear in *A. cancriformis*. In the latter species the main ovarian tubes lie along the sides of the perivisceral sinus, and are incompletely cut off from the more central part of the sinus by a sort of lattice-work of diagonal muscles which traverse the cavity of the sinus. These ovarian tubes are generally filled with mature ova. They open by a short and wide oviduct at the base of the eleventh thoracic limb on either side, and internally they give off a number of tubular-branched diverticula which project through the above-mentioned muscular lattice-work, and nearly fill up the central part of the perivisceral sinus. The walls of the diverticula are lined by a columnar germinal epithelium, from which primitive ova are derived. The primitive ova (oogonia) pass to the extremities of the branches, and there undergo maturation, each dividing into four cells, of which one only develops into an ovum. When ripe, the ova distend the extremities of the diverticula so that the latter look like bunches of grapes. The ova, when ripe, are abundantly provided with food yolk, and have relatively thick chitinous shells. They pass into the brood pouches formed in the manner already described in the eleventh thoracic limbs (oostegopods), and there undergo the first stages of develop-

* The genus *Lepidurus* is distinguished from Apus by the presence of anal scales between and above the caudal setæ.

ment. Passing over the details of segmentation and early development, which indeed are not very accurately known in Apus, we may proceed to the consideration of the development of the larval form into the adult. The eggs, as has been said, lie in the mud of dried-up pools, and on the refilling of the pools larval forms of the character depicted in fig. 24, *A* and *B*, are hatched out from them. This larval form is known as the **Nauplius**. It has an oval body, the anterior two-thirds covered by a dorsal shield. The mouth is ventral, and is overhung by a large upper lip or labrum. The anus is posterior and terminal. Anteriorly is a single median eyespot which survives as the unpaired eye of the adult. There are three pairs of appendages, one pair pre-oral and two pairs post-oral. The pre-oral pair are simple unjointed filiform appendages bearing two terminal setæ; they become the first antennæ of the adult. The second pair of appendages are large biramose swimming limbs. They spring from the sides of the mouth, and each consists of two basal segments, of which the proximal bears a stout masticatory hook directed towards the mouth, and the distal bears two setose branches, an outer "exopodite" and an inner five-jointed "endopodite," probably representatives of the fifth and sixth endites of the typical limb of an adult. It is this pair of appendages, so preponderant in size in the larva, that becomes the minute and rudimentary second pair of antennæ in the adult. The third pair of appendages of the larva resembles the second, but is smaller, and shows only a trace of a masticatory process. It gives rises to the mandibles of the adult. The body behind the third pair of appendages is divided by transverse constrictions into five segments in the larva of Apus, but these segments as yet show scarcely any trace of limbs. On the dorsal shield behind the median eye is a relatively large oval prominence, the neck-organ, which persists as the neck-gland of the adult animal.

The Nauplius larva is of common occurrence among crustacea, and is particularly characteristic of the order *Copepoda*. It is only exceptionally that the posterior part of the body is segmented as in Apus, in most nauplii there is no trace of such segmentation. For this reason the larva of Apus is often called a **metanauplius**.

At the time of hatching the larva of Apus is so opaque

that its internal organs can scarcely be distinguished; the most obvious organ is the gut, which is a relatively wide, straight tube extending the whole length of the body, and swollen at its anterior end into a right and left prominence, the primordia of the digestive glands. The rudiments of new organs are gradually formed beneath the cuticle, but they do not become manifest until the larva has cast off its chitinous cuticle, which it does by a succession of moults called **ecdyses**.

After the first ecdysis the larva is more elongated and has completely lost its oval shape. The three pairs of nauplius appendages have not undergone any material change except that the basal joint of each mandible bears a large masticatory process as yet unprovided with teeth. The second antennæ are still very large, and the most remarkable thing about them is the development of a coiled tubular excretory gland opening at the base of each. These are the larval excretory glands, which eventually disappear, and are replaced by the adult excretory organs or shell-glands. Their position is noteworthy, for they occupy the position of, and are no doubt homologous with, the permanent excretory organs of the higher crustacea —*e.g.* the crayfish. The first antennæ have undergone no change of note, but in front of them, just behind the unpaired larval eye, there is a small pair of tentaculiform projections which in all probability represent the sense organs of the pre-oral lobe or prostomium, and therefore may be considered homologous with the cephalic tentacles borne on the prostomium of so many Annelids. The first pair of maxillæ, which were not represented in the nauplius, are now visible as a pair of simple plate-like outgrowths behind the mandibles. The altered shape of the body is chiefly due to the changes which have taken place in the posterior or thoracico-abdominal region. There are five well-marked segments, and behind them indications of two or three more can be distinguished beneath the cuticle. The three or four most anterior of these segments bear limbs, in the shape of oblique ridges divided into lobes at their free edges. These lobes represent the endites. The posterior extremity of the body ends in a pair of short but distinct caudal processes, between which the anus is situated. After the second ecdysis the larva has attained a length of about 1 mm., and has undergone further changes. The thoracico-abdominal region has grown longer

by the addition of two more segments, making ten in all, of which the first seven bear limbs in a more or less developed condition. The limbs of the first five pairs have developed exites as well as endites, and begin to resemble the typical limbs of the adult. The second maxillæ are represented by

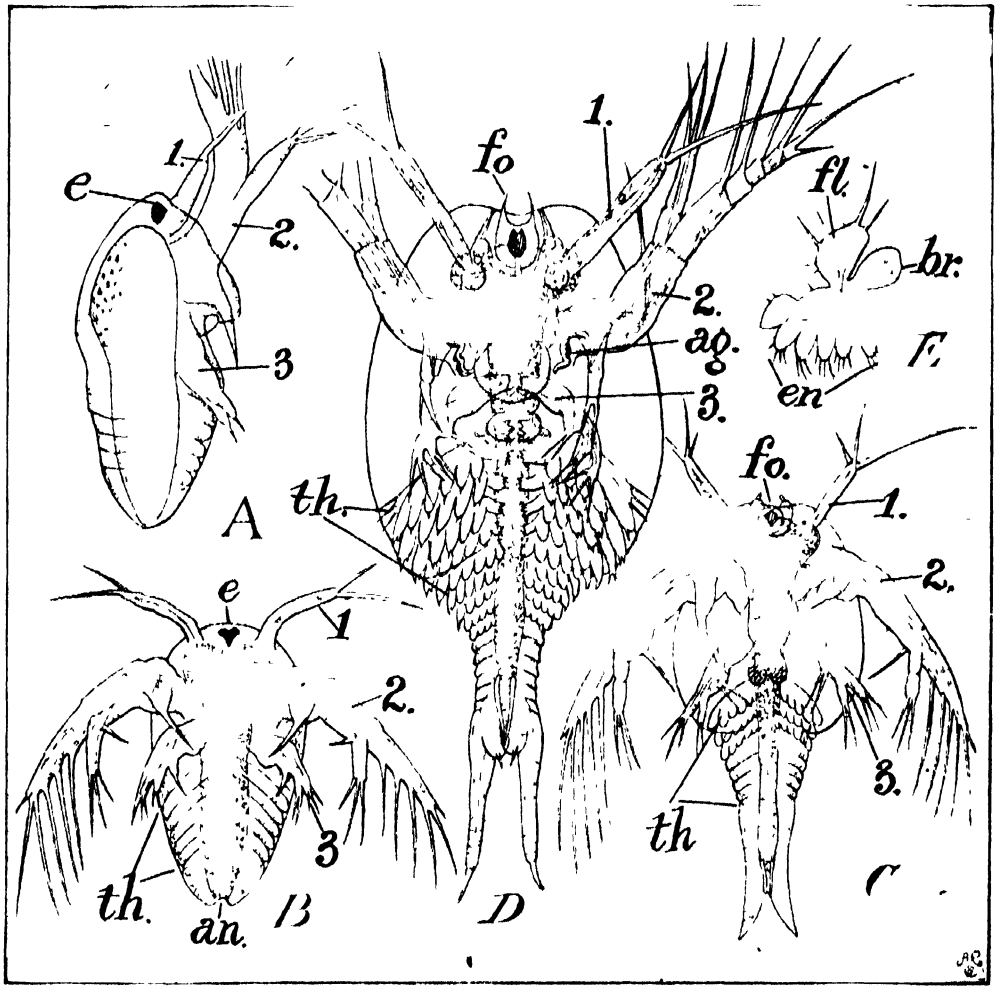


Fig. 24

A. Lateral view of the metanauplius larva of *Apus cancriformis*. *B*. The same larva seen from the ventral surface *C*. Ventral view of a larva after the first ecdysis. *D* Ventral view of a larva after the third ecdysis. *E*. A single thoracic limb of a larva of the same age as that shown at *D*. All the figures after Claus. *1*, the first antennæ; *2*, the second antennæ; *3*, the mandibles; *ag*, antennary gland, the provisional excretory organ of the larva; *an*, anus; *br*, bract; *e*, eye; *en*, endites; *fl*, flabellum; *fo*, frontal organ; *th*, thoracic segments.

a pair of minute outgrowths lying just behind the rudiments of the first maxillæ. The biting process of the mandible is larger and stronger, and its inner edge is furnished with two

or three fine teeth. The two pairs of antennæ show little change, the second pair continuing to be of large size, and acting as the principal locomotory organs. The excretory organs at their bases are distinct and functional. The shell-gland, of which traces could be seen even in the earlier stage, is now clearly visible in the dorsal shield, but it should be noted that the shield extends only a little way backwards. At this stage it scarcely overlaps more than the two first thoracic segments. In the interior of the body the heart, extending as far back as the sixth thoracic segment, has made its appearance.

After the third ecdysis many of the more important organs of the adult are definitely established, but the larva is still far from resembling the adult animal, chiefly because of the still preponderant size of the second antennæ. The body is further elongated by the addition of new segments behind those already existing: the caudal styles are much longer, and twelve pairs of thoracic limbs are present, the first seven pairs furnished with exites as well as endites. The cephalic shield extends backwards to cover the third or fourth segment. The paired eyes are being formed behind and above the median larval eye, and beneath them the rudiment of the cerebral ganglion can be distinguished, sending forward a pair of nerves to the frontal tentacles. The digestive glands are being formed as simple finger-shaped outgrowths from the anterior part of the gut, and the shell-glands have advanced so far in development that they have nearly attained their adult character, and receive a blood supply from a pair of lateral arteries given off from the anterior end of the heart. The heart itself extends as far back as the ninth thoracic segment, and the circulation of the blood is established. The ventral nerve chain can be distinguished reaching back to the ninth thoracic segment. The second pair of maxillæ is only represented by a small conical process bearing a single bristle, but the first maxillæ are fairly advanced, and their anterior biting lobes are differentiated. The first and second antennæ have not undergone much change, but the mandibles are losing their original character of swimming limbs and are becoming powerful toothed biting organs, of which the distal biramose limb is little more than an appendage. At each successive ecdysis the larva becomes progressively more and more like an adult

Apus. After the fifth ecdysis the second antennæ degenerate rapidly in size and importance, and as they undergo reduction, so do the provisional excretory organs which opened at their bases disappear. The frontal tentacles are aborted, and the paired eyes attain their ultimate structure and dimensions. The first antennæ acquire a joint, the limb of the mandibular appendages becomes reduced to a mere palp, and after the ninth ecdysis disappears altogether. The full number of thoracic and abdominal limbs and appendages is gradually established by continued addition of new parts behind those already existing, and after the eighth ecdysis the eleventh thoracic limb of the female shows signs of the differentiation which leads to its being converted into the oostegopod. The caudal styles increase in length, the cephalic shield extends further and further backwards over the body segments, and eventually, on the acquirement of all the adult characters, the larva becomes a full-grown Apus.

CHAPTER XXIII

THE CRAYFISH—ASTACUS FLUVIATILIS

APUS cancriformis affords so good an example of the leading features of crustacean anatomy that it will not be necessary to enter into minute details of the anatomy of the crayfish, the more so because this species is fully described in Marshall and Hurst's "Practical Zoology," and is the subject of an admirable memoir by the late Professor Huxley, a book which should by all means be read by young zoologists. They will find in it a full and interesting account of the habits and structure of crayfishes, as well as a description of the different species of crayfishes and their distribution in different parts of the globe.

The common river crayfish is found in many rivers of England, particularly in those which flow through chalk or limestone districts and have a good deal of lime dissolved in their waters. It lives in holes which it burrows in the river banks, in the mouths of which it lies in wait for its prey. It is a voracious and indiscriminate feeder; almost any kind of flesh is acceptable to it, and it is able by means of its powerful pincers to overcome animals considerably larger than itself. Some years ago it was very abundant in the Thames and Cherwell, and was the subject of a regular fishery, for its flesh is esteemed a greater delicacy even than that of the prawn or lobster. But in 1887 there was a pest among the crayfishes in the Upper Thames and its tributaries; they died in great numbers, and so few survived that the fishery became unprofitable and has practically ceased to exist. In recent years the number of crayfishes has increased, and they are common enough in some small tributaries of the Thames, such as the Glyme. Crayfishes were as abundant in Continental rivers, but they too suffered from a pest which greatly thinned their numbers in 1876, and they are so persistently fished for, that they are no longer as common

as they were. They are reared, however, in crayfish "farms," in both Germany and France. In general appearance, and indeed in almost every detail of its structure, the crayfish resembles a small lobster, and dwellers by the seaside who may find it more convenient to take the latter animal as their type will find little in it that differs from the following description :—

The English crayfish is of a dull greenish-grey colour, and seldom attains a greater length than three, or three and a half inches, but a variety commonly found in France and Germany is larger, attaining a length of five inches or even more, and it is further distinguished by the red colour of its pincers and walking legs.

The crayfish's body, like that of Apus, is divisible into a cephalic, a thoracic, and an abdominal region, each region being composed of a number of segments bearing appendages. The grouping and external aspect of these regions, however, presents many differences. In the first place, the number of segments in the crayfish's body is fewer than in that of Apus: there are nineteen in all, excluding the posterior piece or **telson** on which the anus opens, and each segment bears a pair, and never more than one pair, of jointed appendages.

In the second place, the cuticular armour or exoskeleton of the crayfish is far more developed than in Apus, and attains considerable thickness and strength by the deposition of salts of lime in its chitinous organic basis. The salts of lime may be dissolved out by placing the animal in dilute acid, and the organic residue which is left, though preserving faithfully the outlines of the exoskeleton, is soft and yielding.

In the third place, the fusion of segments, found only in the cephalic region of Apus, is carried to a much greater extent in the crayfish, for in the latter animal the thoracic segments are firmly fused to one another and to the head, and thus constitute a **cephalothorax**. The dorsal integument forms a continuous shield known as the carapace. The abdomen, on the contrary, is composed of six distinct rings or segments in addition to the terminal telson, the last named structure corresponding to the caudal piece of Apus, but differing from it in being devoid of caudal styles.

The abdomen of the crayfish is flexible; it can be extended in a straight line with the cephalothorax or can be bent down

underneath the cephalothorax, and it is the principal swimming organ of the animal. As is well known, crayfishes, lobsters, and all their tribe swim backwards by means of powerful strokes of the abdomen which is alternately flexed by a rapid contraction of its ventral muscles and more slowly straightened out by the dorsal muscles. The principle on which the joints of an arthropodous animal are formed has already been explained (p. 94), and is well exemplified in the abdomen of the crayfish. Each segment consists of a ring of thick calcified cuticle, united to its fellows before and behind by an intervening section of soft cuticle. The upper surface of each ring is wide from front to back, and evenly arched from side to side. This part is known as the **tergum**. Its sloping sides are continued below the level of the abdominal floor into a pair of broadly lanceolate plates, the **pleura**. Ventrally the segment is completed by a transverse skeletal bar, the **sternum**. The outer ends of the sternal bar forms the inner sides of a pair of articular cavities for the limbs, the outer sides of each cavity being formed by a short skeletal piece extending to and continuous with the pleuron. This piece is known as the **epimeron**. It should be observed that the first abdominal somite has no pleura, and is overlapped by the posterior edge of the carapace. In turn it overlaps the second abdominal segment, and this and each succeeding segment overlaps the one behind it.

The telson is flattened dorso-ventrally, has no pleura, bears no appendages, and is imperfectly divided by a transverse joint into two pieces.

In the cephalothorax the great dorsal carapace, when viewed from above, has an oval contour truncated at both ends. From the centre of the anterior end projects a beak-like prominence, the **rostrum**. It has a broad base, ends in front in a sharp spine, and has two principal and some smaller accessory lateral spines.

The carapace shows no trace of segmentation except that the head region is marked off from the thorax behind by a **cervical groove** running transversely across the carapace at about the middle of its length and continued forwards and downwards on each side towards the lower anterior edge of the carapace. Behind the cervical groove a pair of longitudinal **branchio-cardiac grooves** mark off a median cardiac from the lateral branchial regions of the carapace. If one

tries to lift up the posterior edge of the carapace one finds that its median or cardiac part is firmly attached to the body-wall beneath, and is in fact the thickened and calcified cuticle of the fused thoracic segments. It differs, therefore, from the shield of Apus, which belongs to the head region, and simply overlies without being attached to the thoracic segments.

The sides of the crayfish's carapace, however, are separated by a space from the body-wall, and can easily be removed by cutting along the outside of the branchio-cardiac groove and continuing the cut forwards on the outside of the anterior continuation of the cervical groove. The piece thus removed is the **branchio-stegite**; it is a lateral fold of the cuticle of the cephalothorax ending behind, below, and in front in a free margin. The space between it and the body wall is the branchial chamber, in which may be seen the gills or **branchiae** lying close against the body-wall. Their structure and relations will be described later.

Though the carapace is not jointed, examination of the ventral surface of the cephalothorax shows that between the bases of every pair of limbs there is a skeletal piece corresponding in position to the sterna of the abdominal segments. Every such piece is the **sternum** of a segment. The sternum of the last pair of thoracic limbs is fairly wide and movable. (In the lobster it is immovably fused to the one in front of it.) As one proceeds forwards, the sterna of the thoracic limbs become narrower, until those of the anterior thoracic and oral limbs become very narrow and keel like. The sterna are immovably fused together and lie in a straight line. In front of the mouth the sternum of the segment bearing the second antennæ is broad and slopes upwards, that of the segment bearing the first antenna is narrow and set nearly at right angles to the sternum behind it so that it looks directly forwards. This disposition of the two anterior sterna gives rise to the cephalic flexure, conspicuous in a lateral view of the animal. Noticing that, as in Apus, the mouth is placed on the ventral surface and well behind the anterior extremity of the animal, while the anus opens on the under surface of the anterior joint of the telson, we may pass to a consideration of the appendages.

The eyes of the crayfish are situated in cavities at the base of the rostrum, and being placed upon short movable stalks they

resemble modified limbs, and are reckoned as such by some

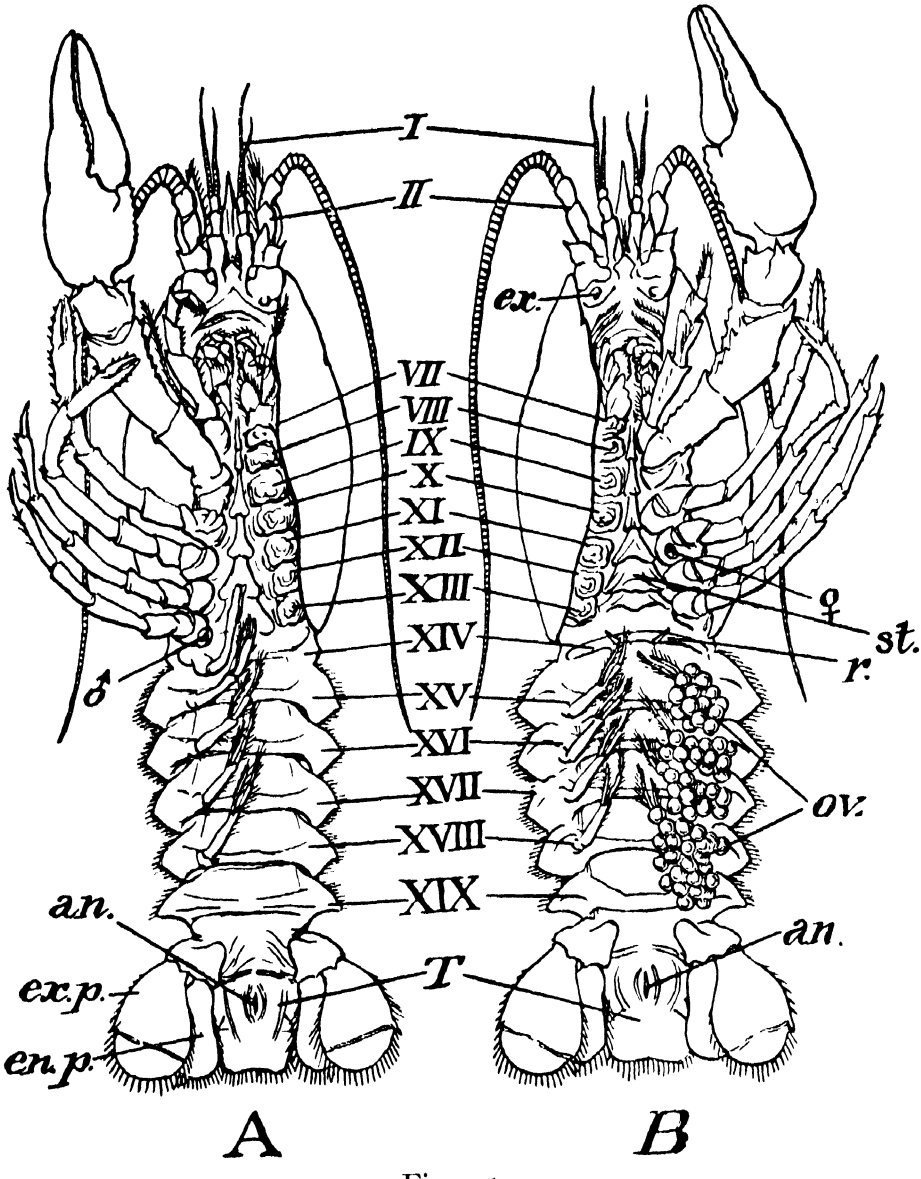


Fig. 25

A. Ventral view of the male, and *B*, ventral view of the female crayfish. The thoracic limbs of one side are removed, as also the ova from the right side of the abdomen of the female. *I*, the first antennæ; *II*, the second antennæ; *VII*, the second maxillipeds; *VIII*, the third maxillipeds; *IX*, the chelæ; *X-XIII*, the four pairs of pareiopods; *XVII-XIX*, the six abdominal segments with their appendages; *T*, the telson; ♂ male generative aperture; ♀ female generative aperture; *an*, anus; *ex*, opening of the green gland on the basal joint of the second antennæ; *r*, rudimentary first abdominal limb of the female; *st*, sternum; *ov*, ova, carried on the abdominal limbs of the female; *ex.p*, exopodite, and *en.p*, endopodite of the last pair of abdominal limbs.

authors, including Huxley. But we shall not adopt this view,

considering them homologous with the sessile eyes of Apus, and therefore as organs belonging to an original prostomial region devoid of limbs. Omitting the eyes, we can count nineteen pairs of appendages, of which two pairs, the first and second antennæ, lie in front of the mouth. Three pairs lie close round the mouth and are modified as masticatory organs; they are the **mandibles** and first and second **maxillæ**. Three pairs succeeding these are turned forwards, and more or less modified to form foot-jaws—viz. the first, second, and third **maxillipeds**. The next pair forms the large pincers or **chelæ**. The next four pairs are the walking legs or **pareiopods**, and on each of the six segments of the abdomen is a pair of swimming legs or **pleopods**, the first five pairs being small, the last pair expanded to form broad swimming plates lying alongside the telson. The first five pairs of appendages we may regard as cephalic appendages, and it should be observed that they correspond with the cephalic appendages of Apus. The maxillipeds, chelæ, and pareiopods are thoracic appendages, and the remainder are abdominal.

Taking the right limb of the third abdominal segment, the sixteenth of the whole series, as an example, we find (fig. 26, *XVI*) that it consists of a two-jointed basal stalk bearing an inner and an outer branch at its extremity. The basal stalk is known as the **protopodite**; its very short proximal joint is the **coxopodite**, its long and cylindrical distal joint is the **basipodite**. Of the two distal branches the inner is known as the **endopodite**, the outer as the **exopodite**. They resemble one another in all essential points, but the exopodite is rather shorter than the endopodite, and is articulated rather lower down than its fellow to the inner margin of the basipodite. Each branch consists of a proximal flattened piece bearing at its distal end a flagelliform appendage imperfectly divided by transverse constrictions into ten or eleven joints bearing a number of plumose setæ on their outer and inner margins. The fourth and fifth pairs of abdominal limbs are practically identical with the third, but the last pair, the nineteenth of the whole series of appendages, is modified. The basal stalk is short and broad, and is not divided into a coxopodite and basipodite. The exopodite and endopodite are expanded and flattened, forming broad swimming plates fringed at their margins with plumose setæ. The exopodite is divided by a transverse suture into two joints, but the endopodite is unjointed.

The sexes in the crayfish are separate, and the females are distinguished from the males by several secondary sexual

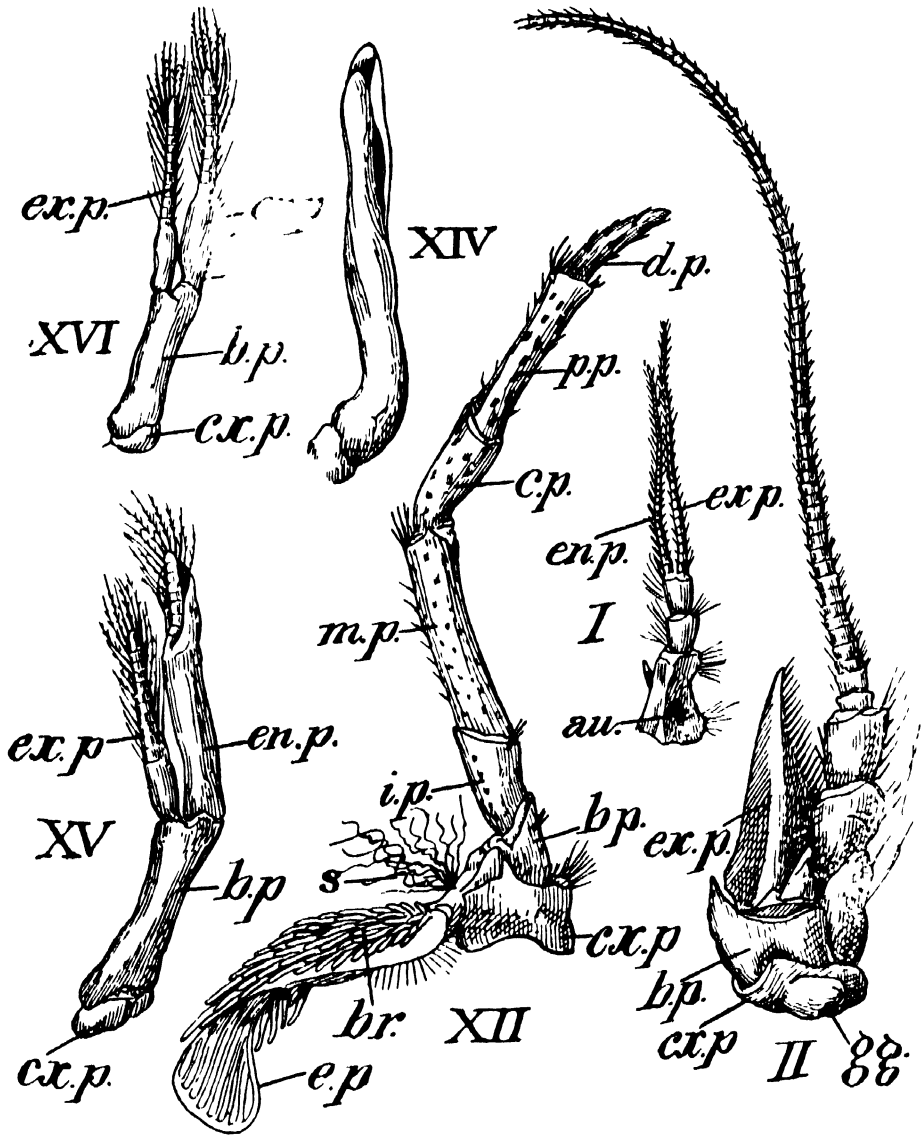


Fig. 26

XVI. Third abdominal limb of the right side of *Astacus fluviatilis* seen from behind. *cx.p*, coxopodite; *b.p*, basipodite; *en.p*, endopodite; *ex.p*, exopodite. *XV.* Second abdominal limb of the male. *XIV.* First abdominal limb of the male. *XII.* Seventh thoracic limb of the right side, seen from behind. *i.p*, ischiopodite; *m.p*, meropodite; *c.p*, carpopodite; *p.p*, propodite; *d.p*, dactylopodite; *e.p*, epipodite; *br*, branchial filaments; *s*, coxopoditic setæ. The other letters as in *XVI.* *II.* The second antenna of the right side, seen from below. *g.g*, the opening of the green gland. *I.* The first antenna of the right side, seen from above. *au*, opening of the auditory organ; *en.p*, internal filament; *ex.p*, external filament.

characters. The abdomen of the female is decidedly broader than that of the male, and the two first pairs of abdominal limbs

(the fourteenth and fifteenth of the whole series) are markedly different in the two sexes. In the female the second abdominal limbs resemble the third, but the first abdominal limbs are very small, consisting of a small unjointed protopodite bearing a single short imperfectly jointed filament, the representative of the endopodite.

In the male both the first and second abdominal limbs are of relatively large size, and are turned forwards so as to underlie the bases of the last thoracic limbs. The second limb consists of a protopodite of the normal structure bearing an exopodite and an endopodite. The exopodite presents no remarkable characters, but the endopodite is much modified, its proximal joint being enlarged and its outer distal margin expanded into a thin plate rolled up in the form of a scroll lying alongside the short distal filament (fig. 26, *XIV*). The first pair of abdominal limbs of the male is still more modified. The coxopodite is present, but the exopodite is absent, and the basipodite appears to be fused with the endopodite. The proximal joint only of the latter is represented, and forms an expanded plate whose sides are rolled in so as to form a canal open at both ends (fig. 26, *XIII*). These modified limbs serve as sperm conduits by means of which the spermatozoa of the male are conveyed to their appropriate position between the bases of the posterior thoracic limbs of the female.

The abdominal limbs of the crayfish do not present, at first sight, any obvious resemblance to the foliaceous limbs of Apus, nor, except for the imperfectly jointed filaments of the exopodites and endopodites, do they resemble the first thoracic appendages of that animal to any great extent. But it should be remarked that they are comparable with the second antennæ and mandibles of the nauplius, having like them a jointed basal piece or stalk bearing an outer and an inner branch.

Passing now to the thoracic limbs. The four pairs of walking legs are long, slender, and made up of a series of seven joints. The great chelæ are stout, and the penultimate joint is expanded and modified to form the pincers, but they too are made up of a series of seven joints, and neither they nor the walking legs show any trace of the division of the distal part of the limb into an inner and an outer branch.

But this feature reappears in the third pair of maxillipeds

(third of the thoracic, eighth of the whole series of appendages), and we will accordingly examine it to see what light it throws on the structure of the thoracic limbs behind it. When the limb is removed from the body, by carefully cutting through the arthrodial membrane at the base of its proximal joint, we see (fig. 27, *VIII*) that it consists of two stout basal joints or segments which we have no difficulty in recognising as the coxopodite and the basopodite. The coxopodite is produced externally into a stout process which bears a large plume-like appendage, the **gill** or **branchia**, sometimes distinguished as the **epipodite**: the details of its structure may be neglected for the moment. The basipodite bears on its outer margin a relatively short and slender branch, the exopodite, which is very like the exopodite of a typical abdominal limb, consisting, as it does, of a longish proximal joint bearing a jointed terminal filament. The endopodite is borne at the extremity of the basipodite, is stout and leg-like, and consists of five joints, named from the proximal to the distal end as follows:—**ischiopodite, meropodite, carpopodite, propodite, dactylopodite.** (In the crayfish the basipodite of the third maxilliped is immovably fused with the ischiopodite.) If now we place the seventh thoracic leg (twelfth of the whole series) of the same side alongside the third maxilliped it is obvious that it is made up of the same parts, minus the exopodite; it consists, in fact, of the protopodite with its two joints coxopodite and basipodite (the former bearing a gill or epipodite), and the endopodite composed of five joints, named as above (fig. 26, *XII*). The last thoracic limb is similar to the seventh, but has no epipodite.

The fifth and sixth thoracic limbs (tenth and eleventh of the whole series) are chelate—that is to say, the penultimate joint or propodite is somewhat expanded and its inner side is produced distally into a finger-like process upon which the terminal joint or dactylopodite shuts down to form a pincer. The great chelæ have exactly the same structure, but the joints are larger and stouter, the propodite is much expanded, and its cavity is enlarged to give room for the powerful muscles which work the dactylopodite. In it also, as in the third maxilliped, the ischiopodite is immovably fused to the basipodite.

Passing forward to the second maxillipede we find (fig. 27, *VII*) that it has much the same structure as the third, except

that the exopodite is relatively larger, and in the endopodite it is the meropodite which is the longest joint, not the ischiopodite. In the first maxilliped the same essential structures

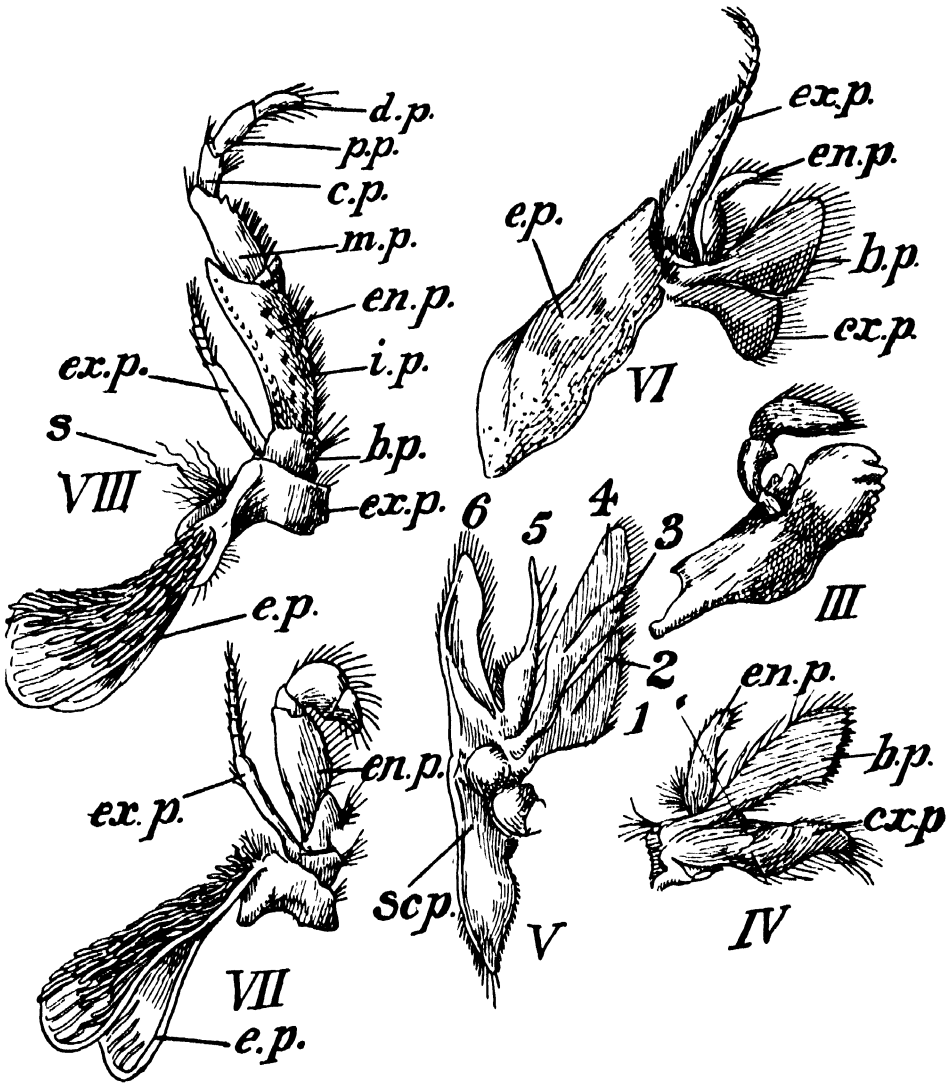


Fig. 27

VIII. Third maxilliped of the right side, seen from behind. *ex.p*, coxopodite; *b.p*, basipodite; *ex.p*, exopodite; *en p*, endopodite; *i.p*, ischiopodite; *m.p*, meropodite; *c.p*, carpopodite; *p.p*, propodite; *d.p*, dactylopodite; *e.p*, epipodite bearing branchial filaments; *s*, coxopoditic setæ. *VII.* Second maxilliped; lettering as in *VIII.* *VI.* First maxilliped. *e.p*, the membranous epipodite. *V.* The second maxilla. *1* and *2*, the two lobes of the coxopodite; *3*, *4*, the two lobes of the basipodite; *5*, the endopodite; *6*, the exopodite. (These figures should be compared with the similar numerals on the abdominal limb of Apus, fig. 22.) *scp*, scaphognathite *IV.* The first maxilla. *III.* The mandible with its palp.

can be distinguished, but the proportions and relative size of the parts are very much altered. The coxopodite and basi-

podite are modified to form broad thin plates with sharp setose edges. The epipodite is no longer a functional gill, but a thin membranous plate entirely devoid of branchial filaments. The endopodite is small and has only two joints, while the exopodite is relatively large (fig. 27, *VI*). The second maxilla, though it bears some resemblance to the first maxilliped, is very unlike any of the other limbs that follow it, and its flat foliaceous appearance at once recalls an abdominal limb of Apus. The coxopodite and basipodite are represented by two thin lamelliform lobes, each of which is deeply sub-divided by a fissure which extends from its inner edge. The endopodite is small and unjointed, though in shape not unlike the endopodite of the succeeding limb. The exopodite is profoundly modified, being converted into a broad thin anterior lobe and produced backwards to form a similar posterior lobe. The whole structure has some resemblance to a human ear. It is an accessory respiratory organ used for baling water out of the branchial chamber, and is known as the **scaphognathite**. Let us now see whether there is anything more than a superficial resemblance between this second maxilla and one of the typical limbs of Apus. The maxilla consists of a median or axial piece to which lobes are attached: this is itself attached by one end to the body and represents the axis or corm of the limb of Apus. On its inner side are the bifid coxopodite and basipodite, standing for the four proximal endites. Beyond these is the endopodite, standing for the fifth endite, and the sixth endite is represented by the exopodite or distal lobe of the scaphognathite. The proximal lobe of the scaphognathite suggests a flabellum, which is fused with the sixth endite, yet this is probably not the case, but the lobe simply represents a great extension of the dorsal process of the sixth endite which is so conspicuous in the second thoracic limb of Apus. The exites of the phyllopod limb are probably represented in the crayfish by the epipodite which in the second maxilla may be represented by two small prominences on the outer side of the axis.

Having once established these homologies, it is easy enough to trace the connection between the other limbs of the crayfish and the phyllopod pattern. In the first maxilliped of the crayfish the broad lobes of the coxopodite and basipodite are shown, by comparison with the second maxilla, to represent the four proximal endites, and the same comparison shows

that the endopodite and exopodite represent the fifth and sixth endites. The epipodite represents the exites, and more probably the flabellum than the bract, the latter structure having disappeared altogether. The transition to the second maxilliped shows how the four proximal endites are reduced, and the joints of the axis which bore them become the coxopodite and basipodite; the fifth endite being as before the endopodite and the sixth the exopodite. A similar comparison shows the homologies of the rest of the series. Thus we are able, by means of the graduated change of form and of relative size of parts in the foot-jaws of the crayfish to trace the connection between such apparently different structures as the chelæ or walking limbs of a decapod and the foliaceous appendages of a phyllopod.

To return to the remaining appendages of the crayfish. The first maxilla (fig. 27, *IV*) is much reduced: the coxopodite and basipodite are there, as two broad setose plates, the endopodite (fifth endite) is also there, but is small and unjointed, the exopodite (sixth endite) and epipodite have disappeared altogether. In the mandible (fig. 27, *III*) the protopodite is very large and transversely elongated, its inner edge being divided by a groove into two toothed ridges. The endopodite or fifth endite is represented by a three-jointed appendage of the protopodite, usually known as the **palp**, and it should be noticed that, in this respect, the mandible of the crayfish does not attain to the same degree of differentiation as that of Apus. In the second antennæ of the crayfish (fig. 26, *II*) we can recognise protopodite, exopodite, and endopodite. The coxopodite is small, but furnished with a large tubercle on its lower surface, upon which the opening of the green gland is situated. The basipodite is divided by a deep longitudinal groove into two pieces, and bears at its distal extremity the expanded lancet-shaped **squame**, representing the exopodite, and the long feeler, representing the endopodite. The feeler has two stout basal joints, succeeded by a very long many-jointed filament beset with setæ.

The first antenna (fig. 26, *I*) consists of a large and peculiarly shaped proximal joint succeeded by two shorter joints; the distal one bearing two terminal many-jointed filaments, of which the outer is thicker and longer than the inner. The outer filament bears two groups of curiously

modified setæ on the under sides of most of its joints; these are known as Leydig's organs, and are supposed to serve as an olfactory apparatus. The basal joint of the first antenna is triangular in section; the upper side, corresponding to the base of the triangle, is concave, and in the middle of it there is a narrow slit-like aperture guarded by a fringe of closely set setæ. This is the aperture of the auditory organ, the structure of which will be referred to later.

The course of the gut in the crayfish is shown in fig. 28. It will be observed that it has the same relations as the gut of Apus, the œsophagus being almost at right angles to the longitudinal axis of the body, the remainder of the gut being straight, situated in the mid-dorsal line, parallel to the longitudinal axis of the body, and ventral to the heart and anterior and posterior blood-vessels, which emerge from the heart. The difference in detail is, however considerable.

The œsophagus of the crayfish leads into a capacious sac, commonly called the stomach, which, like to the similarly named organ in Apus, lies in the head region. But there are these differences, that the "stomach" of the crayfish is lined by a chitinous cuticle, whereas that of Apus is not, and the digestive glands of the crayfish do not open into the so-called stomach, but into a smaller sac lying behind it, which, for reasons which will presently become apparent, should properly be called the stomach. The large sac lined by chitinous membrane we will call the **proventriculus**. This name has the possible inconvenience that it has been already applied to another and different structure, the gizzard of the earthworm; but if the fact that the two organs have no relation to one another is borne in mind, the practical inconvenience will be very slight.

The proventriculus of the crayfish, then, is lined by a chitinous cuticle continuous with that of the œsophagus, and the cuticle of the œsophagus is in turn a continuation of the external hardened and calcified cuticle forming the exoskeleton. In fact, both œsophagus and proventriculus are formed from the stomodæum, which in the crayfish is of very much greater extent than it is in Apus, and the true stomach is therefore pushed back, and lies in the thorax. The proventriculus is divided by a constriction into a larger anterior portion, called the **cardiac** division, and a posterior smaller portion called the **pyloric** division. The name "cardiac" was given to the

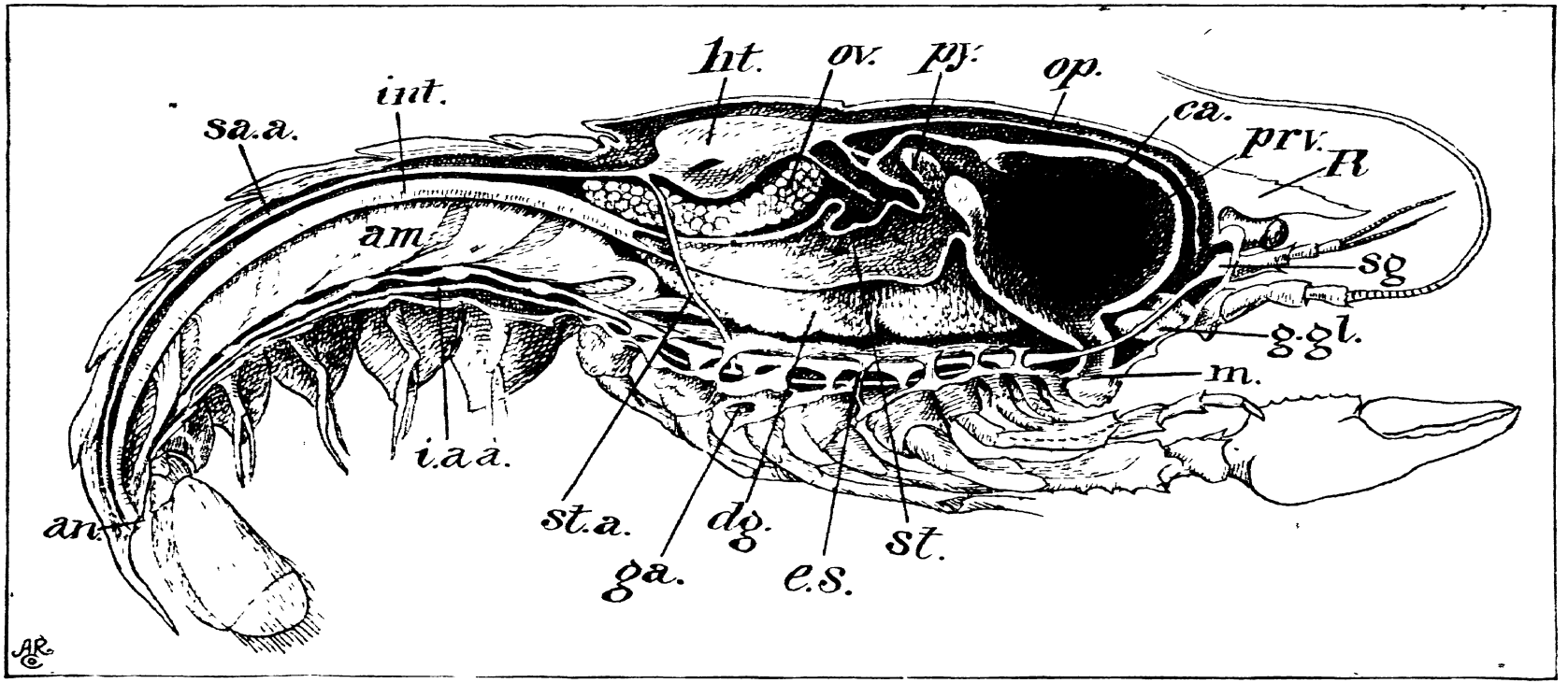


Fig. 28

A sagittal section through the body of a female crayfish. The right walls of the proventriculus, stomach, and anterior part of the intestine have been removed, but the abdominal part of the intestine, the heart, and the nervous system have been left entire. *am*, flexor muscles of the abdomen; *an*, anus; *ca*, cavity for lodgment of the left gastrolith; *dg*, left digestive gland; *e.s*, part of the endophragmal skeleton enclosing the thoracic part of the ventral nerve cord; *ga*, generative aperture; *g.gl*, green gland; *ht*, heart; *i.aa*, inferior abdominal artery, above it are the abdominal nerve cord and ganglia; *int*, intestine; *m*, mouth; *op*, ophthalmic artery; *ov*, ovary; *prv*, cardiac section of the proventriculus; *py*, pyloric section of the same; *R*, rostrum; *sa.a*, superior abdominal artery; *sg*, supra-œsophageal ganglion; *st*, stomach with duct of digestive gland opening into it; *st a*, sternal artery

anterior division from a fancied analogy to the human stomach, and is unfortunate, for, as the diagram shows, it is the part farthest away from the heart of the crayfish. The roof of the posterior part of the cardiac division, and the whole roof of the pyloric division of the proventriculus, is occupied by a series of peculiarly shaped plates and bars, some calcified, and some merely chitinous, called ossicles, which together form the internal masticatory apparatus or gastric mill of the crayfish. The structure and working of this gastric mill have been explained with such admirable fulness and clearness by the late Professor Huxley in his work on the crayfish, that a brief description of this piece of mechanism will suffice here, the reader being referred to his memoir for a fuller account. In the roof of the posterior part of the cardiac division is a plate called the **cardiac ossicle**, whose shape is shown in fig 29, *car.* To the hinder end of this is attached a short stout bar, the **urocardiac ossicle**, *ur.c.*, which runs backwards and downwards on the front limb of the fold or constriction separating the cardiac from the pyloric division of the proventriculus. To either side of the expanded cardiac ossicle is attached a small curved three-cornered piece, the **pterocardiac ossicle**. All these parts being connected by joints, are freely movable on one another, and they form a figure something like a crossbow of which the handle is bent at an angle to the bow itself. A somewhat similar crossbow is formed by four other pieces—namely, the **pyloric ossicle**, situated in the roof of the pyloric division of the proventriculus; the **prepyloric ossicle**, passing downwards and forwards from the centre of the pyloric ossicle to articulate with the posterior end of the urocardiac ossicle, and two lateral **zygocardiac ossicles**, which, fused to either end of the elastic pyloric ossicle, run downwards and forwards in the side walls of the proventriculus, and are articulated to the extremities of the pterocardiac ossicles. The lower end of the prepyloric ossicle is produced into a stout conical tooth, and the inner edge of each zygocardiac ossicle is produced into a thickened ridge bearing a number of large lateral teeth. The whole forms a jointed hexagonal framework, the front and back pieces of which are connected by two jointed rods in such a manner that when these pieces, the cardiac and pyloric ossicles, are approximated, the prepyloric rod is bent back under the pyloric ossicle, and the

urocardiac rod lies nearly in a straight line with the cardiac ossicle. At the same time the lateral pieces of the frame, the pterocardiacs and zygocardiacs are bowed outwards and recede from one another. When, on the contrary, the cardiac and pyloric ossicles are pulled apart from one another, the prepyloric ossicle is moved vertically downwards and forwards, and the lateral pieces of the frame are straightened out and approximated, causing the teeth on the

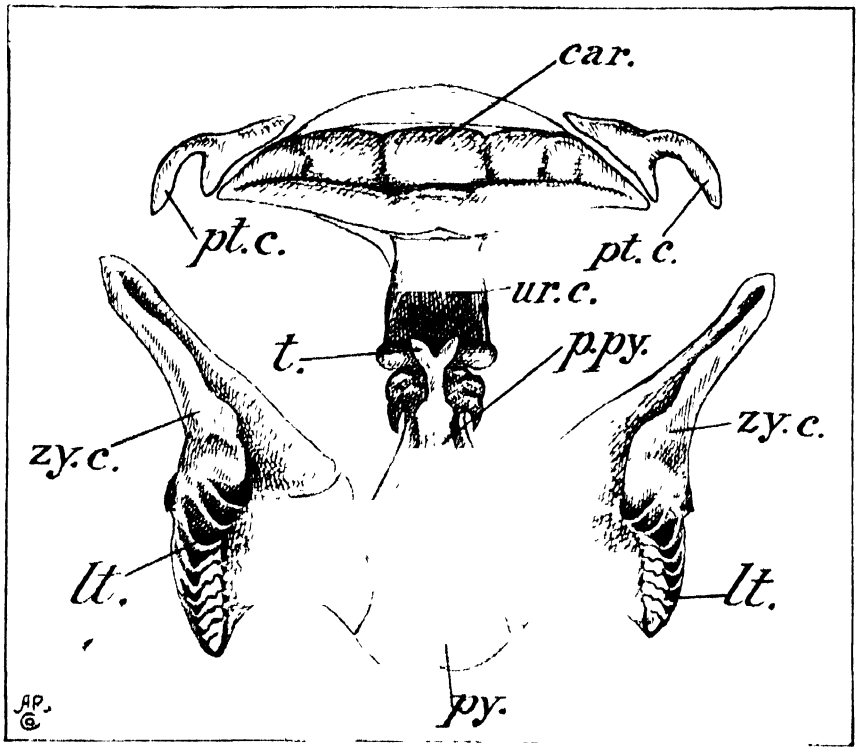


Fig. 29

The gastric mill of the crayfish. The zygocardiac have been disarticulated from the pterocardiac ossicles, and the cardiac ossicle has been pulled forward so as to straighten out the angle formed by the urocardiac and prepyloric ossicles. *car*, cardiac ossicle; *pt c*, pterocardiac ossicles; *ur c*, urocardiac ossicle; *p.py*, prepyloric ossicle; *t*, its median tooth; *py*, pyloric ossicle; *zy.c*, zygocardiac ossicles; *lt*, their lateral teeth.

inner sides of the zygocardiacs to come together and clash against the median teeth of the prepyloric and urocardiac ossicles. The tension of the walls of the proventriculus tends to keep the cardiac and pyloric ossicles approximated, but they can be pulled apart by powerful muscles, one pair of

such passing forward from the cardiac ossicle to be attached to the carapace near the base of the rostrum, another pair passing back from the pyloric ossicle to be attached to the roof of the carapace behind the proventriculus. By the alternate contraction and relaxation of these muscles, the gastric mill is set in motion, and the food contained in the proventriculus is reduced to the necessary state of fineness. At times two peculiar calcareous nodules are found in the lateral walls of the cardiac division of the proventriculus. They are known as **gastroliths**, or, popularly, as "crab's-eyes": nothing is really known about their function, though they are supposed to form a reserve of calcareous matter to supply material for the new armour formed after ecdysis. In pre-scientific days they were credited with mysterious curative properties, and were used as sovereign remedies in all sorts of diseases.

The passage from the cardiac into the pyloric division of the proventriculus is guarded by a large valvular process rising from the floor of the passage between them, and there is a further arrangement of setose ridges projecting into the cavity of the pyloric division, which effectually prevents any but the most finely comminuted food from passing into the mid-gut. The mid-gut, though extremely short, represents the stomach and the greater part of the intestine of Apus. It consists of a short segment of the gut, the internal surface of which is devoid of a cuticle, and is produced dorsally into a pouched process, the cæcum. Right and left it receives the wide ducts of the digestive glands. The mid-gut is succeeded by the intestine or hind-gut, a straight tube running back to the anus. It is lined by a chitinous cuticle raised into six prominent longitudinal ridges, covered by small papillæ, and this character, as well as its development, shows it to be an invagination of the external ectoderm—in other words, a proctodæum. The digestive glands, more commonly called the "liver," are large lobed, yellow masses lying on either side of the gut in the cephalothorax. Each moiety of the gland is divisible into three lobes, an anterior, a posterior, and a dorsal, and each lobe is composed of a number of short tubules or cæca, which are really digitiform outgrowths of the main duct forming the axis of the lobe. The ducts of the three lobes unite to form the wide hepatic duct opening into the

mid-gut. The cæca are lined by a glandular epithelium, containing numerous yellow fat globules, and zymogen granules. These are eventually discharged into the lumen of the cæcum, and pass through the ducts into the gut. There are no other glands connected with the gut.

The circulatory system of the crayfish consists of a muscular heart, a number of efferent tubular vessels or arteries with definite walls, and a system of wide lacunar blood sinuses like those of Apus.

The heart is median and dorsal, lying in the thorax, beneath that part of the carapace bounded by the branchio-cardiac grooves. It is not an elongated tube like that of Apus, but a short rhomboidal sac with muscular walls, and three pairs of valvular ostia opening into the pericardial sinus in which it lies. One pair of ostia is dorsal, another pair lateral, and the third pair ventral. The heart is connected with the walls of the pericardial space by six bands of fibrous tissue, the **alæ cordis**, similar to the structures called by the same name in Apus. Five arteries spring from the anterior end of the heart. Of these the two outermost are given off from the under side, and pass straight to the digestive glands; hence they are called the **hepatic arteries**. Inside, and above the hepatics, an **antennary artery** passes out from the heart on either side, runs forwards along the sides of the proventriculus, and divides into two branches—one, the gastric artery, going to the proventriculus, the other running forward to the head, and giving off branches to the antennæ and green gland. Between the antennaries is a median unpaired vessel, the **ophthalmic artery**, which runs straight forward in the middle line over the surface of the proventriculus, and supplies the anterior part of that organ, the œsophagus and head. Posteriorly, a single median artery is given off from the heart, and it immediately divides into two branches. One of these, the **superior abdominal artery**, runs back, just above the intestine, to the hinder end of the body, giving off numerous branches to the gut and abdominal muscles. The other branch, the **sternal artery**, runs vertically downwards, passes between the ganglia supplying the sixth and seventh pairs of thoracic limbs, and divides below the nerve chain into an **inferior abdominal artery** running backwards, and an **inferior thoracic artery** running forwards; these vessels supply the ventral muscles and limbs

with blood. It will be observed that, though the heart is very short in comparison with that of Apus, it may be regarded as a muscular dilatation of the median blood-vessel formed by the ophthalmic artery in front and superior abdominal artery behind; it is, in fact, a specialised contractile portion of a great dorsal longitudinal vessel, such as is represented by the heart of Apus and the dorsal vessel of the earthworm.

All the arteries enumerated above ramify in the organs to which they are supplied, and their ultimate ramifications are

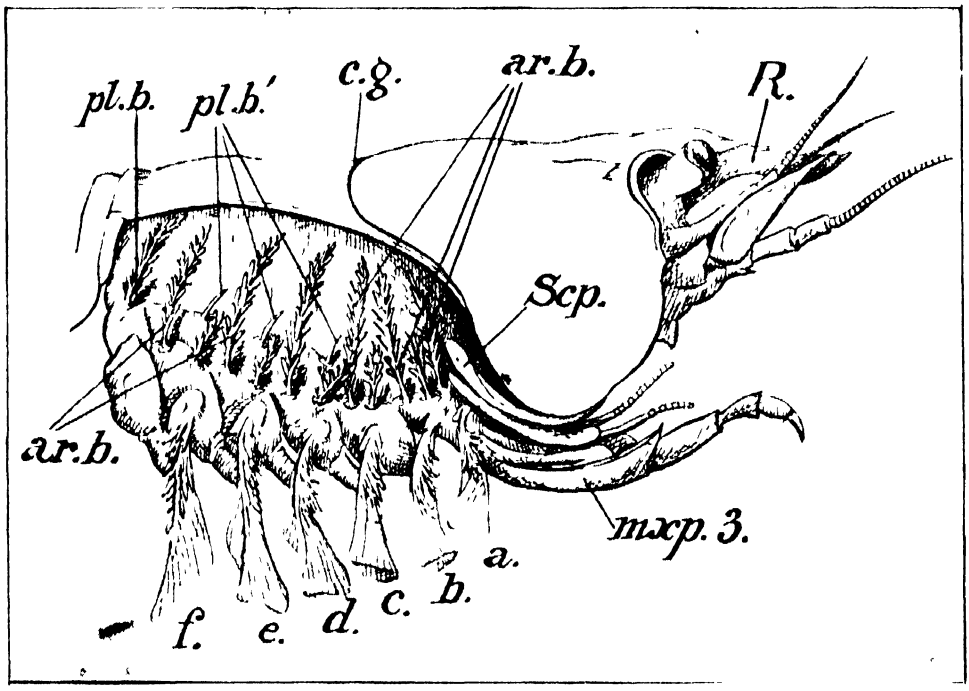


Fig. 30

The right branchial chamber of the crayfish, exposed by cutting away the branchiostegite. The podobranchiæ are turned downwards, and every alternate arthrobranch is cut short. *a-f*, podobranchiæ borne on the seventh to the twelfth limbs inclusive; *ar.b*, arthrobranchiæ; *pl.b*, functional pleurobranchia on the thirteenth segment; *pl.b'*, rudimentary pleurobranchiæ on segments 10, 11, and 12; *c.g*, cervical groove; *mxp. 3*, third maxilliped; *R*, rostrum; *Scp*, scaphognathite.

so fine as to have received the name of capillaries; but there is no true capillary system as in vertebrates. Eventually the ramifications open into larger or smaller spaces or blood sinuses lying between the tissues, and the blood is returned by special passages to the heart. One of the most important of these sinuses is the pericardial space, which has the same

relations as, though it is of less extent than, that of Apus. There is a large perivisceral sinus in the cephalothorax, whose relations again are fundamentally the same as those of Apus, and a system of branchio-cardiac canals running from the bases of the gills up the sides of the thorax, and converging to enter the pericardial sinus. After traversing the various organs of the body the blood is returned to a large ventral blood sinus in the thorax, and thence is conducted to the gills. The last-named structures are attached either to the coxopodites of the thoracic limbs, or to the arthrodial membranes of the thoracic limbs, or to the walls of the thorax, and according to position are known as **podobranchiæ**, **arthrobranchiæ**, or **pleurobranchiæ**. There is a functional podobranch on the coxopodite of every limb from the seventh (second maxilliped) to the twelfth (third pareiopod) inclusive. The first maxilliped does not bear a functional gill, but its membranous epipodite is the representative of an aborted gill. There is a single arthrobranch on the arthrodial membrane of the seventh limb, and two arthrobranchs on the arthrodial membranes of each of the next succeeding five limbs—viz. the eighth, ninth, tenth, eleventh and twelfth. The thirteenth limb bears neither podobranch nor arthrobranch, but a single functional pleurobranch is attached to the wall of the thirteenth segment, and the walls of segments ten, eleven, and twelve bear each a minute filament or rudimentary pleurobranch.* Thus, there are eighteen functional and four rudimentary gills on each side of the body. They lie close against the thoracic wall, covered over by the branchiostegite, and are bathed by the respiratory current flowing in at the hinder end and out at the front end of the branchial chamber. This current is produced by the scooping or paddling motion of the scaphognathite of the second maxilla. The branchial chamber is, for the most part, deep from above downwards, but narrow from side to side. Anteriorly, however, as it follows the line of the cervical groove, it becomes much shallower from above downwards, and at the same time wider from side to side, forming a groove or channel which opens just below the base of the second antenna. In this groove lies the scaphognathite,

* This is true for the "Écrevisse à pieds rouges," *Astacus nobilis*. I have never found more than two rudimentary pleurobranchs in the common English crayfish, *A. torrentium*.—G. C. B.

and it is in constant motion, ladling the water out through the anterior opening. The edges of the branchiostegite being free, the branchial chamber is open both below and behind—the former passage is largely blocked by the bases of the limbs, but the latter is unobstructed, and water flows freely in through it to replace that baled out by the scaphognathite. The arthrobranchiæ and functional pleurobranchia are plume-like structures, consisting of an axis or stem to the sides of which a number of delicate branchial filaments are attached. The cavity of the axis is divided by a longitudinal partition into an outer and an inner blood channel, from which lateral channels are given off to the filaments. The podobranchiæ have a somewhat different structure, the stem arising from a broad basal piece covered with setæ and attached to the coxopodite, while its distal part is modified in that its inner and posterior face is produced into a wide membranous lamina, plaited longitudinally and folded once upon itself longitudinally in such a manner that the edge of the fold looks forward (fig. 27, *VII*). The anterior and outer faces of the stem are covered with filaments like those of the arthrobranchiæ.

The blood in the ventral sinus, rich in carbonic acid after its passage through the tissues, passes up the outer channels of the axes of the gills, circulates in the gill filaments, whose thin walls admit of a free interchange of the gases dissolved in the blood and the water, and having got rid of its excess of carbonic acid and taken up oxygen, is returned down the inner blood channels of the axes into the branchio-cardiac sinuses, whence it is conveyed to the pericardial sinus, and thence is admitted into the heart by the ostia.

The excretory organs of the adult crayfish consist of a pair of "green glands" situated in the head and opening to the exterior on the hinder faces of the tubercles on the basal joints of the second antennæ, in the same position, be it noted, as the provisional excretory organs of the larval Apus. A "green gland" consists of a duct, a bladder, and a green glandular mass, from which it derives its name. The duct is a short tube lying in the coxopodite of the second antenna, behind which it turns sharply backwards, and enlarges to form a considerable membranous sac with thin walls, lying in front and to the side of the œsophagus. The glandular mass lies below the bladder, close against the sternite of the second antenna,

and if its dorsal face is examined with a lens after removal of the bladder, it may be seen to consist of the following parts:— (1.) A triangular mass of brownish-yellow colour, occupying the centre of the upper surface of the gland, the apex of the triangle directed posteriorly: this is the **end-sac**. (2.) A medullary mass of greyish-white colour surrounding the end-sac. Closer inspection shows that this is composed of a coiled tube, which opens by one end into the bladder by a relatively large oval aperture, situated just behind the posterior angle of the end-sac. The other end of the tube passes into (3) the intermediate substance occupying the posterior part of the gland, and this in turn is connected with (4) the **cortical substance**, a layer of bright green tissue investing the whole surface of the gland except the central and posterior parts of its dorsal face. The end-sac may be described as a vesicle whose cavity is divided into numerous chambers by irregular partitions extending inwards from its walls. It communicates by several openings at its anterior end, with the cortical substance, the latter being a labyrinth of reticular canals lined by a cubical glandular epithelium containing numerous green globules. The intermediate substance is really a reflection of the cortical substance over the posterior edge of the gland, and differs from it chiefly in the fact that the green globules are not present in its epithelial cells. The network of tubes forming the intermediate substance opens by several apertures into a relatively wide transparent tube, which is thrown into the several coils constituting the medullary substance. The greater part of the cavity of this tube is sub-divided by numerous irregular ingrowths from its walls, so that it is of a spongy texture. Eventually the tube opens just behind the posterior angle of the end-sac into the bladder. The end-sac and all the regions of the labyrinth are lined by a cubical epithelium, differing somewhat in character in the different regions, but glandular throughout. It has been shown that ammonium carminate injected into the blood-vessels is taken up and excreted by the cells of the end-sac; indigo carmine similarly injected is taken up by the cells of the labyrinth. Clearly, then, the different parts of the green gland have different excretory activities, but as yet little is certainly known about the composition of the fluid excreted. The most that can be said, in view of recent contradictory state-

ments, is that the green gland excretes, among other substances, a nitrogenous substance, which has been called carcinuric acid.

It is interesting to note that the larvæ of many decapods allied to the crayfish have a pair of provisional excretory organs opening at the bases of the second pair of maxillæ, so that in the decapods we have an exact reversal of the conditions which obtain in phyllopod crustacea. It is possible, though there is no direct evidence on the subject, that the ancestral crayfish had a pair of excretory tubes opening at the bases of each pair of limbs, and we do know that in the very primitive arthropod, *Peripatus capensis*, there is a pair of excretory tubes opening at the bases of each of the seventeen pairs of legs. These excretory tubes are formed as ventral outgrowths of as many pairs of cœlomic sacs, and in the adult condition the originally spacious cœlom is reduced to the cavities of the gonads, and to a series of small vesicular sacs forming the internal ends of the excretory tubules. It has been suggested that the end-sac of the excretory organs of crustacea are homologous with the internal cœlomic vesicles of the excretory tubules of Peripatus, and if this comparison is just, we have the representatives of a pair of cœlomic sacs in the second and fifth segments of the crustacea; the green glands or shell glands being tubular outgrowths of these sacs, are therefore peritoneal funnels, homologous with the genital ducts of Annelida. It should be possible to settle the question by reference to the development of the organs in question, but unfortunately the evidence is contradictory. It is stated that in the lobster the body of the green gland is formed out of a group of mesoderm cells, which acquires a cavity, grows towards the base of the second antenna, and there meets and fuses with an invagination of the ectoderm. This would confirm the supposition that the green glands are peritoneal funnels. But it has been stated again that in the phyllopod, *Leptodora hyalina*, both antennary and maxillary glands are formed from the ectoderm, and in this case there can be no question of cœlomic cavities. It is best to await further evidence on the subject, and, meanwhile, to suspend our judgment as to the homologies of the excretory organs of the crustacea.

The nervous system of the crayfish is depicted in fig. 31.

Like that of Apus and of Annelids it consists of a pre-oral cerebral ganglion connected by a pair of perioesophageal connectives with a ventral nerve chain. The points which should be particularly noticed are the following:—The cerebral ganglion is a compact mass from which both the antennary as well as the optic nerves are given off. Adopting the same reasoning that has already been applied in the case of Apus, we must

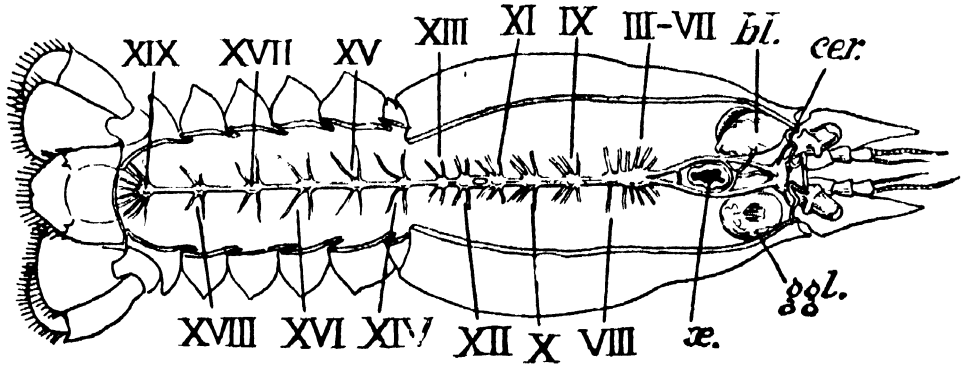


Fig. 31

Central nervous system of the crayfish. *cer*, supra-œsophageal or cerebral ganglion; *œ*, œsophagus; *ggl*, right green gland, *bl*, bladder of left green gland. *III-VII* Suboesophageal ganglion mass supplying nerves to the mandibles, maxillæ, and first two maxillipeds *VII*. Ganglion supplying the third pair of maxillipeds *IX-XIII*. Ganglia supplying the remaining thoracic segments. *XIV-XIX*. Ganglia supplying the abdominal segments.

regard the cerebral ganglion of the crayfish as a syncerebrum, into which the two antennary ganglia have been incorporated. Thus the cerebral ganglion or "brain" of the decapod is a step in advance of that of the phyllopod in respect of integration, for in the latter only the first antennary ganglia are incorporated with the brain, those of the second antennæ retaining their more primitive position at the sides of the mouth A similar tendency to integration of the thoracic ganglia is clearly marked in the crayfish. The perioesophageal connectives are united behind to a large ganglionic mass from which nerves are given off to the mandibles, maxillæ, and first and second maxillipeds. Immediately behind this, and scarcely distinguishable from it, is a second ganglionic swelling supplying the nerves of the third maxillipeds, but there is a distinct ganglion pair for each of the remaining segments from the ninth to the nineteenth inclusive. It is obvious that the first five postœsophageal ganglia have been fused to form the anterior thoracic ganglion, while the ganglion of the eighth segment is

partially fused with the compound mass. It should further be noted that whereas in Apus the ganglia and nerve cords of the ventral chain are widely separated, and the space between them is bridged over by relatively long transverse commissures, in Astacus the elements are so much approximated in the middle line that the members of each pair of ganglia are fused together, and the double nature of the connectives is only apparent on close inspection. They diverge, however, between the ganglia of the eleventh and twelfth segments to admit of the passage of the sternal artery.

The abdominal ganglia lie beneath the ventral or flexor muscles of the abdomen, and are exposed when these muscles are removed; but the thoracic ganglia lie in an arcade formed by the projection of a number of skeletal pieces into the cavity of the body. These pieces must be removed in order to see the thoracic nerve chain; though they appear to lie inside the body they are really infoldings of the external cuticle, and are shed along with the other hard parts during ecdysis.

In addition to the brain and ventral nerve cord, there is a visceral or stomatogastric nerve system, consisting of a median **azygos nerve** running back from the ventral surface of the brain between the periœsophageal connectives to the roof of the proventriculus. Here it is joined on either side by a pair of nerves arising from a stomatogastric ganglion on the connectives, and is continued backward as a median nerve lying on the roof of the proventriculus: near the pylorus it branches right and left to form the lateral nerves, each of which is joined by an infero-lateral nerve coming from the stomatogastric ganglion, and a branch to the liver is given off from their point of union.

We may now consider the organs of special sense. The olfactory hairs, or "Leydig's organs," on the first antennæ have already been mentioned, and the position of the orifice of the auditory sac has been described. The auditory organ itself is a small sac with thin chitinous walls. The posterior end of the sac is pointed, and just above it the auditory nerve —a branch of the antennary—divides into two branches and spreads along the posterior and inferior walls of the sac. Beneath the branches of the nerve the walls of the sac are raised internally into a curved ridge whose sides are beset

with a number of delicate and peculiarly shaped setæ, the auditory hairs. The cavity of the sac is filled with particles of sand and other foreign matter to which the name "otoliths" has been given.

The eyes of the crayfish are compound, like the paired eyes of Apus; there is no trace of a median unpaired eye. Viewed with a lens the eye appears as a convex oval area at the extremity of the eyestalk. It is covered with a soft colourless cuticle, the **cornea**, divided into a great number of quadrangular facets, by two sets of fine lines crossing each other nearly at right angles. The eye looks black, because of the large quantity of pigment associated with its inner parts and seen through the cornea. A vertical section shows that the eye is made up of a large number of elongated visual elements, one corresponding to each facet of the cornea. These elements converge from the convex cornea towards a ganglionic mass situated in the eyestalk, the optic ganglion, and from this the optic nerve runs back to the cerebral ganglion. The paired eyes of Apus are formed on the same principle.

It is not possible to enter into a long description of the compound eyes of Arthropods, still less to consider the different theories that have been put forward to account for their origin. But it may be stated shortly that every compound eye is made up of a large number of visual rods called **ommatidea**, and each ommatideum is an eye more or less perfect in itself, and isolated from its fellows by a sheath of dark pigment contained in special pigment-bearing cells. All the different parts of the ommatideum are formed by the multiplication and differentiation of the layer of columnar ectoderm which underlies the cuticle, a layer which in the Arthropoda is known as the **hypodermis**. Over the general surface of the body the hypodermis is but one cell thick, but at the spot where the eyes are formed it becomes several layers thick, and its cells are arranged in groups about a number of ideal lines converging from the surface of the eye to the optic nerve beneath. Every such group gives rise to an ommatideum consisting essentially of an outer group of cells, the **vitrellæ**, which form a refracting body, the **crystalline cone**, and an inner group of cells, the **retinula**, which give rise to a peculiar rod-like structure, the **rhabdom**. The inner ends of the retinular cells are continued into the fibres of the optic

nerve. The external cuticle may either be flat and continuous, as in Apus, or may be divided into as many facets as there are ommatidea, as is the case in Astacus. In either case the cuticle is transparent, and beneath it is a layer of hypodermis cells, which are grouped together in fours above each ommatideum in those eyes in which corneal facets are developed,

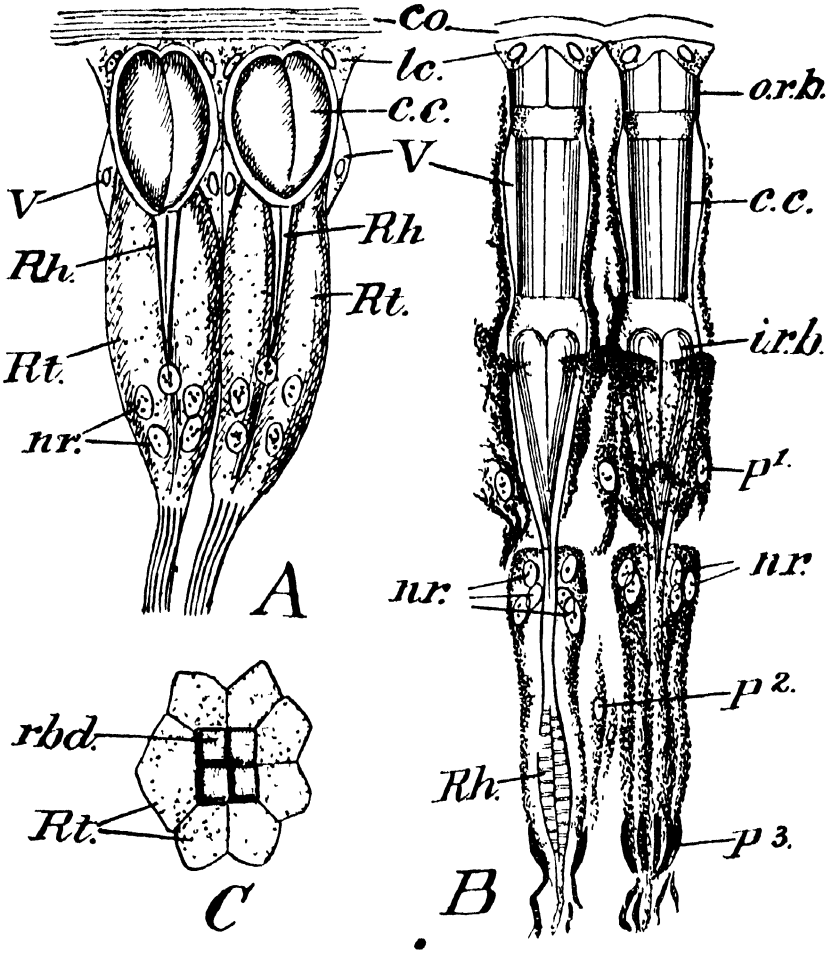


Fig. 32

A. Two ommatidea from the paired eyes of *Apus cancriformis*. *B* Two ommatidea from the eye of *Palæmonetes varians*. *C*. Transverse section through the retinula of *Palæmon squilla*, showing seven retinular cells surrounding four rhabdoms. *co*, cornea; *lc*, lentigen cells; *c.c*, crystalline cones; *V-V*, vitrellæ; *o.r.b*, outer refractive body; *i.r.b*, inner refractive body; *Rt*, retinula; *Rh*, rhabdoms; *nr*, retinular nuclei; p^1, p^2, p^3, pigment cells. (*B* original, *A* and *C* after Grenacher.)

and are known as Semper's cells, or better as **lentigen cells.** Turning now to the actual eye of Apus. The transparent external cuticle or cornea is not facetted, and the lentigen cells beneath are attached to it by their broader ends, their narrower

internal ends dipping down between the crystalline cones of the ommatidea. In each ommatideum the crystalline cone is an ovoid refractive body, surrounded by the four vitrellæ which have given rise to it. The cone itself is formed of four pieces, one piece for each vitrella cell. The hinder ends of the vitrellæ abut upon the retinula. There are five elongated retinular cells grouped together about the optical axis of the ommatideum, and each gives rise along its inner margin, where it is in contact with the remaining four retinular cells, to a chitinous rod or **rhabdomere**. The five rhabdomeres are united together to form the rhabdom. Each ommatideum is surrounded by pigment cells.

In the eye of Astacus, the cuticular lens surmounting each ommatideum is followed by a group of four lentigen cells. Beneath these is the "crystalline cone," a complex structure formed by four crystalline cone cells or vitrellæ, and consisting of an outer refractive body, a median four-sided crystalline cone proper and an inner refractive body (*o.r.b.*, *c.c.*, *and i.r.b.* in fig. 32). The retinular cells are seven in number, and co-operate in the formation of a spindle-shaped rhabdom, which is shown in transverse section to consist of only four rhabdomeres. The rhabdom is marked by transverse alternately light and dark bands, and hence is often called the striated spindle. The position and relation of the pigment cells may be gathered from the figure.

The general anatomy of the ovary and testis have already been described. The latter resembles a racemose gland, consisting of a number of ramifying ducts ending in small dilatations. The cavities of the vesicles are lined by large nucleated germinal cells, which undergo division, and their products eventually become changed into remarkable wheel-shaped spermatozoa. Each spermatozoon consists of a discoid body produced at the circumference into a number of tangential tapering curved processes. Inside the body is a ring-shaped thickening, and lying to one side of this a smaller oval corpuscle which is considered to be the nucleus. During their passage through the vasa deferentia the spermatozoa are enveloped in a viscid secretion, and on discharge are aggregated into white chalky-looking strings which are deposited by the male on the sterna of the posterior thoracic and anterior

abdominal segments of the female, where they may be seen adhering as a white mass. The ova are formed from the germinal cells lining the walls of the saccular ovary. Certain of these cells increase in size and become ova; they are surrounded by a follicle and project into the cavity of the ovary, into which, when ripe, they fall by the bursting of the follicle, and pass to the exterior through the oviducts. During their passage through the oviducts the ova are invested by a viscid transparent substance, and on passing to the exterior are attached by short stalks of this substance to the abdominal limbs. A female crayfish may often be seen with a mass of eggs fastened beneath the abdomen, and is then commonly said to be "in berry." The manner in which the ovum is fertilised by the spermatozoon is not known, but segmentation sets in soon after the eggs are extruded, and all the principal stages of development are passed through whilst the eggs are attached to the mother.

The ovum of the crayfish is abundantly supplied with food-yolk, in which the nucleus occupies a central position. The nucleus divides repeatedly, and the products of division pass to the periphery of the ovum, where they form a layer of nuclei embedded in a continuous sheet of protoplasm not yet segmented into separate cells. The protoplasm and yolk are then divided into as many elongated cells as there are nuclei. Each cell is called a **yolk-pyramid**, reaches from the periphery nearly to the centre of the ovum, and is made up of an external protoplasmic part containing the nucleus, and a large internal part consisting of little else than yolk (fig. 33, *C*). In the next stage the protoplasm surrounding the peripheral nuclei is separated to form a single layer of cells or blastoderm investing a central mass of yolk formed by the fusion of the inner ends of the yolk-pyramids (fig. 33, *D*). An oval thickening, known as the primitive streak, is now formed on what will be the ventral side of the blastoderm, and immediately afterwards five other thickenings are formed near it—viz. a pair of rounded areæ at its anterior end, the optic lobes; a pair of lateral thickenings called the thoraco-abdominal plates, and posteriorly a median thickening called the endoderm plate, which is continuous anteriorly with the primitive groove. In the next stage the endoderm plate is invaginated, forming a small pocket projecting into the yolk and opening to the

exterior by a wide mouth or blastopore. The pocket is the mid-gut or mesenteron, and the cells forming its walls are hypoblast. During, and even before the invagination, the cells of the primitive streak lying in front of the blastopore divide rapidly, and give rise to a small mass of cells lying between

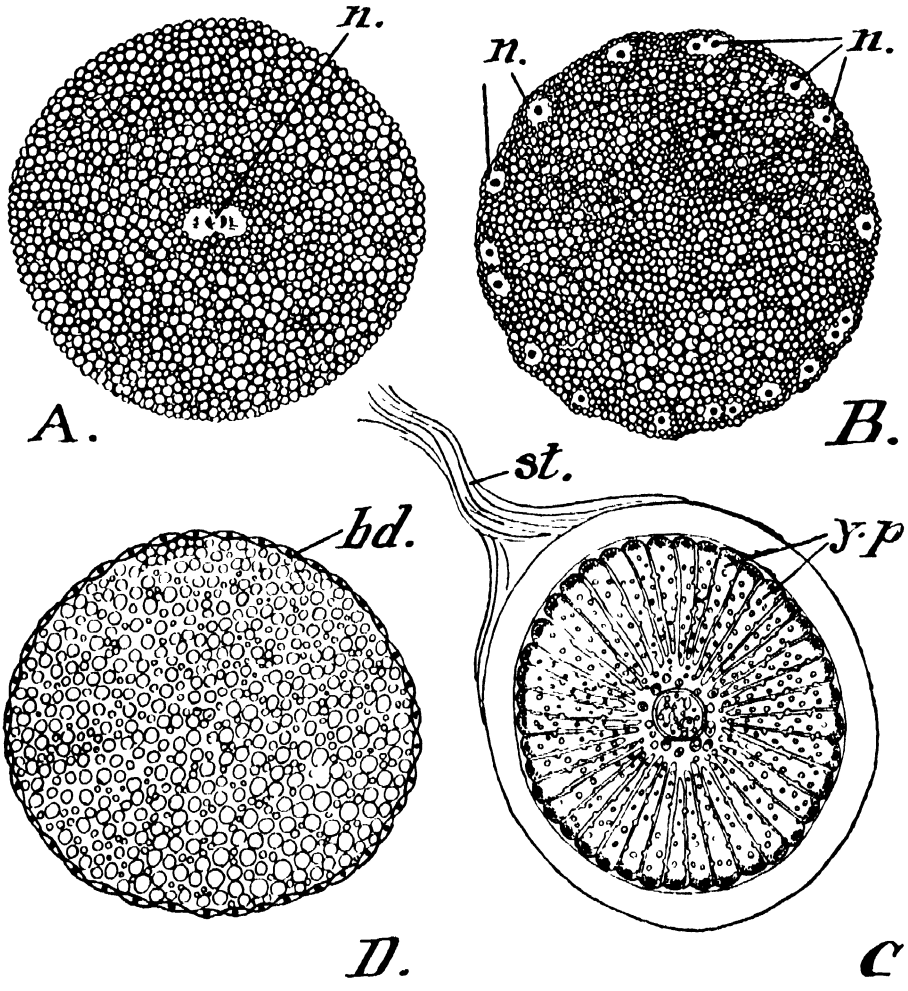


Fig. 33

A. A recently fertilised ovum of Astacus showing the central nucleus *n*, in the act of dividing. *B*. A later stage in which the nuclei form a peripheral layer enclosing the yolk. *C*. The ovum is divided into a number of yolk-pyramids, *yp*. *D*. The inner ends of the yolk-pyramids have fused to form a central mass of yolk enclosed by *bd*, the blastoderm, composed of flattened cells. *st*, the stalk by which the egg is attached to the limbs of the parent. (*A*, *B* and *D* after Morèn, *C* after Reichenbach.)

hypoblast and blastoderm in front of the blastopore. This mass of cells is the mesoblast. The invagination of the mesenteric cavity progresses some little way till a flattened sac is formed lying between the yolk and the epiblast; then the

blastopore closes, and for a while there is no communication between the mesenteron and the exterior. Even before the blastopore is closed, the hypoblast cells forming the walls of the mesenteron begin to absorb the yolk lying outside them.

They actually engulf the yolk spherules, and soon become greatly distended. It should be noticed that the nucleus of each cell, surrounded by a mass of granular protoplasm, takes up a position nearest to the seat of activity—namely, on the outside of the cell nearest to the yolk; and the yolk spherules which have been absorbed are passed into the interior of the cell, and are aggregated at that end which is adjacent to the cavity of the mesenteron. This process of absorption of the yolk continues until the whole of the yolk is stored up in the walls of the mesenteron, the hypoblast cells becoming enormously long and pyramidal so as to resemble the yolk-pyramids of an earlier stage (fig. 34, *F*).

Meanwhile, important changes have been taking place in the embryonic area on the ventral surface. The optic lobes become more distinct, and project as low, rounded swellings from the surface. Behind them, on either side, two pairs of simple bud-like outgrowths indicate the primordia of the first and second antennæ, and a little later a third pair of buds, the primordia of the mandibles, is formed behind them. Between the first antennæ a shallow depression of the ectoderm marks the commencement of the stomodæum; from the first its anterior edge is overhung by a fold, the future upper-lip or labrum. Posteriorly, just in front of the spot where the blastopore closed, the thoraco-abdominal rudiment rises from the surface of the egg as a large median swelling, in the centre of which the proctodæum is formed as a narrow but deep invagination extending through the abdominal swelling towards the closed mesenteric sac. This embryonic stage, with three pairs of limbs, is considered by many to represent the nauplius larva of other crustacea, but it is not expedient to attach too much importance to it.

The further growth of the embryo may be followed in fig. 34, *A*, *C*, *E*, representing ventral views of successive stages of development, and the longitudinal sections, fig. 34, *B*, *D*, *F*, and fig. 35, should be carefully compared with these. It will be seen that new pairs of limbs are successively added behind those already existing, and that each pair soon

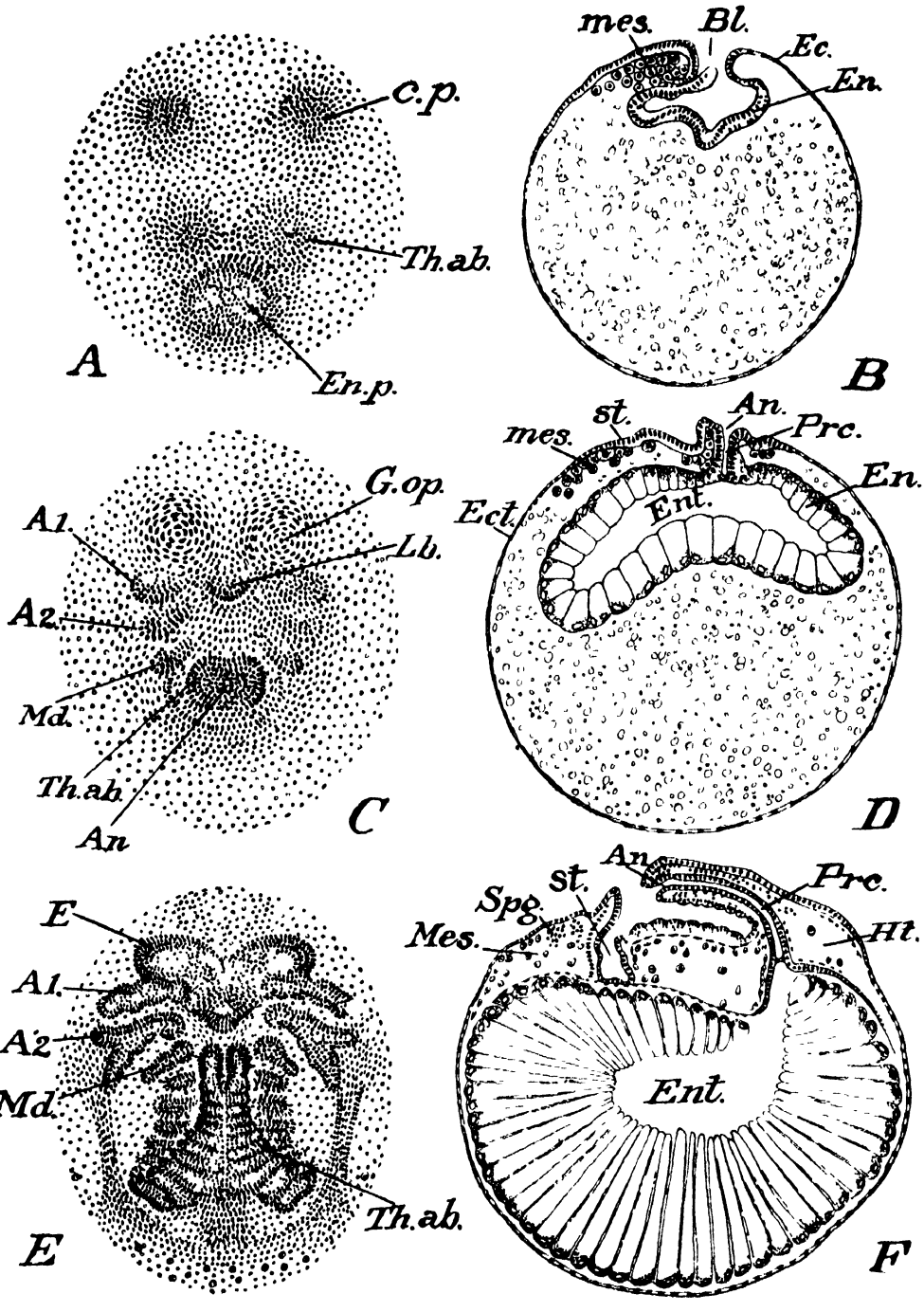


Fig. 34

A. Ventral view of an egg of Astacus in an early stage of development. *cp*, optic lobes; *En.p*, endoderm plate; *Th.ab*, thoraco-abdominal plate. *B*. Sagittal section through a slightly older egg. *Bl*, blastopore; *Ec*, epiblast; *En*, hypoblast; *mes*, mesoblast. *C*. Ventral view of the so-called nauplius stage. *A1*, first antenna; *A2*, second antenna; *An*, anus; *G.op*, optic ganglion; *Lb*, labrum; *Md*, mandible. *D*. Sagittal section through an embryo of nearly the same age as *C*. *Ent*, enteron; *Prc*, proctodæum; *st*, commencement of the stomodæum, other letters as before. *E*. Ventral view of a more advanced embryo; the thoraco-abdominal rudiment *Th.ab*, is well developed and turned forwards; *E*, eyes. *F*. Sagittal section through an embryo of the same age as *E*. *Ht*, heart; *Spg*, supraœsophageal ganglion; other lettering as before. It should be noticed that the yolk has been entirely absorbed by the hypoblast cells lining the enteron, so that the latter resemble the yolk-pyramids of the earlier stage, shown in fig. 33, *C*. (All the figures after Reichenbach.)

assumes the distinctive characters of the adult limb. Thus the first and second antennæ soon become biramous; the mandibles are never biramous, but at an early stage show a differentiation into a thickened proximal joint, and a conical appendage which will become the jointed palp. In the first maxillæ the endopodite is from the first predominant, the exopodite being represented only by a small swelling. The second maxillæ and the maxillipeds, which have both endopodite and exopodite in the adult, are from the first biramous. The chelæ and first two pairs of pareiopods seem to be biramous at an early stage; the terminal branches, however, do not represent endopodite and exopodite, but the rudiments of the chelæ characteristic of the adult limbs. The abdominal limbs are biramous from the first. In short, the limbs grow directly from mere buds into their permanent form without passing through any ancestral stages. The growth of the thoraco-abdominal swelling requires close attention. It projects more and more from the surface of the egg, and as it grows it is folded down beneath the anterior part of the embryo, so that its extremity nearly touches the labrum. It is divided by a series of constrictions into eleven segments — namely, five thoracic bearing the rudiments of the chelæ and the four pairs of pareiopods, and six abdominal bearing the six pairs of pleopods. At the end of all is the terminal piece or telson, divided by a deep median incision into two lobes. As the telson increases in size, the anus is shifted from its original posterior position to the ventral surface.

While these changes are in progress, the eyes grow out as two conspicuous prominences in front of the first antennæ. Beneath them a pair of thickenings of the ectoderm gives rise to the optic ganglia, and a little further back a similar pair of thickenings is formed in connection with the first antennæ, and yet another in connection with the second antennæ. These three pairs of thickenings eventually fuse to form the cerebral ganglion, and it is interesting to note that the "brain" of the crayfish is shown by its development to be a syncerebrum, formed by the fusion of the optic and two succeeding pairs of ganglia appropriate to the appendages. The thoracic and abdominal ganglia are formed from ectodermic thickenings in connection with the successive pairs of limbs.

Turning now to the internal changes, fig. 34, *D*, shows the relatively small size of the embryonic area at the time when the mesenteron is still a closed sac of relatively small extent. The thoraco-abdominal swelling is shown, traversed by the proctodæum, *prc*; the latter is in contact with the wall of the mesenteron at its lower end, but has not yet established communication with it. The commencement of the stomodæal invagination is seen at *st*, and the mesoblast appears as a number of scattered cells lying below the epiblast of the embryonic area. The mesenteron has only absorbed a small part of the yolk, and the hypoblast cells are comparatively small. In fig. 34, *F*, great changes have taken place. The embryonic area is much larger, and the cephalic and thoraco-abdominal regions are well marked. The stomodæum and proctodæum have increased to a marked extent, and the latter touches but does not yet open into the mesenteron. The rudiment of the cerebral ganglion is conspicuous, and the mouth is overhung by a large labrum. The anterior thoracic region is distinctly segmented, as also is the thoraco-abdominal outgrowth, the latter being now bent forwards nearly as far as the mouth. The segmentation, however, affects the epiblast only, and is expressed in the section by the epiblastic thickenings which will give rise to the ventral chain of ganglia. The limbs do not appear, as the section passes through the middle line of the body. The mesoblast has no share in the segmentation, consisting as it does of numerous scattered cells lying between hypoblast and epiblast; but posterior to the proctodæum a certain number of mesoblast cells have united to form the walls of a hollow vesicle, the heart. The hypoblast cells have completely absorbed the yolk, and have increased enormously in size; their external nucleated ends are in contact with the epiblast over the upper two-thirds of the embryo, and their inner ends, swollen by the yolk they have absorbed, delimit the now spacious mesenteric cavity. The latter, the mid-gut, has at this stage attained its largest size; as development progresses, the yolk stored up in the hypoblast cells is withdrawn for the nourishment of the other tissues of the growing body, and the mid-gut becomes relatively smaller and smaller.

In the stage shown in fig. 34, *F*, there is a band of mesoblast cells lying dorsal to the proctodæum in the thoraco-

abdominal region. In the next stage, this band is divided up into a number of paired groups corresponding with the external segmentation of the embryo, and in the abdominal region each group acquires a lumen, so that there is a transitory stage in which the mesoblast of the abdomen is divided up into a series of segmentally-arranged, paired pouches, bearing a close resemblance to the mesoblastic somites of the Annelida. This condition, however, is not of long duration. The walls of the pouches are differentiated to form the flexor and extensor muscles of the abdomen, and all trace of their cavities is lost. It is probable that, while they exist, the mesoblastic pouches are representative of the somites of worms, and their cavities are to be regarded as cœlomic cavities. Unfortunately we have no definite information about the development of the gonads in Astacus. They make their appearance late in embryonic life, and so far as our information goes, they do not appear to have any connection with the transitory mesoblastic pouches which have just been described. This, it must be admitted, tells against the cœlomic nature of the cavities of the pouches, for the cavities of the adult gonads must, according to the principles already laid down (p. 52), be regarded as the representatives of the true cœlom of the adult. Nor does the development of the excretory organs of the crayfish throw much light on the question of the cœlom. The green glands appear, at an early stage, as a pair of epiblastic invaginations at the bases of the second antennæ, and in subsequent stages there is no trace of their entering into connection with any mesoblastic cavity or structure which could be regarded as cœlomic. On the other hand, the green gland of the lobster is described as being formed as an epiblastic invagination which meets and communicates with a mesoblastic vesicle, the latter becoming the end-sac of the adult organ, while the epiblastic tube forms the labyrinth, bladder, and duct. Larval excretory organs have not been described in the crayfish, but in many decapod crustacea a pair of such organs is formed at the bases of the second maxillæ.

A late embryonic stage is represented in fig. 35. The ventral flexure is pronounced, the head and telson being in contact. The general organisation of the body can easily be followed in the figure, and it should be noticed that all the characteristic anatomical features of the adult are represented. The

stomodæum has grown into a large sac, the proventriculus, in which the cardiac and pyloric divisions can be distinguished. It opens into the mesenteron, now short in length, but produced dorsally into a large saccular lobe lined by hypoblast cells, still distended with yolk. Several digitate diverticula from the sides of the mesenteron indicate the commencement

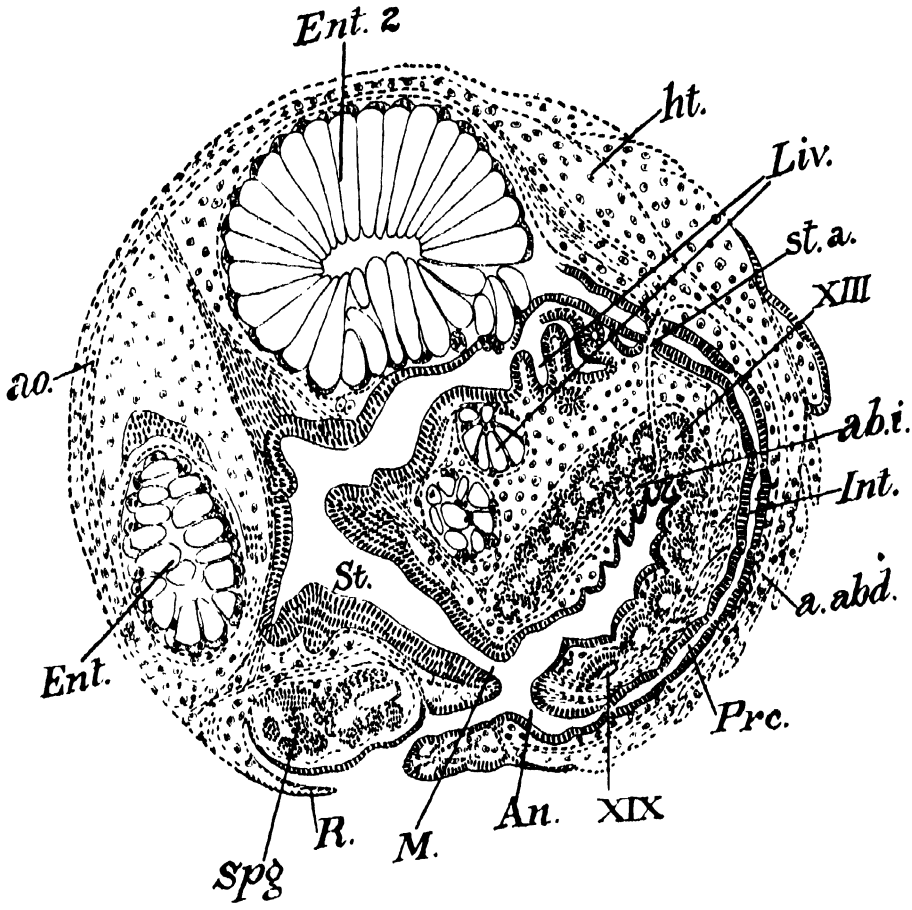


Fig. 35

Sagittal section through an advanced embryo of Astacus (after Reichenbach). *a abd*, superior abdominal artery; *ab i*, inferior abdominal artery; *ao*, ophthalmic artery; *An*, anus; *Ent*, anterior division of the enteron; *Ent* 2, dorsal division of the enteron; *ht*, heart; *Int*, intestine, formed from the proctodæum *Prc*; *Liv*, outgrowths of the mid-gut which will form the digestive gland; *M*, mouth; *R*, rostrum; *Spg*, supraœsophageal ganglion; *St*, stomodæum; *st.a*, sternal artery; *XIII*, ganglion of the thirteenth segment, or eleventh post-oral ganglion; *XIX*, ganglion of the nineteenth segment (seventeenth post-oral ganglion).

of the digestive gland. The proctodæum is still shut off by a partition from the mesenteron, and is intersegmentally constricted. The vascular system is well developed, and the principal arterial channels are established. The cerebral,

thoracic, and abdominal ganglia can easily be seen; the first five pairs of post-oral ganglia are still distinct, and have not yet fused to form the composite postœsophageal ganglion of the adult.

Shortly after this stage, the young crayfish is hatched, with practically the full characters of the adult. There are considerable differences, it is true, such as the shape of the rostrum, the dome-shaped carapace, the form of the telson, and the absence of the first and last pair of abdominal limbs, but none of so much importance as to lead us to describe the newly-hatched young as a larval form. As soon as the young are set free from the egg case, they attach themselves to the abdominal limbs of the mother by their chelæ, the extremities of which are sharply pointed, and incurved, so that when they once lay hold of any soft substance, the grip cannot easily be relaxed. The limbs of the mother being covered with the tenacious material which formed the egg cases, the young crayfishes are firmly fixed, and are carried about by her until they have completed their first moult. Afterwards they leave their parent from time to time, returning to her protection when alarmed, and eventually, after further ecdyses, they leave her altogether, and lead an independent existence.

CHAPTER XXIV

THE INSECTA—PERIPLANETA ORIENTALIS AND AMERICANA

THE Crustacea, of which Apus and Astacus have formed our examples, are essentially aquatic arthropoda breathing by gills. The centipedes, spiders, scorpions, and insects, are terrestrial arthropoda, breathing air by means of tubular or sacculated involutions of the external skin. Of these terrestrial forms it will only be possible in this place to deal with a single example of the very large and highly differentiated class of Insecta, and we cannot select a better example than the common cockroach, both because of its convenient size, and because it represents one of the oldest and most generalised orders of the class.

Ubiquitous as it is in these days, the house cockroach is not a native of England, but has been introduced into this country in comparatively recent years. It came over in ships trading with the East, and was first mentioned as infesting London houses in 1634. It was long before these household pests spread from London into the country; thus Gilbert White writes of "an unusual insect" which had made its appearance in Selborne in 1790, the intruder proving to be the cockroach. But as the communications between seaport and inland towns improved, and imported goods were carried into the country in bulk, the cockroach spread more and more rapidly, and is now almost ubiquitous.

The common species, *Periplaneta orientalis* is a native of tropical Asia; a somewhat larger species, *P. americana*, is a native of tropical America, and is as common as the Oriental form in some English towns. In the former species the wings and wing covers of the female are rudimentary, and in the male do not reach to the end of the abdomen. In *P. americana* both sexes are winged, and the wings and wing covers are longer than the body. The allied genus *Blatta* is a native of Europe, and comprises several species of smaller size and less

domestic habits than Peripianeta. The habits of the cockroach are so familiar as scarcely to require description. It is a nocturnal animal, living by day in crevices and holes, preferably in some warm corner of the house, for it is very susceptible to cold. It is exceedingly voracious, and, as housekeepers know to their cost, attacks every eatable thing that comes in its way.

The familiar name of "black beetle" is a misnomer, for the cockroach belongs to the order *Orthoptera*, and has not the hard glossy wing-cases which, among other characters, are distinctive of the true beetles or coleoptera. The name "cockroach" seems equally inappropriate, but it is probably a corruption of the Spanish *cucarácha*, of which *kakerlak* is the Dutch, and *cancrelat* the French equivalent.

Students of insect anatomy will find a full and admirably lucid account of the anatomy and physiology of the cockroach in Miall and Denny's volume on this animal.* Nothing more will be attempted in this place than to contrast its structure as a typical insect with that of the crustacea described in the two last chapters.

The animal is evidently an arthropod; it has a segmented body protected by a firm chitinous exoskeleton. Certain of the segments are provided with jointed appendages, which bear a sufficiently close resemblance to the walking limbs of a crayfish; the mouth is furnished with three pairs of jaws which are evidently modified limbs, and internally the blood-vascular system, the reduced cœlom, the nervous system, and other characters, correspond in a general way with the anatomical arrangements of the crustacean. But the insect has many characters peculiar to itself. The three regions of the body, head, thorax, and abdomen, are very distinct, the head in particular being separated from the thorax by the intervention of a slender neck. The thorax comprises only three segments, and these alone bear walking-limbs, the abdomen being legless except for the anal cerci, which are proved by development to be the representatives of the eleventh pair of abdominal limbs. Moreover, the two posterior segments of the thorax bear each a pair of membranous expansions of the integument or wings,

* The "Structure and Life-History of the Cockroach," by L. C. Miall and Alfred Denny. London: Lovell, Reeve & Co.; Leeds: Richard Jackson, 1886.

organs which are not present in any other arthropods. Taking the several regions of the body in some detail, the head is relatively small, elongated dorso-ventrally, and compressed from front to back. Viewed from in front it has a somewhat pear-shaped outline, the upper part being broad, and evenly rounded, while the sides narrow downwards towards the mouth. The whole of the front and sides of the head are defended by strong chitinous plates—namely, two **epicranial plates** covering

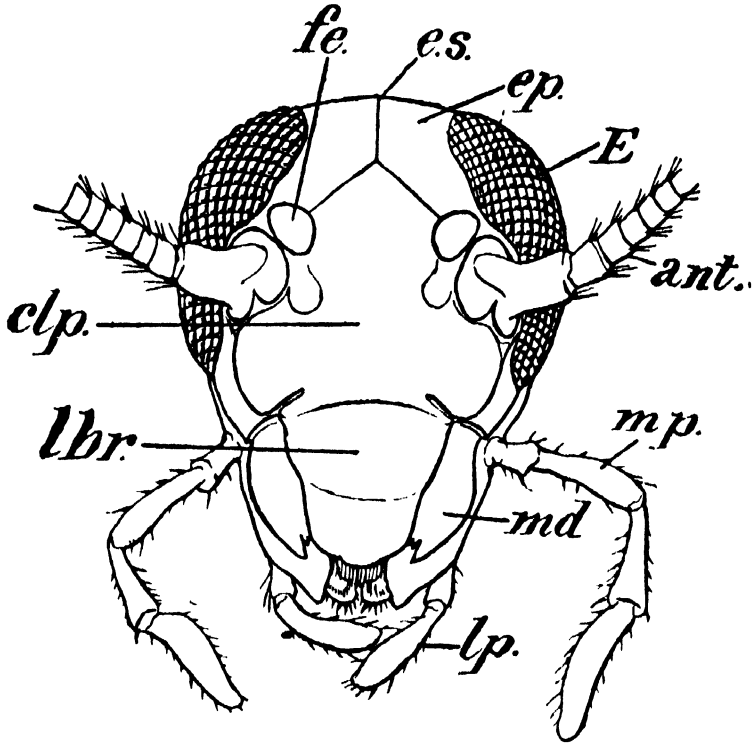


Fig. 36

The head of *Periplaneta orientalis* seen from in front. *ant*, antenna; *clp*, clypeus; *E*, eye; *ep*, epicranium; *es*, epicranial suture; *fe*, fenestra; *lbr*, labrum; *lp*, labial palp; *md*, mandible, *mp*, maxillary palp.

the dorsal and posterior sides; a **clypeus**, forming the lower part of the face; the **genæ**, a pair of plates covering the sides of the head below the eyes. The **labrum** or upper lip is an oblong plate hinged on the lower edge of the clypeus. The arrangement of the plates is shown in fig. 36. The head bears a pair of large compound eyes, a single pair of very long filiform antennæ, and three pairs of foot-jaws -viz. the mandibles and two pairs of maxillæ. The eyes are large reniform swellings at the sides of the head, the surface of each being divided into a

great number of minute hexagonal facets. In all essential characters the structure of the compound eye of the cockroach is the same as that of Astacus. The antennæ are attached to the front of the head immediately below the eyes. Each antenna consists of a tolerably stout basal joint movably articulated by a ring of soft cuticle to a cavity in the clypeus. The basal joint is succeeded by as many as seventy-five to ninety small joints beset with bristles. In the male the antennæ are rather longer than the body, but in the female they are shorter. To the inner and upper side of each antenna is a small circular area of white colour, situated at the end of the suture dividing the epicranium from the clypeus. These areas are called the **fenestræ**. They are covered by soft cuticle, and are supposed to represent aborted ocelli, but their function and significance are altogether doubtful. The mandibles are stout curved bars articulated partly to the posterior downward extensions of the epicranial plates, partly by an anterior joint to the clypeus. Their inner edges are strongly toothed, and they work from side to side; when approximated they are entirely covered by the labrum. The first pair of maxillæ are articulated to the epicranium behind the mandibles. Each maxilla consists of a two-jointed base bearing an inner and an outer branch, and it would be convenient to call these by the same names as the parts of the crustacean limb with which they are apparently homologous—namely, protopodite, endopodite, and exopodite. But entomologists have adopted a different nomenclature, and therefore we must call the proximal joint of the protopodite the **cardo**, the distal joint the **stipes**, the exopodite the **palp**. The endopodite is divided into an inner pointed blade furnished with stiff bristles along its inner border, the **lacinia**, and an outer softer and longer portion called the **galea**. The palp consists of five setose joints, of which the first two are the shortest. The second pair of maxillæ are constructed on the same plan as the first, but the protopodites and endopodites are fused together in the middle line to form a flat-jointed plate called by entomologists the lower lip or **labium**. The fused coxopodites, corresponding to the cardines of the first maxillæ, are called the **sub-mentum**, the fused basipodites, the **mentum**, and the partially fused endopodites are called the **ligula**. Each half of the ligula is further divided into an outer moiety, the **paraglossa**, corresponding to the galea of the first

maxilla, and an inner moiety corresponding to the lacinia. The exopodites or palps of the second maxillæ are three-jointed.

A shield-shaped aperture, called the occipital foramen, marks

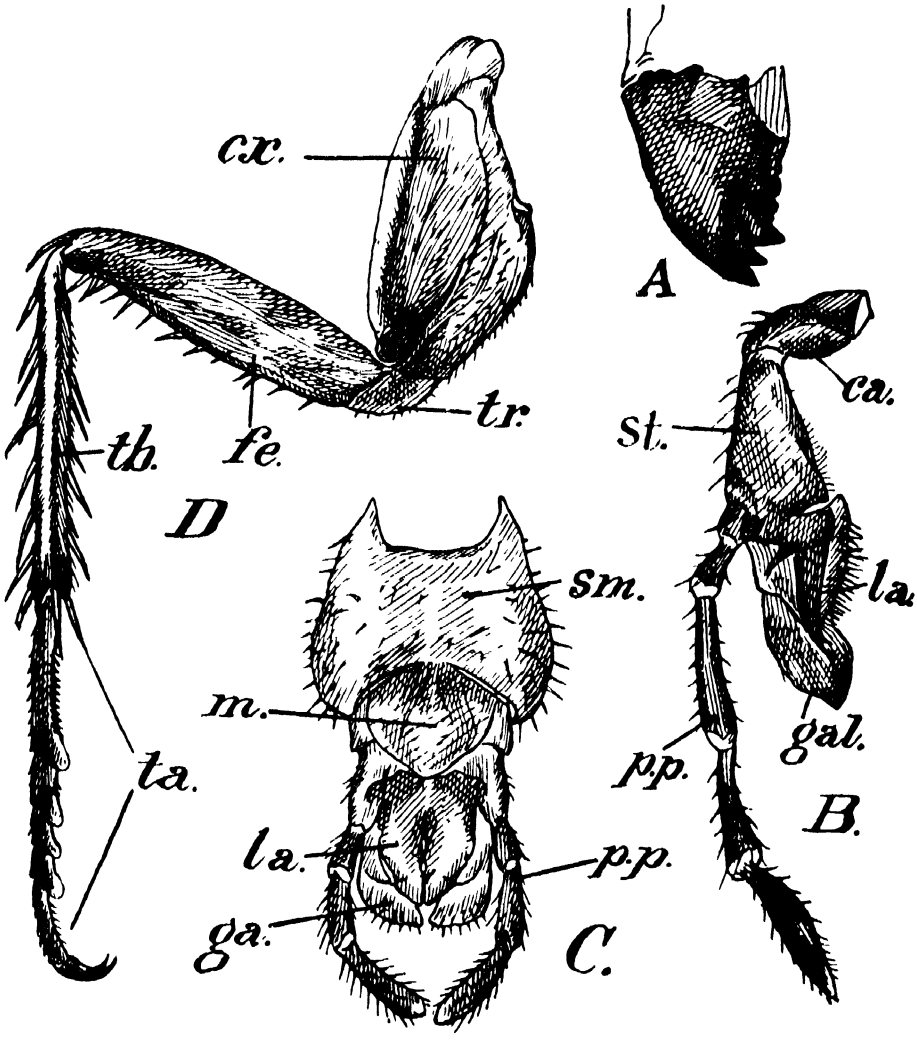


Fig. 37

A. Right mandible of *Periplaneta orientalis*. *B*. Right maxilla. *ca*, cardo; *st*, stipes; *la*, lacinia; *gal*, galea; *p.p*, palp. *C*. The labium seen from behind. *sm*, sub-mentum; *m*, mentum; *ga*, paraglossa, corresponding to the galea of the maxilla; *la*, ligula; *p.p*, palp. *D*. The mesothoracic limb of the right side. *cx*, coxa; *tr*, trochanter; *fe*, femur; *tb*, tibia; *ta*, the five-jointed tarsus. The limb is drawn to a smaller scale than the mouth parts.

the place where the neck joins the back of the head. The neck itself is slender and soft, covered with a soft white cuticle except for seven hard chitinous patches or sclerites, of which one is dorsal, two ventral, and two pairs lateral.

The three segments of the thorax are known as the

prothorax, mesothorax, and metathorax. They are roofed over dorsally by as many slightly arched chitinous plates or terga, generally known as the **pronotum**, **mesonotum**, and **metanotum**. Of these the pronotum is much the largest, and projects forward so much that it not only conceals the neck, but the head can also be withdrawn under it. Ventrally each of the three thoracic segments is provided with a small but distinct median skeletal piece, the sternum, and laterally there are some smaller hard pieces, some of which may be equivalent to the epimera of Crustacea, but others more probably belong to the bases of the limbs. The pro-, meso-, and metathorax bear each a pair of walking legs consisting of a stout basal joint, the **coxa**, a very small articular joint, the **trochanter**, an elongated and fairly stout joint, the **femur**, a more slender **tibia**, and a **tarsus** composed of five short terminal joints terminated by a very small movable piece bearing a pair of hooked claws. The mesothorax and metathorax are further distinguished by the possession of wings movably articulated to the anterior corners of their terga. The wings are membranous expansions of the integument, strengthened by a network of chitinous ridges or **nervures**. The anterior or mesothoracic wings are dark-coloured and horny; they are not used in flight, and when at rest are laid flat back over the metathorax and abdomen, the left wing overlapping the right, so that together they form a protective cover to the more delicate posterior wings, and hence are generally known as the wing covers or **tegmina**. The metathoracic wings are thin and membranous, and when at rest are folded up longitudinally and laid back over the abdomen covered by the tegmina. In *Periplaneta americana* both sexes have wings extending back beyond the posterior end of the body. In the male of *P. orientalis* the wing covers only extend as far back as the posterior edge of the fifth abdominal tergum, and the female is nearly wingless, the tegmina being represented by a pair of oval scales articulated to the mesonotum, and the metathoracic wings by lateral extensions of the metanotum, marked with a few nervures (fig. 38). The young forms of both sexes in both species of Periplaneta are devoid of wings, but the lateral margins of the meso- and metanotum are expanded and produced backwards. It is clear from the study of the young forms and the rudimentary wings of the female *P. orientalis* that the wings are

modified expansions of the terga of the two posterior thoracic segments.

The abdomen of the male differs in several important particulars from that of the female. In both sexes there are

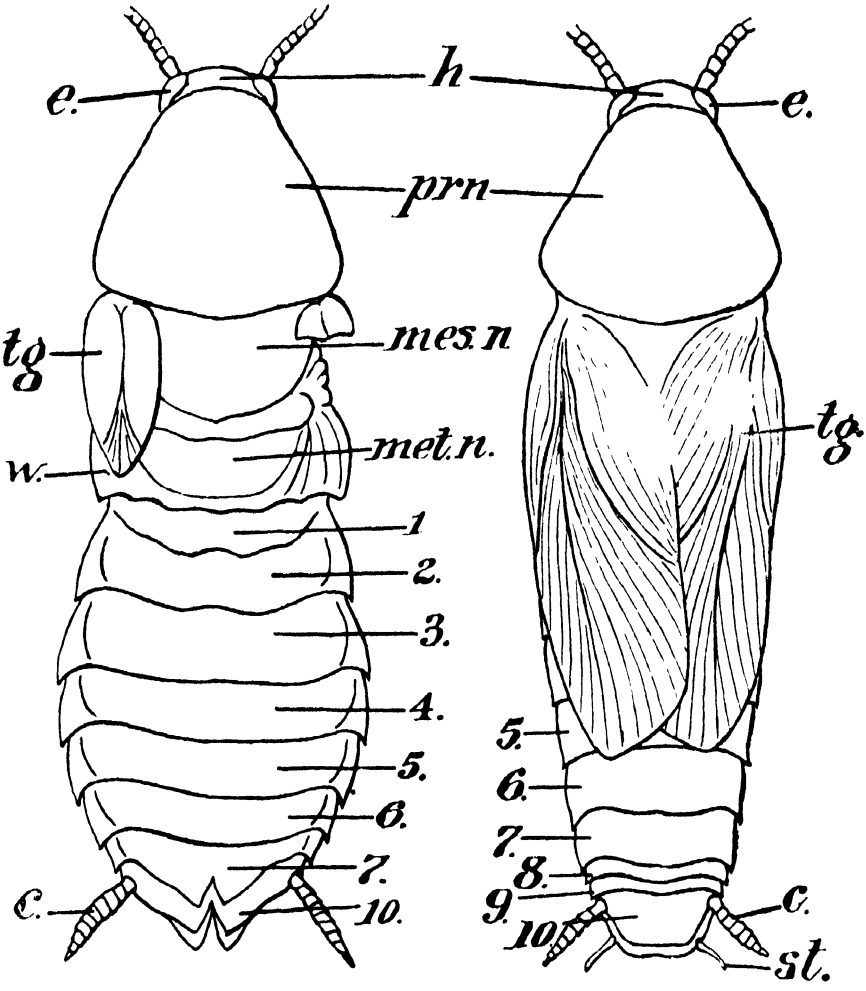


Fig. 38

Dorsal views of the female (left-hand figure) and male (right-hand figure) of *Periplaneta orientalis*. *h*, head; *e*, eye; *prn*, pronotum; *mes.n*, mesonotum; *met.n*, metanotum; *1-10*, the abdominal terga, 8 and 9 are concealed by 7 in the female, but are visible, though small, in the male; *tg*, wing-covers or tegmina; *w*, rudimentary metathoracic wings of the female. The well-developed metathoracic wings of the male are concealed by the tegmina; *c*, anal cerci; *st*, styles of the male.

ten abdominal segments (not counting the podical plates), but in the female several of these segments are modified, and some are concealed from view. A typical segment presents a broad chitinous plate, the **tergum**, above, and an equally broad plate, the **sternum**, below. The tergum and sternum

meet at an acute angle at the sides of the body and are united by a soft colourless cuticle. The tergum projects a little beyond the sternum, and in the first eight abdominal segments a small aperture guarded by a chitinous sclerite is situated under the anterior corners of each tergum. These are the eight pairs of abdominal **stigmata** leading into the respiratory tubes or **tracheæ**.

In the male cockroach the abdomen is narrower and the terga more convex than in the female. The first tergum is comparatively small, and the first sternum is very small, consisting of an oval chitinous plate. Both the terga and sterna of the next six segments are broad chitinous plates, but the eighth and ninth terga are reduced to narrow bands of chitin which in *P. americana* are overlapped and concealed by the posterior margin of the seventh tergum, but in *P. orientalis* are generally visible from the surface without disturbance of the adjacent parts. The tenth tergum is a flat plate with a truncated posterior margin projecting beyond the extremity of the body. To its sides are articulated a pair of spindle-shaped many-jointed **cerci**, and beneath it are two triangular chitinous sclerites, the **podical plates**, between which the anus opens in the middle line. Some authors regard the podical plates as the representatives of the tergum of an eleventh abdominal segment.

Ventrally the abdomen narrows rather suddenly at the seventh sternum. The eighth sternum, though narrow, is rather long from front to back, but is largely overlapped by the seventh, so that its exposed portion is short. The ninth sternum is deeply convex ventrally and concave dorsally, is narrow, and so much overlapped by the eighth, that more than half of its length is concealed from view. Its posterior margin is divided into a median and two lateral lobes by two shallow notches in which a pair of slender unjointed styles are articulated.

The concavity of the ninth sternum encloses a large pouch formed by the infolding of the cuticle. Dorsally this pouch is roofed in by the podical plates, and its anterior extremity is continued into the male genital aperture. Surrounding the aperture is a very complicated genital apparatus consisting of asymmetrically disposed chitinous plates and hooks, the exact relations of which need not be detailed here. Possibly the elements of the tenth sternum are represented by some of these plates.

The abdomen of the female cockroach is broader and flatter than that of the male. The narrow terga of the eighth and ninth segments are overlapped and concealed by the seventh tergum in both *P. americana* and *P. orientalis*. The tenth tergum is divided nearly into two by a notch extending forward from the middle of its posterior margin; under it lie the podical plates and anus, as in the male.

On the ventral surface only seven sterna are externally visible. The seventh is very large and imperfectly divided by a transverse groove into two parts, the posterior of which is boat-shaped and divided into two lateral halves by a median suture. Ordinarily these two halves are closely applied to one another in the middle line; but they are connected by a loose fold of soft and elastic cuticle which allows them to be widely separated for the extrusion of the eggs or the admission of the male organs in copulation. The seventh sternum encloses a wide genital pouch formed by the invagination of the eighth and ninth segments into the segment preceding them. This invagination affects chiefly the sternal moieties of the segments, so that the eighth and ninth terga, though reduced and telescoped under the seventh, retain their proper position on the dorsal surface, but the sterna of the segments are carried far forwards to form the anterior wall and roof of the anterior end of the genital pouch (see fig. 40, *A*). The anterior wall of the pouch is formed by the eighth sternum, a fairly broad semi-transparent chitinous plate sloping from above downwards and forwards and pierced by a median vertical slit, the opening of the female genital duct. The ninth sternum is a small crescentic plate in the roof of the pouch, the anterior edge of which is perforated by a small pore leading into the spermatheca. The genital opening is overhung by three pairs of more or less curved cylindrical appendages called **gonapophyses**. The anterior pair of gonapophyses is the largest, and is attached to the upper edge of the eighth sternum. The two posterior pairs are shown by development to belong to the ninth sternum.

From the above description it follows that in the male cockroach the genital opening is between the tenth tergum and the ninth sternum, while in the female it perforates the eighth sternum.

The alimentary canal of the cockroach, like that of the

crayfish, is remarkable for the great extent of the stomodæum and proctodæum and the small extent of the mid-gut. The mouth opens into a buccal cavity, whose posterior wall is raised into a conical fleshy projection, the **lingua**. The lingua is covered in behind by the labium, and in the angle between the two open the ducts of a pair of salivary glands. In front of the lingua the buccal cavity is continued into the œsophagus, which is very narrow and laterally compressed in the neck, but in the thorax gradually expands into a very long and spacious thin-walled **crop** extending far back into the abdomen. The crop is succeeded by a short conical gizzard or **proventriculus** with thick muscular walls. The inner lining of the proventriculus is raised up into six prominent longitudinal folds covered with hard chitinous plates which, by the contraction of the muscular wall, can be approximated in the middle line so as to form a very efficient grinding and straining apparatus. Behind the tooth-like plates are six cushion-like swellings covered with setæ. The œsophagus, crop, and proventriculus are lined by a chitinous membrane continuous at the lips of the mouth with the external integument, and together they constitute the foregut or stomodæum. The chitinous lining of the proventriculus projects backwards in spout-like form into the mid-gut, and the anterior of the spout is longitudinally folded so that its cavity is reduced to a narrow star-shaped passage.

The mid-gut is a short tube lined by columnar epithelial cells arranged in clusters, which have a fan-shaped figure in transverse section. The anterior end of the mid-gut is produced into eight, or sometimes fewer, short digitiform diverticula known as the **hepatic cæca**. The walls of these cæca are lined by an epithelium similar to that of mid-gut itself, and it has been demonstrated that they secrete a digestive fluid which has a solvent action on proteids and starches.

The hind-gut, which follows directly on the mid-gut, is divisible into three portions. First a short and narrow tube, the so-called **ileum**; following upon this a wider tube nearly an inch in length called the **colon**, and terminally a short pyriform sac with longitudinally folded walls, the **rectum**, which opens to the exterior by the anus between the podical plates. The whole of the hind-gut is a proctodæum lined by a chitinous cuticle which is covered with setæ and thrown into

longitudinal folds in the ileum, is thin and smooth in the colon, thicker and finely setose in the rectum. The internal lining of the rectum is thrown into six prominent longitudinal ridges corresponding with the infoldings visible on the external surface.

The commencement of the hind-gut is marked by the attachment of six bundles of very fine and long **Malpighian**

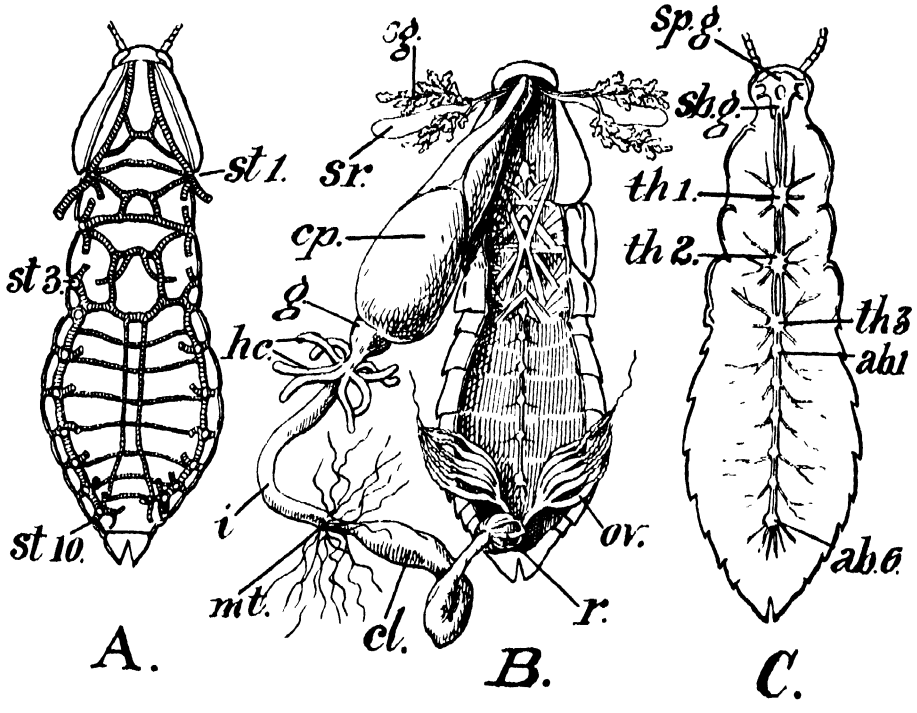


Fig. 39.

A. The principal ventral tracheal vessels of the cockroach (from Miall, slightly altered). *st.1*, first stigma between the prothorax and mesothorax; *st 3*, third stigma of the left side; *st 10*, tenth stigma of the left side. *B*. A dissection of a female cockroach from the dorsal side. *cp*, crop; *g*, gizzard or proventriculus; *hc*, hepatic cæca; *i*, intestine; *mt*, Malpighian tubules; *cl*, colon; *r*, rectum; *sg*, salivary glands; *sr*, salivary receptacle; *ov*, ovaries. *C*. The central nervous system of the cockroach. *sp.g*, supraœsophageal (cerebral) ganglion; *sb g*, suboesophageal ganglion; *th1*, *th2*, *th3*, the three thoracic ganglia; *ab1-ab6*, the six abdominal ganglia.

tubules. Each bundle comprises ten or more thread-like tubes, so that as many as sixty to seventy are present in the adult cockroach. The tubules are lined by a cubical glandular epithelium, and their lumina are often blocked by crystals containing uric acid. The tubules are, in fact, the functional excretory organs of the cockroach, and it is obvious that they differ very much in situation and structure from the green glands or shell-glands of the crustacea. In development the

Malpighian tubules arise as diverticula from the proctodæum, which itself is an invagination of the outer integument. They must therefore be regarded as invaginations of the epiblast, and in spite of their different situation and non-segmental arrangement they can hardly be denied the character of nephridia which have lost their internal openings on the disappearance of the cœlom.

The liver cæca of the cockroach may fairly be homologised with the digestive glands of the crayfish, both being outgrowths of the mesenteron, but the salivary glands of the cockroach have no homologue in Astacus. These glands are developed as diverticula of the stomodæum, and consist of two lobulated glands and a thin-walled sac, the salivary receptacle, lying on either side of the œsophagus. The ducts of the two glands of each side unite and run forwards as a single duct which joins the similar duct of the other side below the nerve cord in the neck. The ducts of the two salivary receptacles similarly unite to form a median duct which opens into the common salivary duct in the head, and the conjoined duct opens into the buccal cavity behind the lingua.

The circulatory apparatus consists of a median contractile dorsal vessel, the heart, and a system of blood sinuses; there are no tubular vessels or very definite blood channels as in the crayfish, unless the blood channels running in the nervures of the wings may be accounted as such. The heart itself extends through the whole length of the thorax and abdomen, and is divided into thirteen chambers, three thoracic and ten abdominal, the two posterior chambers being very small. The chambers are separated from one another by deep constrictions, and the narrow passage between adjacent chambers is guarded by a valve which only permits a forward flow of the blood. Each chamber communicates with the pericardial space by a pair of lateral ostia opening into its hinder end. The anterior chamber is continued into the head as a slender tube, the so-called aorta, which runs forward on the dorsal surface of the œsophagus, and ends in front of the periœsophageal nerve ring in a funnel-shaped orifice through which the blood is discharged into a blood sinus. The chambers of the heart contract successively from behind forwards, the waves of contraction succeeding one another so rapidly that the hinder

chambers may often be observed to contract before the preceding wave has reached the aorta. The blood entering the heart through the lateral ostia is driven forward in a steady stream through the aorta. The heart lies in a pericardial sinus formed by a horizontal membrane stretched across the cavity of the body above the alimentary canal. This membrane is perforated by a number of small openings which admit the passage of blood from the perivisceral blood-space to the pericardial sinus. Both the perivisceral space and the pericardial sinus of the cockroach are largely filled up by a mass of white lobulated tissue. This is the **fat-body**, usually abundant in young insects, but more scanty in adults. Microscopical examination shows that the young lobules of the fat-body are filled with vacuolated nucleated cells, but in older lobules the cell boundaries break down, the nuclei disappear, and the cavity of the lobule is filled with granules and crystals containing uric acid. The fat-body is clearly a metabolic tissue, but it has no ducts, and it must be assumed that the urates and other waste products of metabolism pass into the blood stream, and are taken up and finally excreted by the Malpighian tubules.

There can be little doubt that the feeble development of blood-vessels in insects is correlated with their mode of respiration. Instead of the blood being brought to a respiratory chamber like a lung, or a respiratory appendage like a gill, air is brought to all parts of the insect's body by branched respiratory tubes called **tracheæ**. These tubes are readily seen when a cockroach is dissected under water; being full of air, they look like veins of silver. They are involutions of the external integument, are lined by chitin, and the larger trunks and branches are strengthened by a spiral chitinous thickening. The tracheæ open to the exterior by apertures called **stigmata**, of which there are ten pairs, one pair beneath the anterior edges of the mesonotum, one pair similarly situated beneath the metanotum, and eight pairs beneath the anterior corners of the first eight abdominal terga. The stigmata can be opened or closed by means of valves provided with special muscles, the valves of the thoracic stigmata being external, those of the abdominal series internal. The stigmata lead into short, wide tracheal tubes connected together by longitudinal trunks, from which branches are given off and ramify in all parts of the body, the head being supplied with four large trunks

passing forward from the mesothorax. The minute ramifications of the tracheæ extend to every organ of the body, into the nervures of the wings, and into the long filiform antennæ.

The nervous system of the cockroach (fig. 39, *C*) is constructed on the same plan as that of the crustacea, consisting of a supracœsophageal ganglion connected by cords passing round the gullet with a ventral ganglion chain, and, in addition, a stomatogastric nerve plexus. The supracœsophageal ganglion of the cockroach lies in the head, and is large and complex, consisting of three pairs of fused ganglion masses known as the proto-, deuto-, and trito-cerebrum. It gives off nerves to the eyes and antennæ, and is connected by a pair of very stout cords passing round the gullet with a large subœsophageal ganglion mass, also lying in the head immediately in front of the sub-mentum. The subœsophageal ganglion innervates the mandibles, maxillæ, and labium, and is joined by a long and slender pair of connectives with the first thoracic ganglion-pair lying in the prothorax. There is a large ganglion-pair in each thoracic segment, and in each of the first six abdominal segments, the last of the series being large, and supplying nerves to its own and the posterior segments of the body.

The stomatogastric system is highly developed. Two short nerves pass from the periœsophageal connectives to a frontal ganglion situated in the head on the dorsal side of the gullet, and from this ganglion a median recurrent nerve runs back to a **visceral ganglion** lying on the upper side of the crop. From the visceral ganglion a stout nerve runs outwards and backwards on either side of the crop, and divides into fine branches distributed to the crop and gizzard. About the middle of its course the recurrent nerve is connected with two pairs of small ganglia from which nerves run forward to the supracœsophageal ganglion.

The reproductive organs are somewhat complicated. In the adult male the testes are no longer functional, and are with difficulty distinguished from the fat body in which they are imbedded. In the young males, however, they can be readily discovered as two groups of small spherical vesicles lying beneath the fifth and sixth abdominal terga on either side of the body, and discharging their contents into two narrow tubular sperm-ducts. The sperm-ducts run backwards as far as the seventh tergum, and then turn forwards and upwards to open into a complex organ of relatively considerable size called the

mushroom-shaped gland. This organ consists of two short

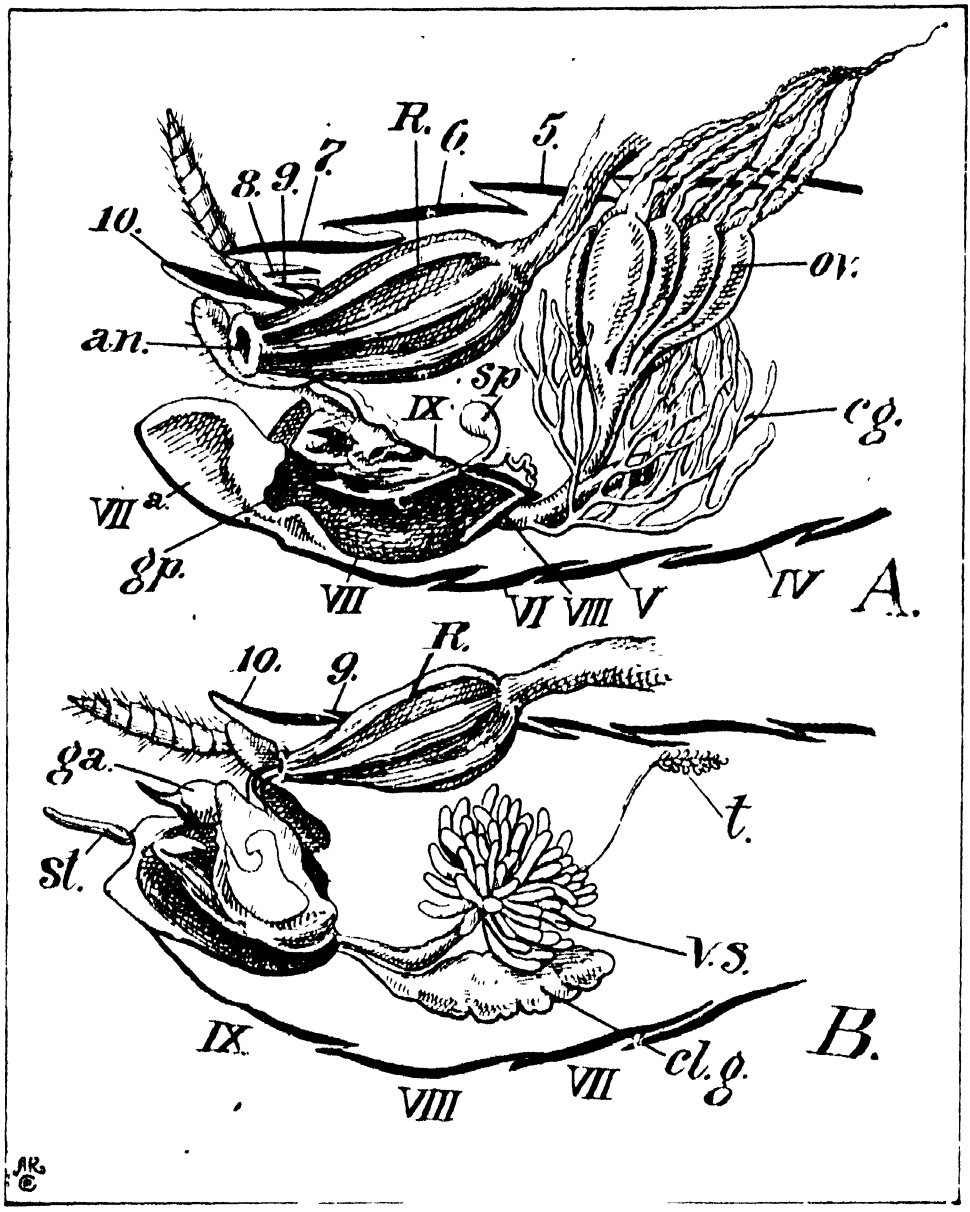


Fig. 40

A The generative organs of the female cockroach as seen from the right side after the removal of the right side of the body and the paired organs of the right side. The terga are numbered by Arabic numerals, the sterna by Roman numerals. *ov*, ovary of the left side; *cg*, colleterial gland; *sp*, spermatheca with its cæcal appendage; *gp*, gonapophyses; *an*, anus; *R*, rectum. The position of the eighth and ninth sterna should be particularly noted. *B*. A similar view of the male organs. *t*, testis of the left side; *v.s*, mushroom-shaped gland or vesiculæ seminales; *cl.g*, conglobate gland; *st*, style; *ga*, genital armature; *R*, rectum. *VIIa*, posterior division of the seventh sternum of the female. For further description, see text.

saccular vesiculæ seminales lying side by side, and bearing at their anterior ends a dense tuft of finger-shaped diverticula. In the adult male these diverticula are filled with spermatozoa and are of a glistening white colour: they were long mistaken for the testes. The vesiculæ seminales receive the sperm-ducts on either side and posteriorly unite to form a muscular tube, the **ductus ejaculatorius**, which opens into the genital pouch by the male pore. The complex apparatus of hooks and plates surrounding the genital pore has already been mentioned. On the lower side of the ductus ejaculatorius is the so-called **conglobate gland**, the function of which is doubtful.

The female organs consist of a pair of composite ovaries communicating by short and rather wide oviducts with a very short median uterus which opens into the genital pouch by a slit-like aperture, the vulva, through the eighth abdominal sternum. On its under side the uterus receives the duct of a much ramified **colleterial gland**, and just above the opening of the vulva into the genital pouch is the orifice of a small tubular **spermatheca** which is filled with spermatozoa by the male during copulation. Each ovary consists of a bunch of eight egg-tubes, distended at their posterior or oviducal ends, but tapering gradually forwards to a point where their diameters suddenly diminish. From this point the tubes are continued forwards as narrow threads which unite to form a single filament running forward till it is lost in the fat-body. The thread-like upper end of each tube contains a mass of granular protoplasm in which numerous nuclei are imbedded. At the point where the thread suddenly expands to form the tube the nucleated mass of protoplasm divides into a number of large cells or primitive ova entangled in a network of protoplasm containing many nuclei. As these cells are passed down the tube they become arranged in a single row, and each is invested by a follicle consisting of a single layer of cells derived from the nucleated network. During their descent the ova increase very much in size, being distended with food-yolk elaborated by the follicular cells, and they bulge out the walls of the egg-tube so that the latter looks like a string of beads. When ripe the ova are elongated oval, something like a sausage in shape, with a slight flexure towards what will be the ventral side of the embryo, and are surrounded by two membranes, an inner or **vitelline membrane** secreted by the ovum itself, and

an outer chitinous **chorion** secreted by the follicle. As the ova are passed out of the vulva they are fertilised by spermatozoa discharged from the spermatheca, and are packed sixteen together, like cigars in a cigar case, in a horny egg-case formed by the secretion of the colleterial glands. The female carries the egg-case for some days in the genital pouch, and eventually deposits it in some sheltered place, preferably near some convenient supply of food for the young when hatched out.

The yolk which forms the bulk of the egg is of so refractory a nature that the study of the earlier phases of the development of the cockroach is a matter of great difficulty, and the intricacies of insect embryology are such that it would be out of place to attempt to describe them in detail in this place. The earlier stages may be briefly summed up as follows:—The nucleus of the fertilised ovum lies at first in the centre of the yolk mass. It divides repeatedly, without any corresponding division of the yolk, till some sixty to eighty nuclei are formed. These nuclei migrate to the surface of the yolk, and continue to divide until a stage is reached in which there is a central yolk mass surrounded by a sheet of protoplasm containing numerous nuclei. Eventually the protoplasm is divided into cells, and the yolk is then invested by a sheet of tissue one cell thick, called the **blastoderm**. On the concave side of the egg the blastoderm cells become columnar and form an elongated band known as the **ventral plate**, elsewhere they are thin and flat like a pavement epithelium (fig. 41, *A*). The ventral plate is at first one cell thick, but a longitudinal groove is soon formed at its hinder end and the cells at the bottom of the groove divide rapidly by tangential divisions, giving rise to a deeper layer of cells which gradually spreads forwards under the outer layer. The latter may now be called the epiblast, the deeper layer will give rise to both mesoblast and hypoblast. As growth proceeds the lateral parts of the deeper layer extend forwards in the form of two bands towards the anterior part of the ventral plate, and there the bands diverge slightly from one another and form a pair of swellings known as the cephalic plates, the bands themselves are the mesoblast bands. The middle part of the deeper layer becomes separated from the mesoblast bands and grows forward more slowly. Eventually it extends to the front end of the ventral plate and bifurcates above the cephalic plates, taking up a position between the

mesoblast bands and the yolk, forming the innermost germinal layer or hypoblast.

While these changes are in progress the ventral plate has become pushed into the yolk in such a manner that it lies in a depression surrounded on all sides by a fold of the blastoderm. This fold increases in size, its edges grow together below the ventral plate, and eventually meet and fuse together. It is obvious that the limbs of the fold consist of an outer and an inner layer of blastoderm cells, and when they meet they fuse together in such a way that the outer limbs are combined into a continuous sheet of tissue, and so are the inner limbs, but all connection between the two is lost. The result is that the embryo is covered in ventrally by two membranes—the inner one, formed by the union of the inner limbs of the fold, is continuous with the edges of the ventral plate and forms a hood known as the **amnion**, covering the lower side of the embryo; the outer membrane is continuous with the blastoderm which elsewhere lies upon and encloses the yolk and is known as the **serosa**. Between the amnion and serosa is a space freely open to the yolk; in some insects the yolk spherules pass into this space, so that the embryo is, as it were, immersed in the yolk, but this does not happen in the cockroach. The relations of these embryonic membranes may easily be understood by reference to fig. 41.

To return to the formation of the embryo. We left the ventral plate as a thickened patch on the lower side of the blastoderm, composed of three layers epiblast, mesoblast, and hypoblast, the two latter layers having been formed by the proliferation of cells from the floor of a groove. From what we know of the development of other insects we must regard this groove as the representative of the blastopore: eventually it disappears, but the anus is formed by a secondary involution of the epiblast at its hinder end.

At an early period the ventral plate is divided into a series of segments by transverse lines, and it should be noted that the segmentation of the insect embryo resembles that of the Annelid much more closely than that of the Crustacean. In Astacus, for instance, the mesoblast consists at first of a number of scattered cells which only at a late period of development arrange themselves into a series of transient mesoblastic pouches, and that only in the abdominal region. In the cockroach the mesoblast is

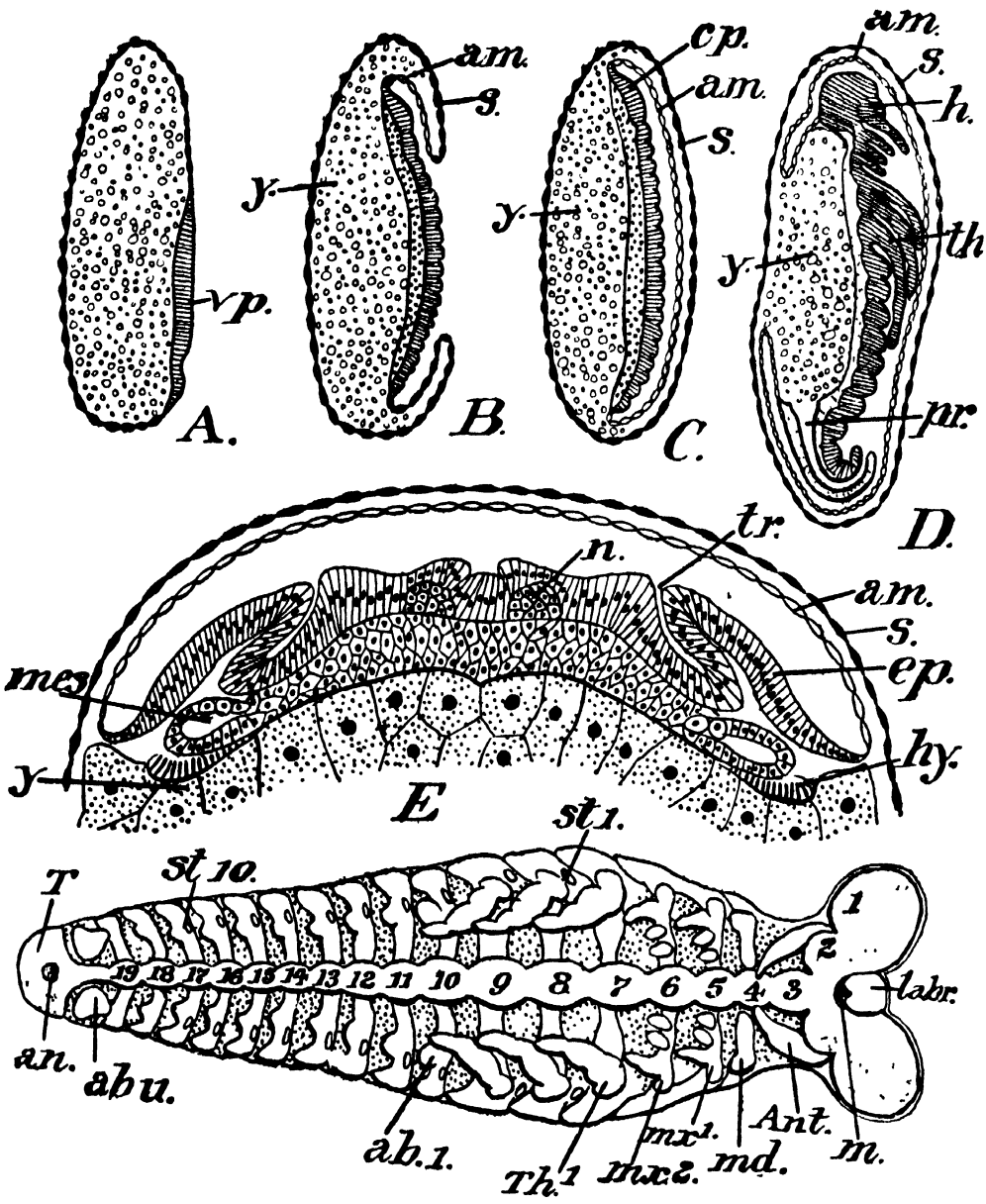


Fig. 41

A, *B*, *C*, *D*. Diagrammatic longitudinal vertical sections through an insect egg at different stages of development. In *A* the yolk is seen surrounded by a single layer of blastoderm cells; at *vp* is the ventral plate. *B* shows the formation of the amniotic folds, *am*; the ventral plate is segmented and consists of an outer layer of epiblast and a deeper layer. In *C* the amniotic folds have coalesced below the ventral plate, and the amnion, *am*, is separated from the serosa. In *D* the limb rudiments are present, and the yolk is nearly enclosed dorsally. *h*, head; *th*, thorax; *pr*, proctodæum; *y*, yolk. *E*. A transverse section through the body of an insect embryo, after Heider. *am*, amnion; *s*, serosa; *ep*, epiblast; *tr*, tracheal involution; *n*, nerve cord; *mes*, mesoblastic somite with cavity; *hy*, hypoblast; *y*, yolk. The lowest figure is a ventral view of an advanced insect embryo, after Heymons. *1*, the ganglion of the cephalic lobes (proto-cerebrum); *2*, ganglion of the antennary segment (deuto-cerebrum); *3*, ganglion of the intercalary segment (trito-cerebrum); *4*, *5*, *6*, gangha of the mandibles, maxillæ, and labium; *7-19*, thoracic and abdominal ganglia; *labr*, labrum; *m*, mouth; *ant*, antennæ; *md*, mandibles; mx^1, maxillæ; mx^2, labium; Th^1, prothoracic limb; *ab1*, first abdominal limb rudiment; *ab11*, eleventh abdominal limb rudiment; *an*, anus; *T*, telson; *st1*, the first, and *st10*, the last stigma of the right side.

formed as a pair of bands which are divided into as many pairs of somites as there are true segments in the body of the embryo. The somites are solid at first, but soon become hollow vesicles in much the same manner as do the somites of the earthworm, and as the germ cells are formed from the walls of some of the abdominal somites there can be no doubt that the cavities of the vesicles are true cœlomic spaces homologous with those of Annelid worms.

In all, nineteen pairs of somites are formed in the embryo of the cockroach, in addition to an anterior and a posterior section in which no cœlomic sacs are developed. The anterior section is bi-lobed, the mouth opens on its ventral surface, and it differs from the true segments of the body both in the absence of cœlomic sacs and in the fact that it never bears any trace of limbs or appendages. It will be distinguished as the cephalic lobe. The posterior section of the ventral plate is known as the caudal lobe or telson, and is similarly characterised by the absence of cœlom sacs and appendages and by the opening of the anus on its ventral surface. Each of the intervening nineteen segments contains a pair of cœlomic sacs, and each, with the exception of the second, bears a pair of lateral limb rudiments in the form of short conical outgrowths. Thus we see that the embryo insect resembles a crustacean, and differs from the adult in having a pair of appendages on each segment. We find also that a pair of ganglia is formed from epiblastic thickenings in the cephalic lobe and in every successive segment, just as in Astacus. The further fate of the cephalic lobe and segments deserves the closest attention, for it affords the clue which enables us to homologise the insect with the crustacean body.

The cephalic lobes and the first five embryonic segments go to form the head of the adult insect. The appendages of the first segment, which are at first post-oral, are shifted forward in front of the mouth and become the antennæ. Their ganglion fuses with the ganglion of the cephalic lobes and becomes the deuto-cerebrum of the adult brain. The second segment is known as the intercalary segment; it does not bear limb rudiments in any winged insect, but a pair of such rudiments has been discovered in the embryo of one of the primitive wingless insects belonging to the family Poduridæ. Its ganglion becomes incorporated into the brain and forms the

trito-cerebrum. Eventually the intercalary segment is aborted and disappears, but its existence is of great importance, for there can be little doubt that it represents the somite of the second antennæ. The limb rudiments of the third, fourth, and fifth embryonic segments give rise to the mandibles, maxillæ, and labium, and their ganglia fuse together to form the subœsophageal ganglion of the adult. The sixth, seventh, and eighth somites become the three thoracic segments, and their limb rudiments become the three pairs of thoracic legs. In the remaining eleven abdominal segments lying in front of the telson the limb rudiments disappear at an early age, except in the first and last. Those of the first abdominal segment give rise to a peculiar embryonic organ which disappears at a later stage, those of the eleventh abdominal segment give rise to the cerci. The ganglia of the thoracic and first five abdominal segments remain distinct, but those of the last six embryonic segments fuse together to form the last abdominal ganglion of the adult.

The cœlom sacs are larger in Periplaneta and its allies than in other insects. They become divided into dorsal and ventral moieties, the latter extending into the limb rudiments. The dorsal moieties persist for a long time, and eventually the genital organs, the heart, the pericardial septum, the fat-body, and the muscles of the body are formed from their walls. Their cavities are completely broken up, and give place to the extensive system of blood-spaces which surround and run between the viscera of the adult. The ventral moieties of the cœlom sacs disappear at an earlier stage: their walls break up and give rise to groups of irregularly shaped cells whose fate is not clearly understood, but it is probable that they enter into the composition of the limb muscles in the thoracic region.

As the embryo is formed on the ventral side of the egg, the yolk is naturally on the opposite or dorsal side. For a long time the embryo is little more than a plate on the ventral surface, and the head, body segments, rudimentary appendages, etc., are all formed while it is in this condition, the yolk being enclosed only by the outer of the two embryonic membranes or serosa. At a comparatively late period, when the hypoblast is established, all the three layers of the ventral plate grow upwards, and eventually meet and fuse above the yolk, so that the latter comes to lie entirely in the mid-gut or enteron. The

overgrowth of the yolk is complicated by the presence of the amnion, but the course of events will be readily understood by an inspection of the diagrams, fig. 41, *A-D*. The enteron is at first of considerable size, owing to the bulk of the yolk contained in it, but as the yolk is absorbed, it becomes smaller and smaller, and is finally reduced to very small dimensions, the larger part of the alimentary tract being formed from two epiblastic invaginations, the stomodæum and proctodæum.

The young cockroach is not hatched till it has assumed nearly all the characters of the adult, and when it leaves the egg it is an active insect, not, as is the case in so many other insects, a fleshy grub or caterpillar. The young males are wingless, like the females, and the tenth tergum is notched posteriorly in both sexes. The young forms are generally known as **nymphs**, and they attain their full sexual characters after a number of moults or ecdyses, in each of which the chitinous cuticle is entirely thrown off and replaced by a new one.

Insects which are hatched like the cockroach, with practically the full adult characters, and undergo no metamorphosis, are known as *Homomorpha* or *Ametabola*. Those which are hatched out as grubs or caterpillars, and afterwards enter into a resting stage from which they emerge as perfect insects, are known as *Heteromorpha* or *Metabola*. Our common butterflies are good examples of the latter division. The caterpillar is a larval form produced from the egg. After a free life of some length, during which it feeds on plants, the caterpillar forms a protecting case or cocoon for itself and becomes a **pupa** or chrysalis. During this stage it undergoes profound modifications, and eventually emerges from the pupa-case as a perfect insect or **imago**.

It is clear, from the study of the development of the cockroach, that there is a closer correspondence between the structure of insects and crustacea than their adult anatomy would lead one to suppose, and zoologists are abundantly justified in classing them together in the phylum Arthropoda. It is possible to go even further, and to compare the structure of the Arthropoda with that of the Chætopod worms. In both these groups we find an elongate segmented body, bearing lateral hollow appendages (parapodia in Polychæta). The alimentary tract is a more or less straight tube traversing the

whole body; its anterior opening, the mouth, is overhung by a prostomium; its posterior opening, the anus, opens on the terminal segment. The nervous system consists of a supra-œsophageal ganglion connected by cords passing round the gullet with a ventral chain of ganglia. The principal blood-vessel is dorsal in position. Though the cœlom has practically disappeared, and its place has been taken by blood-spaces in adult arthropods, we find paired cœlomic pouches well developed in the embryo of the cockroach. It seems evident that in the arthropods the limbs or parapodia lying nearest to the mouth have been modified to form tactile organs (antennæ) or masticatory organs, and that the segments to which they belong have become more or less intimately fused with the prostomium and peristomial segment to form a head. There is some reason to believe that the green glands and shell-glands of the crustacea are homologous with the nephridia of worms, and though these organs are absent in insects (unless indeed they may be represented by the Malpighian tubes), as also in the air-breathing scorpions, spiders, and centipedes, yet we have the instance of the remarkable arthropod, Peripatus, which is a terrestrial animal breathing air by means of tracheæ and has nephridia opening at the bases of each of its numerous pairs of legs. These questions, however, are among the most debatable in the domain of comparative anatomy, and it would be quite out of place to attempt to discuss them in an elementary treatise. But even a beginner can hardly fail to be impressed by the many indications of relationship revealed by the study of the anatomy and embryology of such apparently unlike animals as those which have been described in this and the preceding chapters as examples of the cœlomate invertebrata.

CHAPTER XXV

THE CEPHALOCORDA—AMPHIOXUS LANCEOLATUS

In the first volume of this work the frog, a vertebrated animal, was selected as an example of animal organisation, and in studying it the beginner will have gained a tolerably clear idea of the leading features of vertebrate structure. But the frog is by no means a simple vertebrate: almost every detail of its anatomy exhibits a complexity which forbids our regarding it as a near representative of that primitive stock from which, on the theory of evolution, we must suppose all vertebrate animals to have sprung. Happily for the study of comparative anatomy, we have an excellent example of a primitive vertebrate in the remarkable fish-like animal **Amphioxus**, found somewhat rarely on sandy bottoms in shallow waters off the English coast, but more abundantly in other parts of Europe, especially in the Mediterranean. Nor is Amphioxus confined to European waters; it has been found in shallow seas in almost every part of the world, and several species have been described, some exhibiting such well marked characteristics that they have been thought worthy of generic rank. The common European species is named *Amphioxus lanceolatus*, and it is the only one that will be referred to in the present chapter.

Although Amphioxus is fish-like in form, it has neither the structure nor the habits of a true fish. It has neither head nor jaws, is destitute of paired fins, and has many anatomical peculiarities that are not found in any fish. It can swim rapidly in the water by sinuous movements of its narrow, knife-shaped body, but in its most usual posture it is buried vertically in the sand, the anterior end of its body projecting into the water. In this position it obtains its nourishment from the minute organisms drawn into its mouth in the currents created by the ciliated apparatus to be described further on. It has the most astonishing powers of burrowing,

and when alarmed will disappear into the sand at the bottom of an aquarium in the twinkling of an eye.

The external features of the animal are shown in fig. 42. The body is about one and a half inches long, compressed from side to side, and tapering to a point at either extremity (hence its name ἀμφιώξυς, sharp at both ends). There is no trace of a specialised anterior head. Examination with a lens shows that the walls of the body are divided into a number of muscle-segments or **myotomes**, separated from one another by partitions or septa of connective tissue. These myotomes are not simple rings like the annuli of a worm, but are bent at a sharp angle, the apex of the angle pointing forwards, and one result of this arrangement is that several of them are cut through in any transverse section of the body. The most anterior and posterior myotomes are very small, those in the middle of the body are large, but do not extend to the ventral surface. As many as seven or eight myotomes lie in front of the mouth. It should further be observed that the myotomes of the two sides of the body do not correspond, but alternate with one another.

At either end of the body the tip of an elastic skeletal rod may be seen projecting beyond the myotomes. This rod is the **notochord** or **chorda dorsalis**, and in a very young transparent specimen, or in one that has been cleared in turpentine, it may be seen extending through the dorsal region of the body in the form of a rod lying above the alimentary canal, but below the more dorsally placed central nervous system. The notochord, a structure which recurs in the embryos at least of all higher vertebrata, is one of the most important features in the anatomy of Amphioxus.

The anterior end of the notochord is enclosed in a vertical membranous fin. This fin is continued along the mid-dorsal line as a low ridge, expands posteriorly into a lancet-shaped caudal fin, surrounding the posterior myotomes, and is continued forward as another low ridge on the ventral surface for about a quarter of the length of the body. The dorsal and ventral fins are strengthened by a number of little skeletal rods of cartilaginous consistency, called **fin-rays**. There is no correspondence between the number of fin-rays and the number of myotomes. There are sixty-two of the latter in *Amphioxus lanceolatus*, and as many as 250 to 260 dorsal

fin-rays. The ventral fin-rays are paired, and vary from

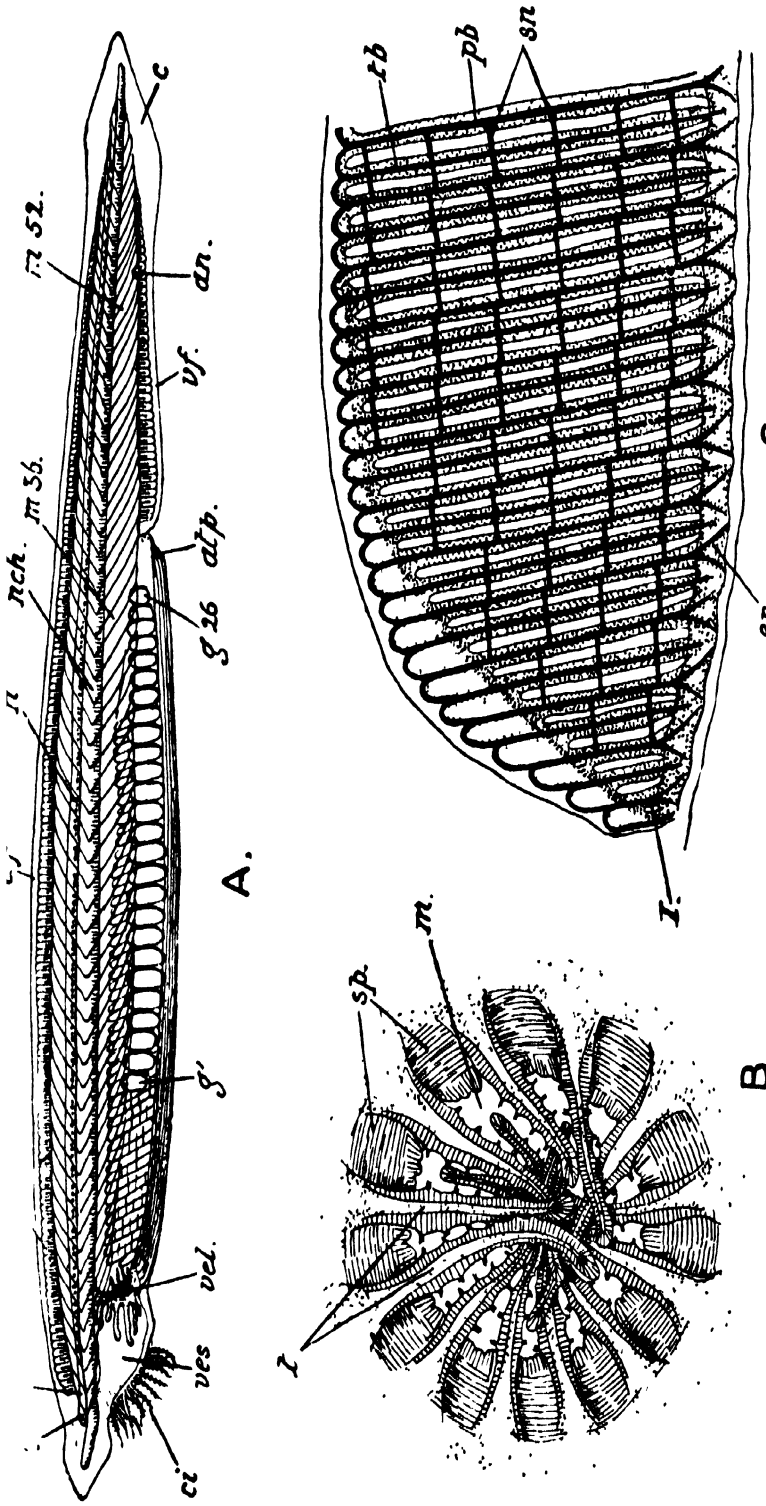


Fig. 42

A. An adult specimen of *Amphioxus lanceolatus*, seen from the left side as a transparent object. *an*, anus; *atp*, atriopore; *c*, caudal fin; *ci*, buccal cirrhi; *df*, dorsal fin; *e*, eyespot; *fr*, fin-rays; g^{1}-g^{26}, the twenty-six pairs of gonadial pouches; m^{1}, the first, m^{35}, the thirty-sixth, m^{52}, the fifty-second myotomes; *n*, neural tube; *nch*, notochord; *vel*, velum, in front of it are the finger-like processes of the wheel organ; *ves*, vestibule; *vf*, ventral fin. *B.* The velum as seen from the inside of the pharynx, after Lankester. *m*, mouth; *sp*, sphincter muscle; *t*, tentacles. *C.* Anterior end of the left wall of the pharynx, after J. Müller, slightly modified. *en*, endostyle; *pb*, primary bar; *sn*, cross-bars or synapticula; *tb*, tongue-bar; *1*, first gill-slit undivided by a tongue-bar.

thirty-two to forty-nine in number. In the region of the ventral fin the myotomes extend to the ventral surface of the

body, but in front of this the ventral surface is flat, marked with several longitudinal wrinkles, and bounded on either side by a fin-like expansion of the integument, called the **metapleur**. The ventral ends of the myotomes only reach down to the metapleural folds. At about the level of the seventh myotome, the metapleur of each side is continued into a triangular flap fringed on its free margin with eleven tentacle-like processes, the **buccal cirrhi**. The flap of the right side is continuous with the anterior median fin. These two flaps form a hood enclosing a wide but shallow funnel-shaped cavity, often described as the buccal cavity, but it will be best to call it the **vestibule**. The mouth is situated at the posterior end of the cavity at the bottom of the funnel. It should be clearly understood that the wide aperture of the vestibule is not to be regarded as the mouth. The buccal folds, as the triangular flaps are called, are formed relatively late in larval life, some time after the true mouth, which they enclose, has been established. The other external openings are the anus, the atriopore, and the so-called olfactory pit. The **anus** opens on the fifty-second myotome, not in the middle line, but on the left side of the body. The **atriopore**, which must not be mistaken for the anus, is a widish, nearly triangular opening on the ventral surface on the level of the thirty-sixth myotome, just in front of the anterior end of the ventral fin. It is the exhalant aperture of a large chamber, the **atrium**, which surrounds the lower part of the anterior end of the body behind the mouth, and receives the water discharged through the numerous gill slits which perforate the body-wall in that region. The "olfactory pit" is a small conical depression situated on the left side of the median dorsal fin on a level with the first myotome. Nothing is known about its function, but it is associated with an important embryonic aperture called the **neuropore**. Just in front of the olfactory pit is a small black pigment spot seated on the anterior end of the nervous tube. This spot is called the eye; it has no lens, cornea, or retina, and is nothing more than a collection of pigment granules, but as Amphioxus is extremely sensitive to light, it is concluded that this spot is specially sensitive. Similar pigment spots occur at intervals along the length of the neural tube.

Before proceeding to the study of the internal organs, it is

necessary that the relations of the atrium should be thoroughly understood. On making a median ventral incision from the atriopore to the vestibule one exposes a cavity which appears to be traversed by the gut, and to contain the gonads, the latter organs having the form of twenty-six pairs of pouches, extending from the tenth to the thirty-sixth myotomes, and projecting into the atrial cavity. This cavity appears to be, and was long mistaken for, the perivisceral cavity or cœlom. But in reality it is external to the body, and is lined with epiblast. The gonads, though they seem to lie in it, are really outside of and only project into it. The relations of the atrial chamber in the adult animal are best understood by imagining the side walls of the body of a fish-shaped animal to be very extensible. If these side walls were pulled out on either side of the body as a longitudinal fold, and the two folds were drawn down below the ventral surface and fastened together in the middle line like the flaps of a coat, there would be a space between the wall of the body and the united flaps which would correspond exactly in position to the atrial cavity. One may realise the relations even more clearly by imagining the sides and back of one's waistcoat to be part of and continuous with one's skin. Then the space between the front of the waistcoat and the body would correspond to the atrial cavity, and the opening below the waistcoat would correspond to the atriopore. It must be remembered, however, that though this illustration serves very well to explain the adult relations, the atrial chamber is not actually formed in Amphioxus by the downgrowth and union below of two flaps of skin, but in a more complicated and curious manner which will be described later. For present purposes we may speak of right and left atrial folds, united in the mid-ventral line. The ventral portions of the folds lying between the metapleurs and the ventral suture are known as the **epipleurs**, the metapleurs being, as it were, lateral offsets of the atrial folds. The atrial chamber is closed in anteriorly, and has no communication with the vestibule in front of it.

The cirrhi which surround the buccal folds are covered with patches of sensory epithelium provided with stiff hair-like processes, or with cilia, and are supported by skeletal rods attached to a jointed skeletal hoop which runs round the margins of the buccal folds. Internally the epithelium of the

buccal folds is modified and drawn out into a number of richly ciliated finger-shaped processes. The combined action of the cilia causes a flow of water towards the mouth and gives the appearance of a rotatory movement, hence the structure has been called the wheel-organ. Close to it, lying against the right side of the notochord, is a ciliated depression known as Hatschek's organ.

At the back of the vestibule is a nearly vertical partition called the **velum**, perforated in the centre by the circular aperture of the **mouth**. The mouth can be closed by a ring of muscle fibres which surround it, and is further protected by twelve oral tentacles which may either project freely backwards into the pharynx, or may be folded across the mouth opening in the manner shown in fig. 42, *B*. The oral tentacles are provided with patches of sensory epithelium like those on the buccal cirrhi, and when folded across the mouth they form a very efficient strainer. Care should be taken not to confuse the oral tentacles with the buccal cirrhi.

The alimentary canal, into which the mouth leads, is a straight tube running to the anus. A little distance in front of the atriopore it is produced ventrally into a simple finger-shaped diverticulum which is directed forwards and applied closely to the right side of the pharynx. This diverticulum ends blindly in front, and is lined with long columnar epithelial cells: it appears to function as a liver; at all events, the blood-vessels have relations to it similar to those existing in the livers of higher forms, and it is known accordingly as the **hepatic cæcum**. The cæcum appears to be in the atrial chamber, but it is really excluded from it by a complete investment of atrial epithelium and mesoblast, representing the body-wall pushed out in front of it as it grew forwards from the ventral side of the gut.

The section of the alimentary canal lying in front of the liver cæcum, extending from about the eighth to the twenty-sixth myomere, is known as the **pharynx**. It is compressed from side to side, but of considerable depth from above downwards, and its side walls are perforated by a great number of elongated **gill-slits**, which place its cavity in communication with the atrial chamber. There may be as many as 180 of these gill-slits on each side in a fully developed specimen, but in young forms they are far less numerous.

In preserved specimens, in which the muscles are contracted by the action of spirit, the gill-slits are not vertical, but their lower ends are directed backwards at a sharp angle so that many of them are cut across in transverse section. The slits are separated from one another by narrow but rather deep partitions called **gill-bars**, and as the gill-slits are formed as outgrowths of the gut which have met, fused with, and eventually broken through the epiblast (here the epiblast lining the atrial chamber), each gill-bar is covered externally with epiblastic epithelium, internally and at the sides, by hypoblastic epithelium, and contains a core of mesoblast. The gill-bars are strengthened by a series of chitinoid skeletal rods whose arrangement is shown in fig. 42, *C*. The dorsal end of every rod curves over to join the rod next behind it, but the ventral extremities are not connected together, and end alternately in simple and bifurcated points. The gill-bars which have bifurcated skeletal rods are known as primary bars, those which have simple rods are known as secondary or tongue-bars, and the two gill-slits lying between two primary bars together constitute a primary gill-cleft. At the time of its first appearance every primary cleft was a simple oval opening. After a time a tongue-like downgrowth was formed from its dorsal margin, which grew across the cavity of the cleft until it met and fused with its ventral margin, thus dividing it into two. The primary bars, then, are the original partitions between the primary clefts, the tongue-bars are secondary growths which divided the primary clefts into two. There are other differences between the primary and secondary bars which will be described later, after the cœlom has been treated of. The primary bars are connected together by several cross-bars or **synapticula**, which at first skip over, but eventually are fused to the tongue-bars. The dorsal wall of the pharynx is indented by a deep but narrow groove, the **hyperbranchial groove**, running along its whole length close beneath the notochord. The sides of the groove are covered with a special ciliated epithelium, which, at the anterior end of the pharynx, is continued right and left into two ciliated tracts, the **peripharyngeal bands**. These bands curve downward and join the anterior end of a ventral groove which runs along the whole length of the floor of the pharynx. This ventral groove

is known as the **endostyle**. It is lined throughout by very attenuated columnar ciliated cells, and on either side of the middle line are two tracts of glandular cells. The cilia at the bottom of the groove are especially long, and serve to drive along the cord of mucus secreted by the glandular cells. Amphioxus, as has been explained, feeds upon minute organisms contained in the currents of water passing in at the mouth. On entering the pharynx, these organisms are entangled in the strings of mucus driven forward by the cilia of the endostyle, are passed by the ciliary action of the peripharyngeal bands to the hyperbranchial groove, and are carried down it to the intestine, while the water escapes through the gill-slits into the atrial chamber, and thence to the exterior by the atriopore.

The notochord, as has already been seen, extends from one end of the animal to the other, and anteriorly projects well in front of the mouth. This anterior extension of the notochord is so characteristic a feature, that Amphioxus and the genera nearly related to it are placed in a separate class, **Cephalochorda**. Throughout the region of the gut the notochord lies close above the roof of the latter. It is formed from a median groove in the dorsal wall of the primitive gut of the embryo, the groove being afterwards separated off as a cord of cells which undergo remarkable histological changes, and give rise to a peculiar form of supporting tissue known as notochordal tissue. In the adult the notochord seems to be made up of a number of vertical discs separated from one another by irregular vacuolar spaces. The nuclei of the cells which formed the notochordal tissue can be seen in transverse section to form dorsal and ventral groups lying near the periphery of the cord.

The notochord is surrounded by a stout connective tissue sheath which is produced upwards to form an investment to the nervous tube, and this investment is again prolonged dorsally into a median band of fibrous connective tissue, which in turn is continuous with the fibrous sheaths of the fin-rays. Laterally the notochordal and neural sheaths and the median fibrous band are continuous with the connective tissue septa separating the muscle segments or myotomes.

A transverse section shows that the upper part of the body, right and left of the notochord and central nervous system, is

formed of a dense mass of muscle divided into a number of squarish blocks by connective tissue septa. In a section taken behind the atriopore these muscular masses extend down the sides of the body to the origin of the ventral fin, but in a section through the pharyngeal region they only form the upper part of the side walls of the atrial chamber, the lower walls and floor being formed by the thin muscular sheets of the atrial folds. It is obvious, on reflection, that these muscle

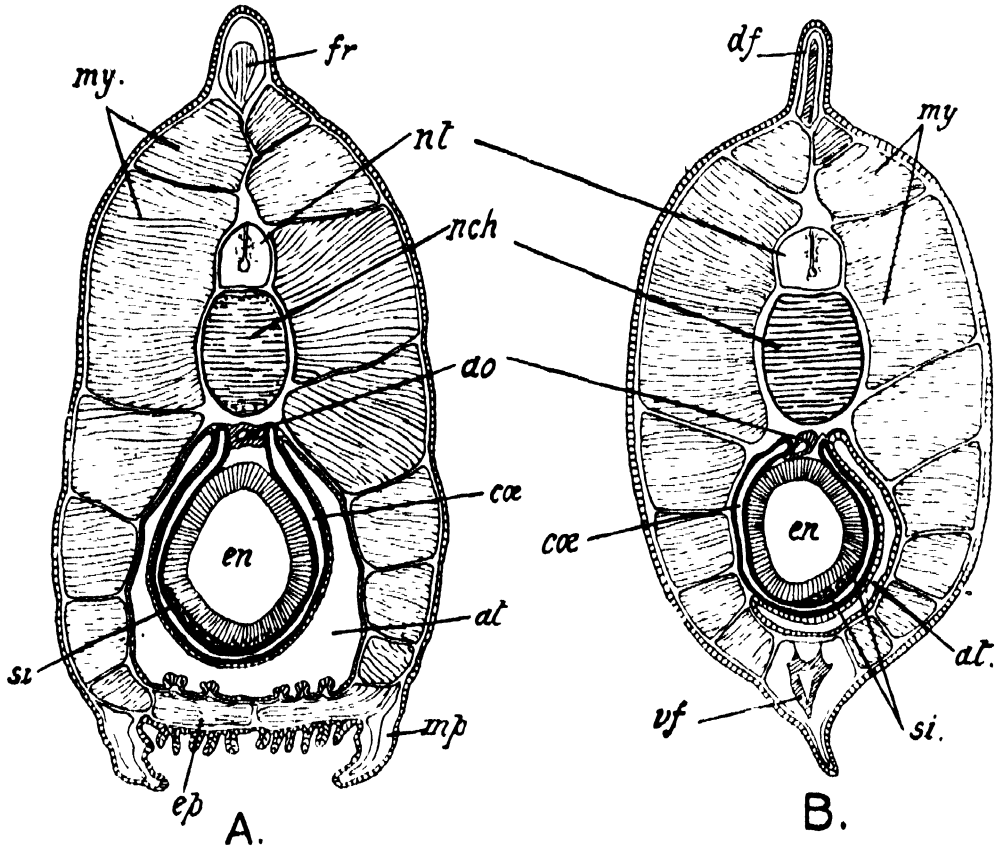


Fig. 43

A. Transverse section taken a little way in front of the atriopore of Amphioxus. *B*. Transverse section taken between the atriopore and the anus. *ao*, dorsal aorta; *at*, atrium; *cœ*, cœlom; *df*, dorsal fin; *en*, intestine; *ep*, epipleu; *fr*, fin-ray; *my*, myotomes; *mp*, metapleural fold; *nch*, notochord; *nt*, neural tube; *si*, subintestinal veins; *vf*, ventral fin.

masses are the myotomes of which several, because of their V shape, are cut across in one section, and for the same reason each myotome is cut twice.

In a section taken just in front of the atriopore, posterior to the hepatic cæcum (fig. 43, *A*), the intestine is seen suspended by a fold of tissue from the lower part of the notochordal

sheath and lying in a cavity which at first sight looks like the peritoneal space or cœlom. This cavity, however, is not cœlom, but atrium, and is lined by an epiblastic epithelium easily distinguished from cœlomic epithelium because of the presence of brown pigment granules in its cells. Examining the section closely, we find that the hypoblastic wall of the intestine is invested by three layers of tissue. Externally there is the atrial epithelium, and within this, and closely adherent to it, a thin sheet of mesoblastic tissue which we may call the **somatopleur**. Then follows a narrow space; then another very thin layer of mesoblastic tissue, the **splanchnopleur**, which closely invests the hypoblastic epithelium of the gut. The space between the somatopleur and splanchnopleur is the **cœlom**. Below, and at the sides of the intestine, it is so narrow as to be scarcely recognisable, but dorsally the splanchnopleur and somatopleur diverge slightly from one another, so that the cœlomic space is more obvious. On either side of the middle line the splanchnopleur turns upwards and outwards, and is continued into the somatopleur, so that the gut appears to be suspended from the notochord by a double membrane, which is, in fact, a very short mesentery. The two layers of the mesentery are not in contact, but are separated by a lymph space, in which lies the dorsal aorta.

Similar relations are seen in a section taken between the atriopore and the anus (fig. 43, *B*), but here the atrium is reduced to a diverticulum lying on the right side only of the intestine, so that the description given above applies to that side only. On the left side the somatopleur is adherent to the connective tissue covering of the myotomes.

Throughout the pharyngeal region the intestine and its coverings are perforated by the gill-slits, and as a consequence the cœlom, instead of being a continuous though narrow space surrounding the gut on all but the dorsal side, is subdivided into dorsal and ventral sections connected by canals running in the primary gill-bars. The manner in which these subdivisions and connections were formed requires a little thought. Before the gill-slits or atrial chamber were formed the pharynx lay, like the intestine, in a cœlomic space, and at first in a relatively large space, for it was not compressed by the presence of the atrial chamber subsequently formed round it. The gill-slits were formed as a succession of oval apertures,

perforating the side walls of the pharynx, and placing its cavity in communication with the exterior. In the natural uncontracted condition of the young animal these slits would be vertical, and would be separated from one another by vertical partitions, narrow from front to back, but deep from side to side. As the gill-slits are confined to the side walls of the pharynx, the cœlomic space below the floor of the pharynx would be unaffected by their presence, as would also be the case with the dorsal spaces right and left of the middle line. But in the side walls the cœlom would be reduced to a series of narrow passages running down the partitions separating the primary gill-slits—*i.e.* the primary gill-bars. And, in fact, we find in the adult that there is a triangular space right and left of the upper part of the pharynx, usually known as the **dorsal cœlom**, which communicates by a narrow canal running down each primary gill-bar with a space underlying the endostyle, and hence known as the **subendostylar cœlom** (fig. 44, *S.co*).

It has already been explained that each primary gill-slit is divided into two by a tongue-like downgrowth from its upper margin. The cœlom does not extend into these secondary downgrowths, and consequently the tongue-bars do not contain cœlomic canals, while the primary bars do, a difference which is obvious enough in a cross section through the gill-bars. On the formation of the atrial cavity the shape of the dorsal cœlomic spaces is somewhat altered, and curious changes occur in connection with the development of the gonads, but the main relations described above are undisturbed, except, of course, that the gill-slits no longer open to the outside but into the atrial chamber. Owing to the contraction of the muscles of adults preserved in spirit the gill-slits slope backwards, and it is because many gill-bars are cut through that transverse sections through the pharynx have so curious and complicated an appearance. The complexity, however, may be readily understood by a study of the plastic diagram given in fig. 44, which has been fully lettered to save lengthy description. Fig. 45, *C* and *D*, are transverse sections through a primary and a tongue-bar, showing the cœlomic canal in the former and its relation to the skeletal rod. It may further be seen that there are three blood-vessels in a primary bar, but only two in a tongue-bar,

It will be noticed that in addition to the cavities described above, there is a considerable cavity in each metapleural fold. These are not part of the cœlom, but lymph spaces. There was a cœlomic cavity in each atrial fold at its first appearance,

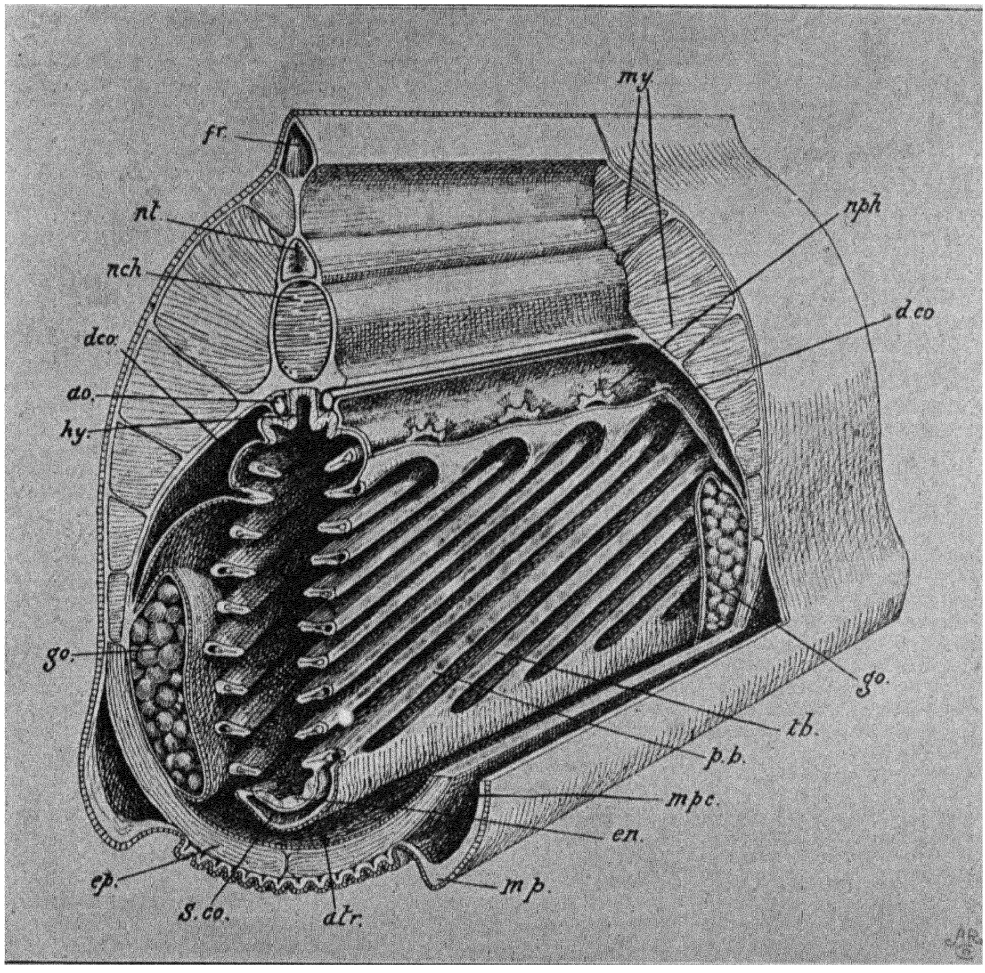


Fig. 44

Diagram illustrating the anatomy of the pharyngeal region of Amphioxus. A segment has been cut out of the pharyngeal region, and a portion of the right wall removed to show the atrial cavity, the pharynx and its gill-slits, and the dorsal cœlom. *ao*, dorsal aorta; *atr*, atrium; *dco*, dorsal cœlom; *en*, endostyle; *ep*. epipleur; *f*, fin ray; *go*, gonads; *hy*, hyperbranchial groove; *mp*, metapleur; *mpc*, metapleural canal; *my*, myotomes; *nch*, notochord; *nph*, nephridium; *nt*, neural tube; *pb*, primary gill-bar; *tb*, tongue-bar; *S.co*, sub-endostylar cœlom.

but it disappeared in larval life, its walls being converted into the muscle fibres of the metapleural and epipleural folds.

The blood-vascular system of Amphioxus differs from that of other vertebrates in the absence of a definite heart. It presents, however, a very characteristic vertebrate feature—namely, a **hepatic-portal system.** The blood from the intestine and posterior end of the body is collected into a large sub-intestinal vein which runs forward below the intestine till it reaches the hepatic cæcum. Here it breaks up into a number of capillaries surrounding the liver. From these the blood is collected into a hepatic vein lying on the dorsal side of the cæcum; the hepatic vein runs backwards to the point where the cæcum joins the intestine, then turns sharply forwards and runs below the floor of the pharynx in the endostylar cœlom as the **branchial aorta.** The branchial aorta contracts rhythmically from behind forwards, and it is obvious that in position and function it corresponds to the heart and truncus arteriosus of higher vertebrates. The branchial artery gives off lateral vessels which run, right and left, into each primary gill-bar. Each lateral vessel is dilated at its base into a contractile bulbil, and immediately beyond it divides into three branches, which run up the bar, one to the outside of the cœlomic canal, one internally to the skeletal rod, and one near the internal end of the bar (fig. 45, *C*, v^3, v^2, v^1). In the tongue-bars there is no cœlomic vessel, but an external and an internal vessel are present, the former embedded in the skeletal rod. The vessels of the tongue-bars have no connection below with the branchial artery, but receive their blood supply through small lateral vessels running in the synapticula. The two or three vessels of each gill-bar unite above to form a single efferent branchial vessel which leads direct into the dorsal aorta. Before opening into the efferent branchial vessels the cœlomic vessel of each primary bar and the external vessel of the tongue-bar next behind it give off branches which unite to form a plexus surrounding the excretory tubule overlying each primary gill-cleft. The blood from the plexus is carried to the dorsal aorta by efferent vessels. In the pharyngeal region there are two dorsal aortæ, one lying on each side of the hyperbranchial groove (fig. 44, *ao*). Behind the pharynx the two aortæ unite into a single vessel which runs back above the intestine, giving off numerous branches which form a rich capillary network on the walls of the gut. From these capillaries the blood passes

into the sub-intestinal vein, and so the circle is completed. It

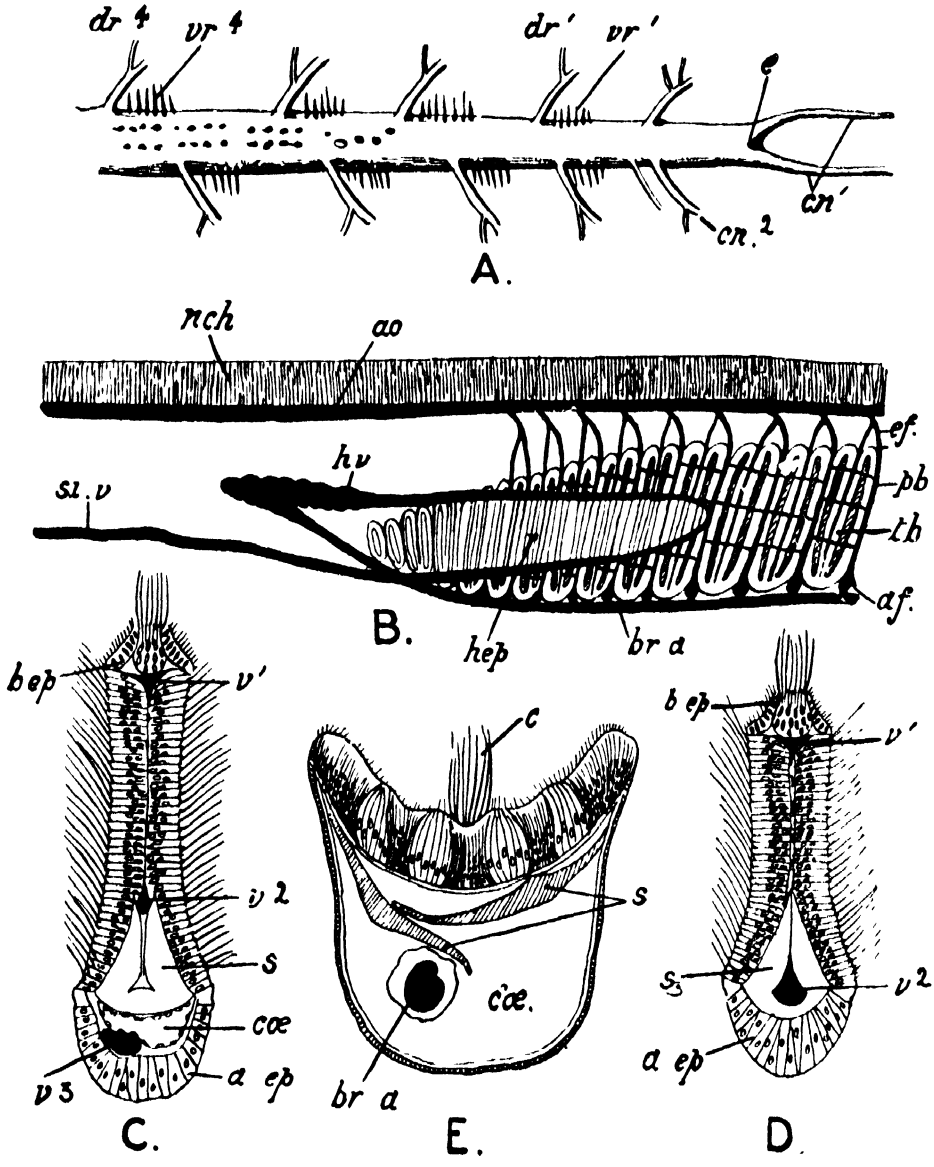


Fig. 45

A. Anterior portion of the nerve cord of Amphioxus, after Schneider. cn^1, cn^2, first and second pairs of "cranial" nerves; dr^1, dorsal roots of the first pair, and dr^4, dorsal roots of the fourth pair of spinal nerves; vr^1, vr^4, the corresponding ventral roots; *e*, eyespot. *B*. Diagram illustrating the circulation in Amphioxus. *af*. afferent branchial vessel with enlarged bulbil; *ao*, dorsal aorta; *br.a*, branchial aorta; *ef*, efferent branchial vessel; *hep*, hepatic diverticulum; *hv*, hepatic vein; *nch*, notochord; *pb*, primary bar; *th*, tongue-bar; *si.v*, sub-intestinal vein. *C*. Section through a primary, and *D*, section through a tongue-bar. *a.ep*, atrial epithelium; *b.ep*, branchial epithelium; *cœ*, cœlom; *s*, skeletal rod; v^1, internal, v^2, external, and v^3, cœlomic blood-vessels. *E*. Section through the endostyle. *br.a*, branchial aorta; *c*, median cilia of endostyle; *cœ*, subendostylar cœlom; *s*, skeletal rods. (*C*, *D*, and *E* after Benham.)

should be noted that in Amphioxus the blood runs forwards in

the ventral vessel and backwards in the dorsal vessel. This is characteristic of all vertebrates, and is exactly the reverse of what happens in worms and Arthropods.

The excretory organs of Amphioxus are remarkable because of their close resemblance to the nephridia of many polychæte worms, and because they differ in some important respects from the excretory organs of fishes and higher vertebrata. They are undoubtedly nephridia, but unlike those of the earth-

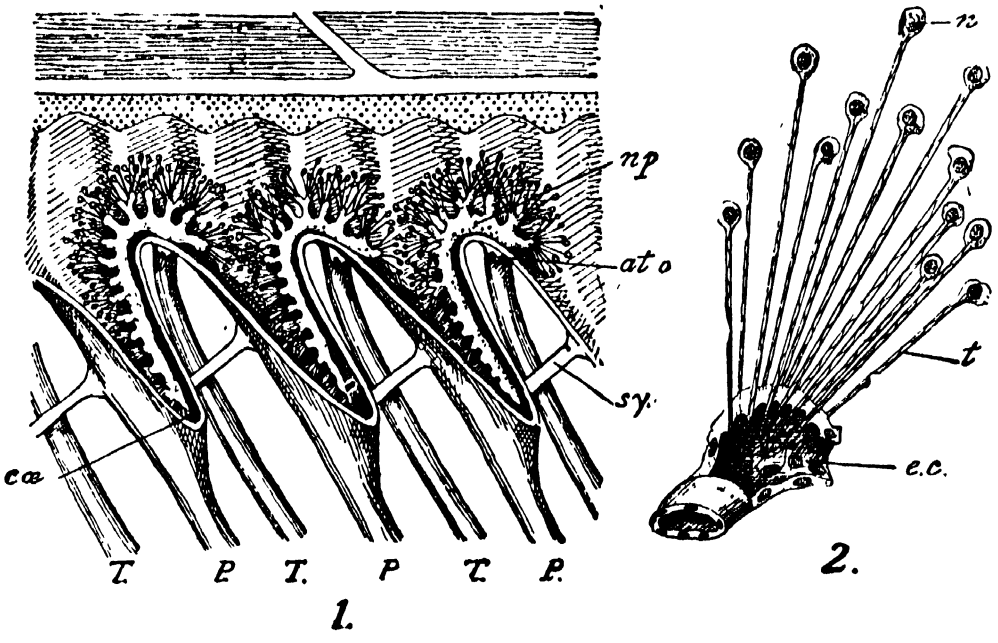


Fig. 46

1. Three nephridia with the neighbouring portion of the pharyngeal wall, after Boveri and Goodrich. *at.o*, atrial opening of a nephridium; *cœ*, dorsal cœlom passing into a cœlomic canal in a primary gill-bar: *np*, a nephridium with short dorsal branches bearing solenocytes; *sy*, cross-bar or synapticulum; *P*, *P*, primary gill-bars; *T*, *T*, tongue-bars. 2. A portion of an excretory canal bearing a group of solenocytes, semi-diagrammatic, after Goodrich. *e.c*, excretory canal; *n*, nucleus; *t*, tube with flagellum.

worm, they have no ciliated funnels opening into the cœlomic cavity, and though they are serially arranged, they do not correspond with the muscle segments of the body, but with the gill slits, which, as has been explained above, are much more numerous than the muscle segments of the pharyngeal region. There are about a hundred excretory tubes or

nephridia on each side of the pharynx of Amphioxus. The nephridia lie in the dorsal cœlom in close proximity to the dorsal ends of the branchial bars. As shown in fig. 46, each consists of a delicate excretory canal bent in the form of a crook. The handle of the crook hangs down in the pocket-shaped extension of the dorsal cœlom lying above, and leading into the cœlomic canal of a primary gill-bar. The decurved extremity of the crook is attached to the atrial wall just above the adjoining tongue-bar, and here it opens into the atrial cavity by a minute orifice situated on the end of a small papilla. Internally the excretory canal does not open into the cœlom, but its dorsal surface is produced into a number of short, simple, or slightly branched closed diverticula, the rounded ends of which are beset with a number of pin-shaped organs known as **solenocytes**. Careful study with a very high power of the microscope shows that each solenocyte has the following structure:—The head of the pin is a knob of protoplasm containing a nucleus. The shaft of the pin is an exceedingly delicate, transparent, thin-walled tube, the cavity of which communicates below with one of the branches of the excretory canal, but has no opening into the cœlom. A long flagellum hangs down from the terminal knob of protoplasm into the cavity of the tube, and projects beyond the latter into the cavity of the excretory canal. In life this flagellum is in constant movement, and its flickering motion recalls the flame-cell of a flat-worm, to which indeed the whole organ bears a close resemblance. Carmine and other colouring matters introduced into the blood system are taken up by the nephridia, whose excretory function was proved by this method, and it would appear that the excretory products pass by osmosis through the thin walls of the tube of the solenocyte, are propelled by the action of the flagellum into the excretory canal, and pass thence by the excretory pore into the atrial cavity, and finally by the atriopore to the exterior.

In addition to the tubules just described, there is a pair of funnel-shaped structures lying in the dorsal cœlom in the region of the twenty-seventh myotome, where the pharynx passes into the intestine. The wide, funnel-shaped mouths of these structures open into the atrium, and possibly their inner narrow ends open into the dorsal cœlom. They are

lined by an epithelium filled with brown pigment like the atrial epithelium, and are clearly epiblastic involutions of the atrial wall. Hence these brown-funnels, as they are called, if they are really excretory—which is not certain—may properly be called nephridia.

The central nervous system of Amphioxus presents many interesting features (fig. 45, *A*). It is a simple thick-walled tube lying dorsal to and nearly co-extensive in length with the notochord. Posteriorly the nerve tube tapers down to a point; anteriorly it ends abruptly at the level of the first myotome, some little distance behind the front end of the notochord. The nerve cord is perforated throughout its extent by a minute central canal, which is evidently the persistent lower part of a cleft which extended from the upper surface of the cord through about two-thirds of its thickness, but the upper walls of the cleft have become closely approximated, leaving only the minute canal below. At the anterior end of the cord the canal widens out to form an almost globular space known as the **cerebral vesicle.** In young specimens this vesicle opens into the olfactory pit by an aperture called the **neuropore**, but in later life the pore closes up and the olfactory pit is only attached to the roof of the cerebral vesicle by a solid cord of cells. Except for this cerebral vesicle, and the specialisation of the two anterior pairs of nerves, there is no trace of a brain. Nerves are given off laterally to the myotomes and body-wall from the whole length of the neural cord. With the exception of the first two pairs, these nerves consist of a dorsal or sensory, and a ventral or motor root, to this extent resembling the spinal nerves of higher vertebrates, but their arrangement is in many respects different and more primitive. In the first place the nerves given off from opposite sides of the cord are not symmetrical, but alternate with one another, this disposition being obviously correlated with the asymmetry of the myotomes. As is the case in higher vertebrates, the nerve fibres of a dorsal root are gathered into a single nerve trunk, while the ventral fibres emerge separately from the nerve cord; but in Amphioxus the dorsal and ventral roots are not given off from the same section of the cord, the latter being placed some way in front of the former. Again, there is no ganglion on the dorsal or sensory root, and the two sets of nerve fibres,

sensory and motor, are not united to form a mixed nerve, as is the case in higher vertebrates, but proceed straight to their destinations without ever becoming connected with one another. The ventral roots, on emerging from the sheath of the nerve cord, spread out and terminate in the muscle fibres of the myotome to which they belong. The dorsal roots run outwards through the myotomes and divide into dorsal and ventral branches, which run upwards and downwards in the cutis below the epidermis, and break up into a number of fine branches, supplying the epidermis, and also, it is said, the muscles of the floor of the atrium and the pharynx.

The two first pairs of nerves have no ventral roots, do not supply muscles, and appear to be exclusively sensory in function. Hence they are frequently distinguished as cranial nerves, but, as Amphioxus has no cranium, the name is hardly satisfactory. The first pair arises symmetrically from the lower side of the front end of the nerve cord and runs forward, dividing into a number of branches which are distributed to the fin-like expansion forming the anterior end of the animal. The second pair of nerves also arises symmetrically from the nerve cord, but more dorsally than the anterior pair. Its branches are also distributed to the snout, and both they and the branches of the first pair enter into curious peripheral ganglionic enlargements before they are finally distributed to the epidermis. The bulk of the nerve cord is made up of longitudinal fibres whose cut ends appear as dots in a transverse section. Round the central canal and dorsal fissure are nerve-ganglion cells and peculiar fibrous "supporting cells." There are also very large ganglion cells scattered along the centre of the cord from which very large "giant fibres" proceed, running longitudinally down the cord. But the minute structure of the nervous system is too complicated to be described in an elementary treatise.

The form and position of the gonads has already been described. The cavities of the twenty-six pairs of gonadic sacs are portions of that section of the embryonic cœlom known as the myocœle (see p. 199), which have been cut off from the rest of the cœlom so as to form a number of vesicles projecting into the atrial cavity. The sexes in Amphioxus are separate. In the breeding season the gonads of the males and females become hugely distended by the genital products and

eventually burst, discharging their contents into the atrium, whence they pass through the atriopore to the exterior. Fertilisation is effected in the water after the discharge of the ova.

The development of Amphioxus is fully as interesting and instructive as its adult anatomy, and the study of it may be regarded as the indispensable introduction to the study of vertebrate embryology. It is, however, beyond the scope of this book to enter into it in any detail. The reader will find a full account of the embryonic and larval development in Dr Willey's excellent treatise on the subject,* and much may be learned from almost any book on vertebrate embryology. The following account will deal only with points of fundamental importance, and the full explanations attached to figures 47-50 will spare the necessity of lengthy description. The first stage of development includes the segmentation of the ovum and the formation of the gastrula. The ovum is spherical, and sparsely furnished with food-yolk. The first cleavage is vertical, and divides the ovum into two equal halves. The second cleavage is also vertical, at right angles to the first, and results in the formation of four equal blastomeres. The third cleavage is nearly equatorial, dividing each blastomere into a somewhat smaller upper cell and a larger lower cell. The fourth cleavage divides all the cells vertically, producing a sixteen-cell stage, with eight upper and smaller and eight lower and larger cells surrounding a central cavity widely open to the exterior above and below. By continued meridional and transverse divisions the sixteen-cell stage is converted into a hollow sphere or **blastula**, with a central cavity (**blastocœle**) surrounded by a single layer of cells. The cells of the lower third of the blastula are somewhat larger, and contain more yolk granules than the upper cells. The lower surface becomes flattened, and the larger cells are then pushed into the blastocœle ; and this process of invagination is continued until the blastocœle is altogether obliterated. The embryo now has the form of a two-layered cup (fig. 47, *K*), the cavity of which is the primitive gut or **archenteron**, and

* "Amphioxus, and the Ancestry of the Vertebrates," by Arthur Willey. Columbia University Biological Series. Macmillan & Co., London and New York, 1894.

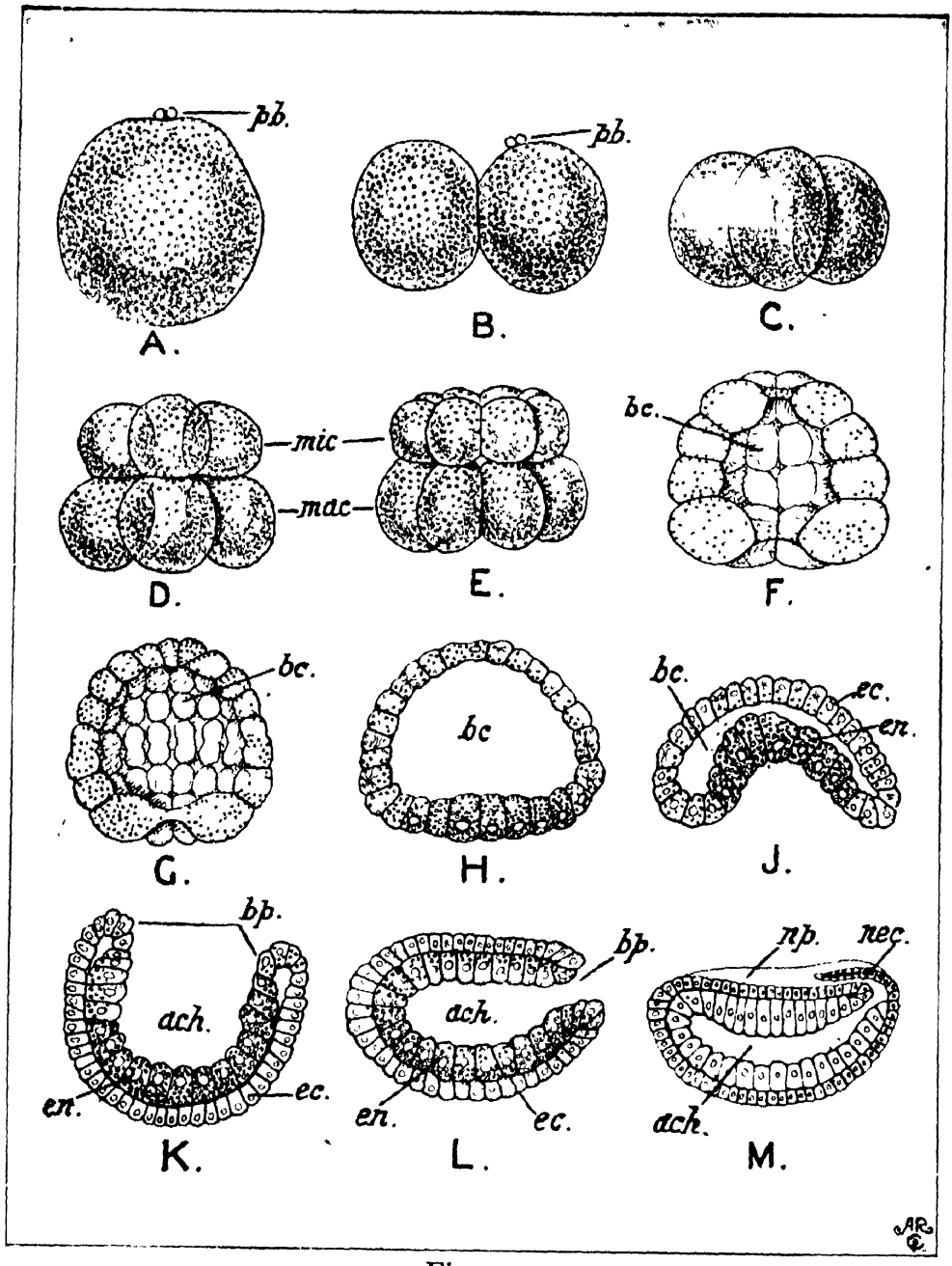


Fig. 47

A to *M*. Various stages of the development of *Amphioxus lanceolatus* (mostly after Hatschek; *H*, *J*, *K*, and *L* modified after Morgan). *A*, the unsegmented ovum; *B*, the first two blastomeres resulting from the first cleavage; *C*, stage with four equal blastomeres; *D*, eight-cell stage consisting of four smaller cells (micromeres) above and four larger cells (macromeres) below; *E*, sixteen-cell stage; *F*, optical section of thirty-two cell stage showing the segmentation cavity or blastocœle, opening to the exterior above and below; *G*, a later stage, the blastocœle completely closed in; *H*, a blastula shortly before invagination; *J*, commencement of invagination of the larger granular cells of the lower pole; *K*, gastrula, with widely-open blastopore; *L*, later gastrula in which the blastopore has been narrowed by the folding together of the walls; *M*, embryo with neural plate and commencing neurenteric canal. *ach*, archenteron; *bc*, blastocœle; *bp*, blastopore; *ec*, epiblast; *en*, hypoblast; *mic*, micromeres; *mac*, macromeres; *nec*, neurenteric canal; *np*, neural plate; *pb*, polar bodies

the widely-open mouth is the **blastopore**. The layer of larger cells lining the hollow of the cup is the **primitive hypoblast**; the outer layer is the epiblast.

Such an embryonic form is known as a **gastrula**. It soon loses its hemispherical shape and becomes elongated, the blastopore at the same time being reduced to a small orifice situated at one extremity of the now ovoid embryo. The manner in which the narrowing of the blastopore is effected has been the subject of much controversy. It would appear that the walls of the widely-open cup, depicted in fig. 47, *K*, are folded together, with the result that the blastopore is narrowed to the dimensions shown in *L*. This folding is accompanied by a multiplication of cells at the lips of the blastopore, so that the orifice is not slit-like but circular. The posterior end of the embryo is indicated by the blastopore, and one side—the dorsal side of the future animal—is flattened.

About this time the epiblastic cells develop cilia, by means of which the embryo rotates within the vitelline membrane. Thus far, development has led to the formation of a two-layered gastrula, not differing in any essential feature from the gastrula of many invertebrate animals. In the succeeding stages the gastrula undergoes important changes, leading to the formation of the mesoblastic somites and of characteristic vertebrate organs, the dorsal nerve tube and the notochord.

The embryo becomes elongated in an antero-posterior direction, and the cells of the flattened dorsal surface are somewhat modified to form an elongated median tract known as the **neural plate**. This plate sinks down below the surface, and the cells of the adjoining epiblast begin to grow over it, and eventually they meet and unite in the middle line above it. During this process the sides of the neural plate are bent upwards, so that it forms a gutter, roofed in above by the epiblast which has grown over it. Eventually, by further upgrowth, and folding in of its sides, the gutter is converted into a tube, the **neural tube** or central nervous system of the adult. While the dorsal epiblast is growing over the neural plate, the epiblast at the lips of the blastopore—particularly that of the ventral lip—grows over the blastopore, and, being continuous in front with the dorsal epiblast, it shuts off the blastopore from the exterior, but roofs over a passage leading round the posterior extremity of the embryo

from the neural tube to the archenteron. This passage, known as the **neurenteric canal**, is present in the embryos

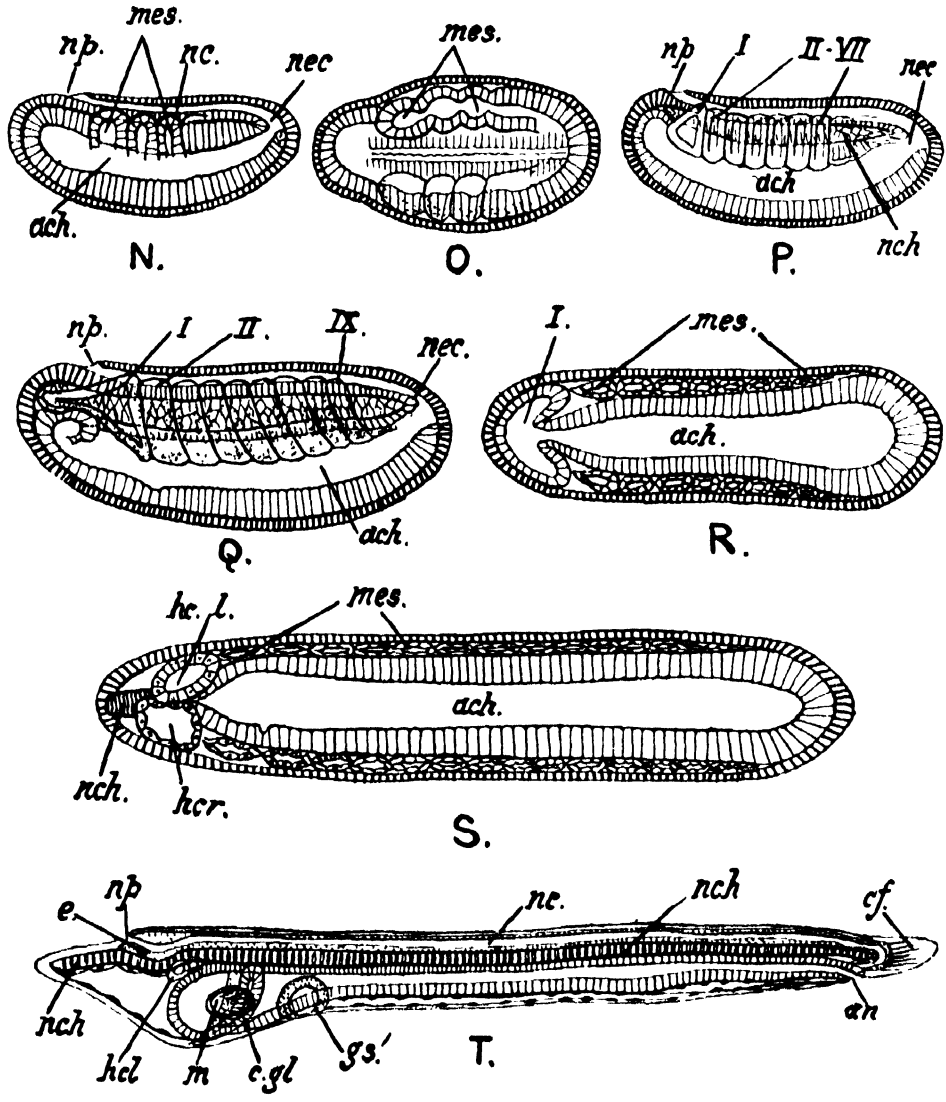


Fig. 48

N to *T*. Further stages in the development of Amphioxus (after Hatschek). *N*, sagittal section of an embryo with three mesoblastic somites; *O*, horizontal section of the same embryo; *P*, sagittal section of an older embryo; *Q*, sagittal section of an embryo with nine pairs of mesoblastic somites; *R*, horizontal section of an embryo of the same age showing the origin of the head-cavities; *S*, horizontal section of an embryo, with fourteen pairs of mesoblastic somites, showing the position of the head-cavities at this stage; *T*, a larva about thirty-six hours old, showing the mouth, first gill-slit, etc. *ach*, archenteron; *an*, anus; *cf*, caudal fin; *c.gl*, club-shaped gland; *e*, eyespot; *gs*^{1}, first gill-slit; *h.cl*, left head cavity; *hcr*, right head cavity; *m*, mouth; *mes*, mesoblastic somites; *nc*, neural canal; *nch*, notochord; *nec*, neurenteric canal; *np*, neuropore. *I-IX*, the several pairs of mesoblastic somites.

of higher vertebrates. As the neural plate is enclosed by

epiblast from behind forwards, the neural groove opens in front by an aperture called the **neuropore.** This aperture is gradually shifted forwards, till it lies near the anterior end of the embryo; but it is not closed till the adult characters are fully established, and traces of it are always to be found in the cord of cells uniting the bottom of the olfactory pit with the nerve cord.

Meanwhile, important changes have been taking place in the roof of the archenteron, leading to the formation of the notochord and mesoblastic somites. The roof of the archenteron is composed of smaller cells than those forming the floor and sides. Partly, it would seem, because of the pressure of the neural plate above, but partly as a result of its own growth, the archenteric roof is furrowed by three parallel, longitudinal grooves, one median and two lateral, the latter being the first to appear, and the deepest. As may be seen in the figures, the median groove gradually becomes constricted off from the archenteron from before backwards, the cells composing its walls grow towards and interdigitate with one another, and eventually they become vacuolated, and take on the characters of notochordal tissue. The notochord, then, is formed from a groove in the dorsal wall of the archenteron. At first it does not extend to the anterior end of the body, but at a later stage it grows forward till it projects beyond the first myotome. The posterior end of the notochord is for a long time confluent with the hypoblast in front of the neurenteric canal.

The lateral grooves give rise to the third and succeeding pairs of cœlomic sacs or **mesoblastic somites** in the following manner:—The anterior end of each groove is constricted off both from the archenteron and from the remainder of the groove behind it, and so forms a small sac or somite containing a cavity which was originally a part of the archenteric cavity. By a series of successive constrictions, new pairs of somites are constricted off from the lateral grooves, the latter increasing in length, *pari passu*, with the increase in length of the embryo. The result is the establishment of a number of pairs of somites, derived from the dorso-lateral walls of the archenteron, containing cœlomic cavities derived from the archenteric cavity. These cavities may be obliterated for a time, but soon reappear. When the cœlom is derived in this

manner from the archenteric cavity, it is usual to call it an **enterocœle.**

The second pair of cœlomic cavities is formed as a pair of outgrowths of the archenteron in front of and rather above the

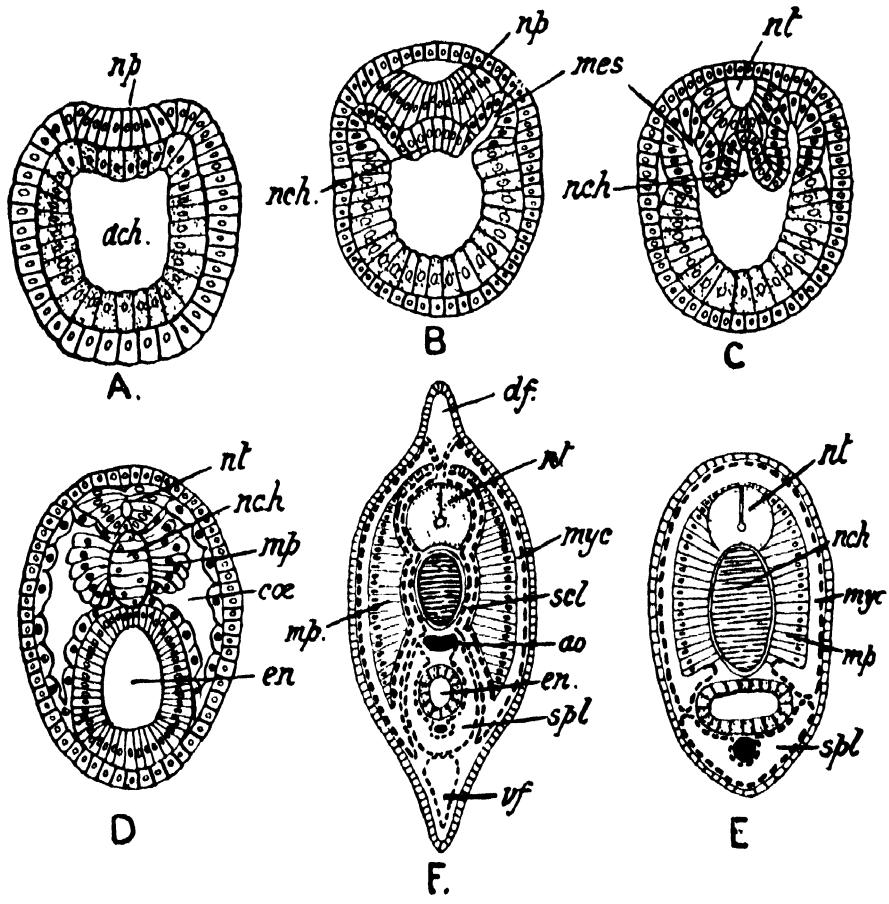


Fig. 49

A, *B*, *C*. Transverse sections of embryos of Amphioxus of different ages, illustrating the formation of the neural tube, notochord, and mesoblastic somites. *ach*, archenteron; *mes*, mesoblastic somites; *nch*, notochord; *np*, neural plate; *nt*, neural tube. *D*. Transverse section through an older embryo in which the mesoblastic somites are completely separated from the archenteron. *mp*, muscle plate; *cœ*, cœlom; *en*, mesenteron; the other lettering as above. *E*. Diagrammatic transverse section through a larva with five gill-slits. *myc*, myocœle; *spl*, splanchnocœle. *F*. Diagrammatic transverse section of a young Amphioxus shortly after the metamorphosis; the section is taken between the atriopore and anus. *ao*, aorta; *df*, dorsal fin; *scl*, sclerotome; *vf*, ventral fin; the other lettering as above. (All the figures after Hatschek.)

lateral grooves. The right outgrowth soon becomes constricted off from the archenteron; the left retains its connection with it for a long time. These cavities have a somewhat complicated history. Their walls give rise to the first myotome,

and the cavities themselves send back ventral prolongations which extend into the atrial folds when the latter structures make their appearance. Eventually the cavities in the atrial folds disappear, and their walls are used up in the formation of the atrial muscles. The anterior end of the archenteron sends forward a pair of outgrowths, and is then constricted off from the rest of the gut. The sac thus formed is divided into two vesicles corresponding to the two anterior outgrowths, and so the first pair of cœlom-sacs or "head-cavities" is established. The head-cavities differ from all the other cœlomic sacs in the fact that their walls never give rise to muscles. Their fate is somewhat peculiar. The right cavity grows to a larger size than the left, passes below the notochord, and forms the pre-oral cavity or cœlom of the snout of the larva. It becomes obliterated in the adult. The left cavity also is shifted below the notochord, but its fate is very different, for it requires an opening to the exterior on the right side, and becomes the pre-oral sense pit, which has been described as a ciliated pit on the inner side of the vestibule.

The early developmental stages of Amphioxus are passed through very rapidly. The blastula is completed about four hours after the ova are extruded from the atriopore; the gastrula is completed about two hours later, the first mesoblastic somites are formed four hours afterwards, and the embryo, covered with a coat of cilia, escapes from the vitelline membrane and swims in the water as a free larva. A few hours later it has the form depicted in fig. 48, *T*, with an elongate attenuated body, a pointed snout, a flattened caudal fin, a swollen pharyngeal region, and the mouth and first gill-slit have made their appearance. From this time onwards the development progresses very slowly, and it is some months before the larva is metamorphosed into the adult.

The growth of the larval Amphioxus is characterised by an extraordinary asymmetry in some of the more important organs. Thus the mouth, when it is first formed, is an oval aperture on the left side of the body. The first gill-slit is formed as a ventral outgrowth of the floor of the gut, but as soon as it has established communication with the exterior it is shifted up on the right side. Other gill-slits, to the number of fourteen or fifteen, are formed behind the first gill-slit, and similarly these are formed on the ventral surface and are

afterwards shifted to the right. The peculiar organ shown in front of the first gill-slit in fig. 50, *B*, is a transient embryonic organ formed from the floor of the pharynx, and known as the **club-shaped gland**. The fourteen or fifteen gill-slits first formed, and shifted to the right side of the body, are known as the **primary gill-slits**. Above them on the right side six **secondary gill-slits** are formed, and as the latter increase in size they push the primary gill-slits first to the ventral side, and ultimately to the left side of the pharynx. The first and some of the more posterior of the primary gill-slits close up and disappear; two additional secondary slits are formed, and so a stage is reached in which there are eight pairs of gill-slits, more or less symmetrically disposed, on the right and left sides of the body. While the gill-slits are being adjusted to their final positions, the mouth also is shifted from the left side to the anterior end of the pharynx;—thus to the position which it occupies in the adult. It should be observed that the gill-slits are simple oval apertures at first, but subsequently become horseshoe-shaped, and finally divided into two by the downgrowth of the tongue-bars from their dorsal margins.

For a detailed account of these remarkable phenomena and the subsequent changes undergone by the larva, the reader should consult Dr Willey's Memoir. We must confine ourselves in this place to a consideration of the formation of the atrial cavity and the fate of the mesoblastic somites.

The atrial folds are formed in a larva with six or seven primary gill-slits, as two low ridges or longitudinal thickenings of the integument on the ventral side of the body. Anteriorly, in correspondence with the asymmetry of the primary gill-slits, the ridges diverge to the right. These ridges enlarge, and become well-marked folds hanging down from the body-wall. Then, from the inner face of each fold a solid ridge, the **epipleural fold**, grows in towards the middle line and meets and coalesces with its fellow of the opposite side. In this way a tube lined by epiblast is formed enclosing the gill-slits. As the epipleural folds do not coalesce behind, the tube opens to the exterior by an aperture, the **atriopore**. Though small at first, the atrial tube soon grows in size and extends itself by dorsal upgrowths right and left of the pharynx, thus reducing the perivisceral cœlom to very small dimensions. The metapleural folds, as the lower edges of the atrial folds are

called, are at first solid, but become hollowed out by the two metapleural lymph spaces.

The mesoblastic somites are shown in fig. 49 as triangular sacs containing very small cavities, and lying right and left of the notochord. Fig. 49, *D*, shows how these sacs have extended dorsally and ventrally between the epiblast and the gut, notochord, and nerve tube. At the same time their cavities have enlarged greatly, so that we may distinguish an

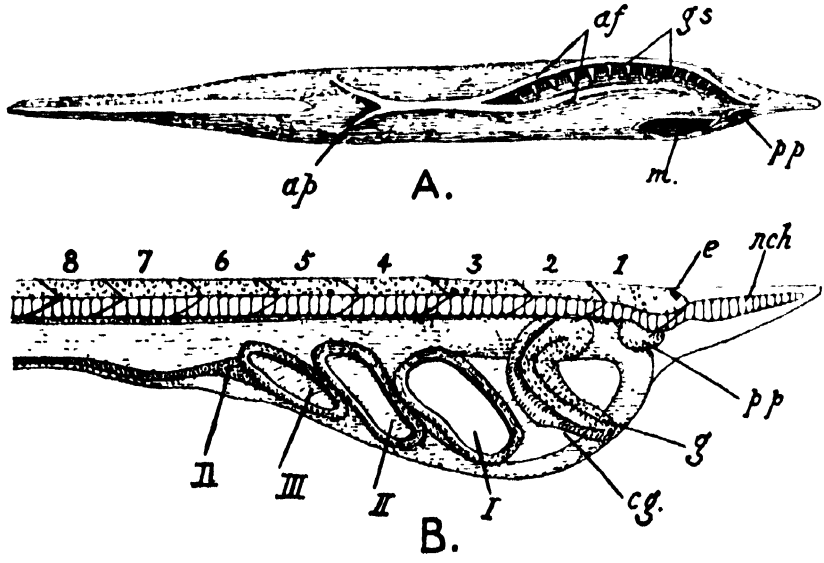


Fig. 50

A. Diagrammatic ventral view of a larval Amphioxus illustrating the formation of the atrial cavity. *af*, atrial folds; *ap*, atriopore; *gs*, gill-slits; *m*, mouth; *pp*, pre-oral pit. *B*. View of the first eight somites of a larval Amphioxus with three gill-slits and a rudiment of a fourth; from the right side. *1-8*. mesoblastic somites; *I-III*, the first three gill-slits; *IV*, the rudimentary fourth gill-slit; *cg*, club-shaped gland; *e*, eyespot; *g*, glandular tract; *pp*, pre-oral pit. (After Lankester and Willey.)

outer layer of cells or **somatopleur** lying against the epiblast, and an inner wall or **splanchnopleur** lying against the gut and notochord. But the cells of that part of the inner layer which lies against the notochord become differentiated at a very early period in the manner shown in fig. 49, *D*. They become elongated and extended in a longitudinal direction, so that they nearly fill up the upper part of the cœlomic space. These cellular growths are the first signs of the myotomes. At a later stage, shown in fig. 49, *E*, the lower limbs of the pouches have grown down to the mid-ventral line, and fused below the gut, so that the latter is surrounded below by a cœlomic

space, and at the same time the upper parts of the cœlomic pouches containing the rudiments of the myotomes have become separated off from the fused lower portions, and constitute dorsal sections of the cœlom, known as **myocœles**. The ventral space lying below and to the sides of the gut is distinguished as **splanchnocœle**. The partitions between the splanchnocœlic sections of successive somites break down, so that the splanchnocœle becomes a continuous cavity from end to end of the gut. But the partitions between the myocœlic sections persist and form the septa between the myotomes of the adult. The figure also shows a short ingrowth or diverticulum of the myocœle below the muscle-plate at the level of the lower edge of the notochord. In fig. 49, *F*, we see that this diverticulum has grown enormously, and has pushed its way upwards, separating the muscle-plate from the notochord and nerve-cord above it. This diverticulum is known as the **sclerotome**. It may further be seen in fig. 49, *F*, that the myocœle has pushed its way downwards, so as to separate the somatopleuric wall of the splanchnocœle from the epiblast.

We may now consider the fate of the walls of these various subdivisions and prolongations of the original cœlomic pouches.

The interior wall of the sclerotome gives rise to the connective tissue sheath of the notochord and nerve chord. The outer wall of the sclerotome gives rise to the inner connective tissue sheath or fascia of the muscles of the myotomes.

The cells of the muscle-plates are converted into the muscle fibres of the myotomes.

The outer or somatic walls of the myocœles are converted into the deeper layer or cutis of the integument. It is said that the dorsal and ventral fin-spaces are also formed from the myocœle.

The inner wall of the splanchnocœle becomes the peritoneal investment of the gut, the outer wall the peritoneal lining of the perivisceral cœlom. The splanchnocœle itself is greatly reduced in size on the formation of the atrial chamber, and in the pharyngeal region is subdivided into the dorsal and sub-endostylar cœlomic spaces and the canals of the primary gill-bars on the formation of the gill-slits. The splanchnocœle, therefore, persists as the body-cavity of the adult, but the myocœle and cavity of the sclerotome are obliterated, and

very slight traces of them are to be found in the full-grown animal.

The cavities of the gonadic pouches, however, are persistent portions of the myocœle, being formed by the evagination of the lower corners of the eleventh to the thirty-seventh myocœles. The details of the development of the gonads are rather complex. A pocket-like projection from the lower end of each of the named myocœles is pushed into the myocœle next in front of it. The germ cells are formed from the epithelium lining the pockets, and, as the latter increase in size, each one thrusts the wall of the myocœle in which it lies inwards towards the atrial cavity, thus giving rise to a gonadic sac projecting into the atrium; within this lies the gonad derived from the wall of the myocœle next behind. The whole process is described at length in Dr Willey's Memoir on Amphioxus.

The remarkable simplicity of the developmental processes of Amphioxus bear witness to their primitive character. The principal organs are formed as infoldings or outfoldings of simple epithelial layers, and only at a comparatively late period are the epithelial cells differentiated to form nervous, muscular, notochordal, and other tissues. Thus the blastula, by infolding, becomes a gastrula; outfoldings of the inner layer of the gastrula give rise to the notochord and mesoblastic somites. The central nervous system is formed by a sinking in and subsequent folding up of a part of the outer layer; the atrial cavity, also, originates as a groove in the outer layer, which afterwards is converted into a tube.

The development of the higher vertebrates pursues a similar course. In them, also, simple epithelial layers are formed, from which the various tissues and organs of the body are subsequently evolved. But in their case the processes are so much complicated and obscured, partly by the presence of food-yolk, partly by the development of embryonic organs, and partly by the precocious differentiation of tissues and organs, that they can hardly be interpreted without reference to Amphioxus.

Again, in the adult anatomy of this remarkable animal, we find the most simple example of the vertebrate plan of organisation. There is an endoskeleton, in the form of an

elastic rod running through the length of the body dorsal to the gut. Mechanically this rod, the notochord, serves as a support to the body, and as an attachment to the muscles. Accordingly we find a great development of dorsal musculature, accompanied by the reduction and obliteration of the cœlom in this region. A similar elastic rod is found in the embryos of all higher vertebrates. In Amphioxus the notochord is simply invested by a connective tissue sheath. In higher vertebrates we have a progressive series in which the notochord is (1) surrounded by continuous cartilage, (2) the cartilage is divided into segments or vertebral centra, (3) the centra are thickened with consequent reduction of the notochord, (4) the cartilage is replaced by bone and the notochord disappears, except for a few traces. The significance of these facts cannot be overrated.

The second characteristic vertebrate feature in Amphioxus is the dorsal position and tubular character of the central nervous system. This tubular character is referable to the mode of its development, and we find that this mode is similar throughout the vertebrate phylum.

A third and very important vertebrate feature is the presence of gill-slits, structures which are always present in the embryos of vertebrates, but are obliterated in the adults of air-breathing forms. Amphioxus is remarkable for the vast number of its gill-slits; this is most probably a secondary feature connected with its habits and mode of feeding. Correlated with the presence of gill-slits, serving as respiratory organs, is the vertebrate type of circulation, a contractile ventral blood-vessel connected by lateral vessels passing up between the gill-slits with a dorsal blood-vessel in which the blood flows backwards. In this connection we may also notice the presence of a hepatic portal system. We may further notice as features that occur in, but are not peculiar to vertebrates, the segmentation of the body expressed by the myotomes and the presence of metamerically repeated excretory tubules. It is, however, a peculiar vertebrate feature that the primitive segmentation is retained only in the dorsal musculature or myotomes, but is lost in the ventral region through fusion of the splanchnocœlic subdivisions of the primitive somites.

But Amphioxus, while exhibiting so clearly the fundamental

characters of vertebrate organisation, differs from all other members of the phylum in several important characters, chief among which is the absence of a specialisation of the anterior end of the body to form a definite head. In the absence of the head, all structures associated with a head are also absent, paired eyes, paired auditory organs, a definite brain, and jaws. Because of this, Amphioxus is sometimes placed apart from all other vertebrates in a section Acrania. But this method of classification is not without inconveniences. As a matter of fact, Amphioxus cannot properly be called a vertebrate, for it has no vertebral column composed of separate vertebræ, but only the precursor of a vertebral column—namely, a notochord. But a notochord is a possession common to the true vertebrates, to Amphioxus, to the group of animals known as "sea-squirts," Ascidia, or Tunicata, and to some other groups, and we may therefore group all these in a phylum **Chordata**. In this phylum Amphioxus is characterised by the forward extension of the notochord to the anterior end of the body, and therefore it and the genera immediately related to it, form a class **Cephalochorda**. The Ascidians having a notochord only in the tail, form a class **Urochorda**: certain worm-like animals with a very imperfect notochord are **Hemichorda**, and the true vertebrates possessed of a definite head are **Craniata**

CHAPTER XXVI

THE ELASMOBRANCH FISHES—SCYLLIUM CANICULA

AMONG the oldest remains of vertebrated animals that have been discovered are teeth and spines, whose structure shows clearly that they belonged to fishes resembling our modern sharks and dog-fishes, and some wonderfully complete specimens of ancient sharks have been obtained from carboniferous deposits. The sharks, then, belong to a very ancient group of fishes, and, as might be expected, the living forms retain so much that is primitive in their organisation, that they are beyond all other animals instructive to the comparative anatomist. If Amphioxus affords us a clue to the general architecture of vertebrated animals, the sharks, dogfishes, and rays are no less important as giving us an insight into the anatomy of craniate and gnathostomatous vertebrates—that is, to vertebrates which have a distinct head, furnished with true jaws.

The larger forms of sharks are happily not common in British waters, though some of them occasionally wander to our coasts. But dogfishes, which, to all intents and purposes, are little sharks, are very abundant and of several kinds.

One of the commonest is *Scyllium canicula*, known to fishermen as the "little rough dog." It is also called the "rough hound," the "lesser spotted dogfish," and other names. A somewhat larger and closely allied species is the "nurse hound" or "greater spotted dogfish," *Scyllium catulus*, but it is not so common as *Scyllium canicula*. Besides these, are the "Toper," *Galeus canis*; the "smooth hound," *Mustelus lævis*; and the "picked dog," *Acanthias vulgaris*. The last named is extremely common, and is easily recognised by its bluish-grey back, its white belly, and by the sharp-pointed, powerful spine situated in front of each of the two dorsal fins. The skates and rays, though differing greatly in appearance, are closely allied to the sharks and dogfishes, their wide flattened shape

being due to a great expansion of the two pectoral fins. The commonest English rays are the thornback, *Raia clavata*, and the skate, *Raia batis*. The following description will apply to the lesser spotted dogfish, *Scyllium canicula*, but except for certain differences in detail, it will be found serviceable for any other species of dogfish, and may even be used as a guide to the dissection of skates and rays.

The lesser spotted dogfish is a voracious and predatory fish, swimming about in large shoals near the bottom of the shallower seas round our coasts. It preys upon fishes, small crustaceans, octopus, and squid, and is caught in large numbers by fishermen, both in nets and by hook and line, but except for anatomical purposes, it has no marketable value.

Comparing its general external features with those of Amphioxus, it is at once evident that we have to do with a true craniate vertebrate belonging to the class of fishes. The whole length of a well-grown specimen is about two feet, and the body is divisible into head, trunk and tail, though there are no distinct boundaries between these regions. The head is triangular in shape, somewhat flattened, and bears the three pairs of organs of special sense characteristic of the higher vertebrates. The olfactory organs are situated in the snout, and open to the exterior by a pair of circular orifices placed on the ventral surface. These nasal openings communicate by wide **naso-oral grooves** with the mouth, the grooves being partly covered and concealed by flaps of skin. The eyes, situated on the sides of the head, are elongated, slit-like, and furnished with movable lower eyelids. The auditory organs are situated on the sides of the head immediately behind the eyes, but, in the absence of any tympanic membrane or external ear, they are not recognisable externally.

The mouth is a wide crescentic opening on the ventral surface of the head, about an inch behind the tip of the snout. It is furnished with jaws, and each jaw is armed with several rows of sharp re-curved teeth. The vent or cloacal aperture is placed in the mid-ventral line, rather nearer to the anterior than to the posterior end of the body. Right and left of the cloacal aperture are the **abdominal pores**, a pair of small apertures leading into the cœlom, and guarded by valves. The general shape of the body can be better understood from an inspection of fig. 51, than from any description. It is much

elongated and tapers gradually towards the tail, the last five inches of which are bent upwards at an angle. The body is furnished with certain flattened expansions of the skin, supported by horny and cartilaginous rays. These **fins** are very important structures, and will be described in detail in connection with the skeleton. For the present it is sufficient to note that there are four unpaired or median fins and two pairs of lateral fins, the latter representing the limbs of the higher vertebrates. The anterior dorsal fin is placed rather far back in the mid-dorsal line of the body; in a specimen 22 inches in length the front edge of the anterior fin was 11 inches, and the posterior dorsal fin 15 inches from the snout. The caudal fin forms a vertical expansion round the posterior five inches of the tail. It starts on the dorsal side as a low ridge, gradually increasing in size to the tip of the tail, round which it is continued into the ventral lobes. The ventral part of the caudal fin is deeper than the dorsal part, and is partially subdivided into two lobes, of which the anterior is considerably the larger. The ventral median fin is situated in the mid-ventral line, some three inches behind the cloacal aperture and opposite to the interspace between the two dorsal fins. On removing the skin from one of the median fins it will be noticed that the greater part of its extent is simply a fold of the integument supported by a large number of very fine horny fin-rays, but its base is thickened and muscular, and supported by a smaller number of cartilaginous fin-rays.

The anterior pair of lateral fins are known as the **pectorals.** They are large triangular expansions attached by their apices to the ventro-lateral margins of the body not far behind the head. In a specimen 22 inches long the anterior edge of the pectoral fin was $3\frac{1}{2}$ inches from the tip of the snout. The posterior or **pelvic** pair of lateral fins are smaller than the pectorals, and rise from near the middle line of the body just in front of the cloacal aperture. In the female the pelvic fins are sub-triangular in shape and their inner margins are free; but in the male the inner margins are fused together, and below the sort of hood thus formed there project a pair of stout styliform processes, deeply grooved along their inner edges, and furnished with a terminal tuft of papillæ. These are the accessory male organs or **claspers,** used in copulation.

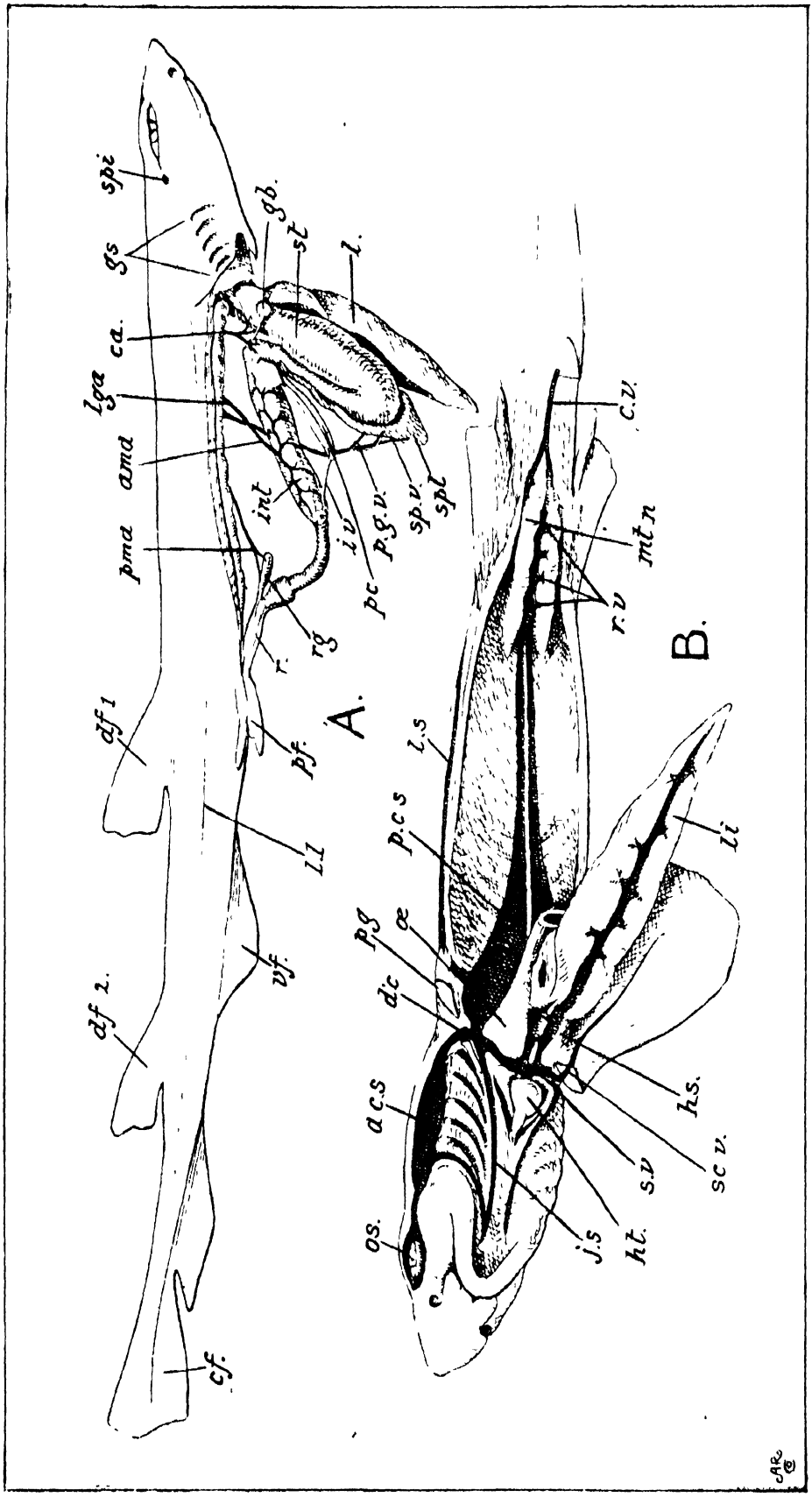


Fig. 51. The Dogfish (*See explanation opposite*)

A. The common dogfish, *Scyllium canicula*, seen from the right side. The pectoral girdle and the wall of the abdominal cavity have been cut away to expose the abdominal viscera. *ama*, anterior mesenteric artery; *ca*, cœliac artery; *cf*, caudal fin; *df1* and *df2*, the first and second dorsal fins; *gb*, gall-bladder; *gs*, the five gill-slits; *int*, intestine; *iv*, intestinal vein; *l*, left lobe of the liver, the right lobe is cut away; *lga*, lieno-gastric artery (the reference line should point to the hinder of the two arteries); *ll*, lateral line; *pc*, pancreas; *pgv*, posterior gastric vein; *pf*, pelvic fin; *pma*, posterior mesenteric artery; *r*, rectum; *rg*, rectal gland; *spi*, spiracle; *spl*, spleen; *sp.v*, splenic vein; *st*, stomach; *vf*, ventral fin.

B. Diagram showing the arrangement of the principal venous sinuses of the dogfish. *acs*, anterior cardinal sinus; *cv*, caudal vein; *dc*, ductus Cuvieri; *hs*, hepatic sinus; *ht*, heart; *js*, jugular sinus; *li*, right lobe of liver, the left lobe is cut away; *ls*, lateral sinus; *mtn*, metanephros; *œ*, œsophagus (cut short); *os*, orbital sinus; *pcs*, posterior cardinal sinus; *pg*, pectoral girdle; *rv*, renal veins; *sc.v*, subclavian sinus; *sv*, sinus venosus.

The paired fins resemble the median fins in that the greater part of their free expansions are supported by numerous fine horny rays, but their bases are very muscular, and supported by a cartilaginous skeleton.

Immediately in front of and above each pectoral fin is a row of five vertical slits, leading obliquely forwards into as many separate branchial chambers, which in turn communicate by separate apertures with the gullet. On looking into one of these gill-slits the tufts of red highly vascular gill-filaments may easily be seen. Immediately behind each eye is a much smaller orifice communicating with the gullet, but only provided with a rudimentary tuft of gill-filaments. These smaller openings are known as the **spiracles**. They are really rudimentary gill-slits, and are specially large and conspicuous in rays, but are absent in many sharks. The presence of a number of gill-slits opening separately to the exterior, and destitute of any plate-like covering or operculum, is characteristic of though not peculiar to Elasmobranch fishes. The lampreys also have separate gill-openings. Though there are usually five gill-slits (in addition to the spiracle when present) in sharks, dogfishes, and rays, there are some forms in which this number is exceeded. The genus *Heptanchus* has seven gill-slits, *Chlamydoselache* and *Hexanchus* have six.

A close inspection of the head and snout of the dogfish reveals the presence of a number of minute pores arranged in symmetrical rows. These are the apertures of the mucous canals, peculiar gelatinous-looking tubes filled with mucus, and richly supplied with nerve endings.

The back and sides of *Scyllium canicula* are of a warm brownish-grey colour, covered with brown spots. The belly and throat are nearly white, and they and the under sides of

the fins often have a pink tinge. The skin is not covered with scales like those of the more familiar bony fishes, but is rough to the touch, and considerable resistance is felt if the finger is drawn from the tail towards the head of the animal. This roughness is due to the presence of innumerable closely set spines or **denticles** (sometimes called "placoid" scales) imbedded in the cutis, whose shape and structure differs entirely from that of true scales, and most closely resembles that of teeth. In fact, the teeth of the dogfish are nothing more than specialised denticles, and in Acanthias and some other dogfishes, though not in Scyllium, the interior of the mouth is beset with numerous small denticles similar to those of the outer skin. In the thornback ray the denticles are relatively few in number, but large, with sharp prominent spines. The spines of the dorsal fins of Acanthias, the long serrated spine on the tail of the sting-ray, the rows of blade-like spines on the rostrum of the saw-fish, are all modifications of skin denticles. Some isolated denticles of *Scyllium canicula* are shown in fig. 53. Each consists of a flat four-lobed basal plate, bearing a backwardly directed spine on its upper surface. A perforation in the centre of the basal plate leads into a canal called the **pulp-cavity**, which traverses the centre of the spine, and in life is filled with the so-called **pulp**, a very vascular form of connective tissue containing large ivory-forming cells or odontoblasts. The bulk of the spine is formed of ivory or dentine, a calcareous tissue traversed by fine ramifying canals communicating with the pulp-cavity. Externally the spine is coated with a layer of **enamel**, a hard structureless substance similar to the enamel of our own teeth. The basal plate is formed of calcified connective tissue, usually described as "cement," though it differs in structure from the cement of our own teeth. A denticle is formed as an upgrowth from the deeper vascular layer of the skin or cutis, covered by the epidermis. The cement, pulp, and dentine are formed from the mesoblastic tissue of the cutis, the enamel from the overlying epiblastic epidermis.

The skin of the dogfish is closely bound by connective tissue to the muscles beneath, and is difficult to remove. On stripping it away from the head and anterior part of the trunk, one can see that the trunk muscles, like those of Amphioxus, are divided by connective tissue partitions into a number of

muscle-segments or **myotomes**. The myotomes, however, are at once complicated and more numerous than in Amphioxus. There are thirty-four pre-anal and as many as ninety-six post-anal segments, and each myotome instead of being bent once at an angle is bent four times. Starting from the mid-dorsal line it runs first forwards, then back at a sharp angle, then forwards again as far as the lateral line. From the lateral line it runs sharply backwards again and then bends forward under the ventral surface to join its fellow of the opposite side. There is also a specialisation of the musculature such as is not found in Amphioxus. In the head the muscles are grouped about the eyes and jaws in such a manner that all trace of metameric arrangement is lost. In the neighbourhood of the gills the muscles are modified in connection with the gill-pouches and the cartilaginous skeleton supporting them ; there is a group of powerful longitudinal muscles on the ventral wall of the throat, and there are special muscles in connection with the paired and median fins. It should be particularly noticed that the primitive segmental arrangement of the muscles is lost in the head, and largely modified in the region of the gills.

The skeleton of the dogfish shows a great advance on that of Amphioxus, but its main or axial portion is moulded upon a continuous notochord, which in the embryo is very like that of Amphioxus, except that it never extends to the anterior end of the body. Considerable remnants of it are found in the adult. The skeleton is divisible into the **axial skeleton**, consisting of the cranium and vertebral column ; the **visceral skeleton**, consisting of the jaws and branchial arches ; and the **appendicular skeleton**, consisting of the cartilaginous supports of the fins. The whole skeleton is composed of cartilage which may be calcified in places, but no true bone is developed either in substitution of the cartilage or in the membrane surrounding the cartilage.

It is convenient to begin with the study of the vertebral column. This is made up of a number of vertebral bodies or **centra**, bearing **neural arches above** and **hæmal** arches below ; the latter, however, are absent or modified in the trunk. The vertebral centra are traversed by the notochord ; the neural arches enclose a canal containing the spinal cord, and the hæmal arches of the tail enclose the caudal artery and caudal vein. Each individual centrum is a short, stout

cylinder of cartilage, deeply excavated at both ends so that it is biconcave, or **amphicœlous** (see vol. i. p. 22). The concavities are connected by a small canal running through the middle of the centrum, and this canal and the concavities are occupied by the remains of the notochord, which is therefore continuous from end to end of the vertebral column. As the biconcave centra are united end to end by ligaments, it is evident that within each centrum the notochord is constricted to a mere thread, but between two centra it swells up to occupy the whole space formed by two apposed concavities. In technical language the notochord is constricted intravertebrally and enlarged intervertebrally.

From the upper sides of each centrum, at the middle of its length, two short neural processes project upwards. To the upper edge of each neural process a pentagonal plate of cartilage, the **vertebral neural plate**, is fused, and the spaces between successive vertebral neural plates are filled in by hexagonal **intervertebral neural plates**, the two sets of plates forming the sides of the neural arch, while the centra form the floor. The arch is completed above by a number of wedge-shaped pieces of cartilage, the **neural spines**, which fill in the spaces between the upper angles of the vertebral and intervertebral neural plates. The lower posterior margins of the vertebral plates are notched to admit the passage of the ventral roots of the spinal nerves, and the upper posterior margins of the intervertebral plates are similarly notched for the exit of the dorsal roots.

In the most anterior vertebræ the hæmal arches are mere ridges projecting horizontally from the lower sides of the centra. Further back they become more prominent and form distinct transverse processes, having small cartilaginous ribs, about half-an-inch in length, articulated to their distal ends. At about the 30th vertebra the transverse processes begin to bend downwards so as to enclose a groove on the ventral surface of the centra, and at the 42nd vertebra the groove is converted into a canal by the processes meeting below and forming a complete hæmal arch, which in life contains the caudal artery and vein. The hæmal arches of the last 48 or 50 vertebræ are produced ventrally into laterally compressed hæmal spines, which afford support to the lower lobes of the caudal fin.

The cranium of the dogfish is made up of a brain-case to which two pairs of capsules of the organs of special sense are fused. As no bone enters into its composition, and it has no covering of bony plates, it is a particularly favourable object for the study of the primitive condition of the vertebrate skull. The brain-case proper is a somewhat oblong cartilaginous box open behind and in front. The hinder opening, situated on the posterior wall of the cranium, is the **foramen magnum**, through which the spinal cord passes to expand into the brain. On the sides of the foramen magnum are the two occipital condyles, for articulation with the first vertebra. The opening in front is a large vacuity in the cranial roof. During life it is covered in by a sheet of connective tissue, with which the pineal body enters into close relations. The **olfactory capsules** are fused to the front end of the cranium, and in the adult are continuous with it, but in embryonic life they were separate. They are large hemispherical sacs with wide openings looking downwards and forwards. Their walls are very thin, and their cavities are separated by a median vertical cartilaginous plate, the internasal septum. Three small cartilaginous rods project forward in front of the olfactory capsules to form the rostrum. The two uppermost spring from the walls of the olfactory capsules, the lowest from the front edge of the internasal septum, and they converge together in front. In Scyllium they are very small, but in some sharks and dogfishes they are relatively large.

The **auditory capsules**, like the olfactory, were separate in embryonic life, but in the adult they are intimately fused with the side walls of the hinder part of the cranium, and form a pair of prominent projections immediately behind the orbits. A ridge running forward and outward on the roof of each capsule, marks the position of the anterior vertical semicircular canal; a similar ridge running backward marks the posterior vertical semicircular canal, and a horizontal shelf marks the external horizontal canal. Between the two auditory capsules, on the mid-dorsal roof of the cranium, is a depression in the sides of which are the openings of the **ductus endolymphatici** or **aqueductus vestibuli** leading into the auditory organs.

The optic capsules are never fused to the cranium in any vertebrate, but they profoundly modify the walls to which they

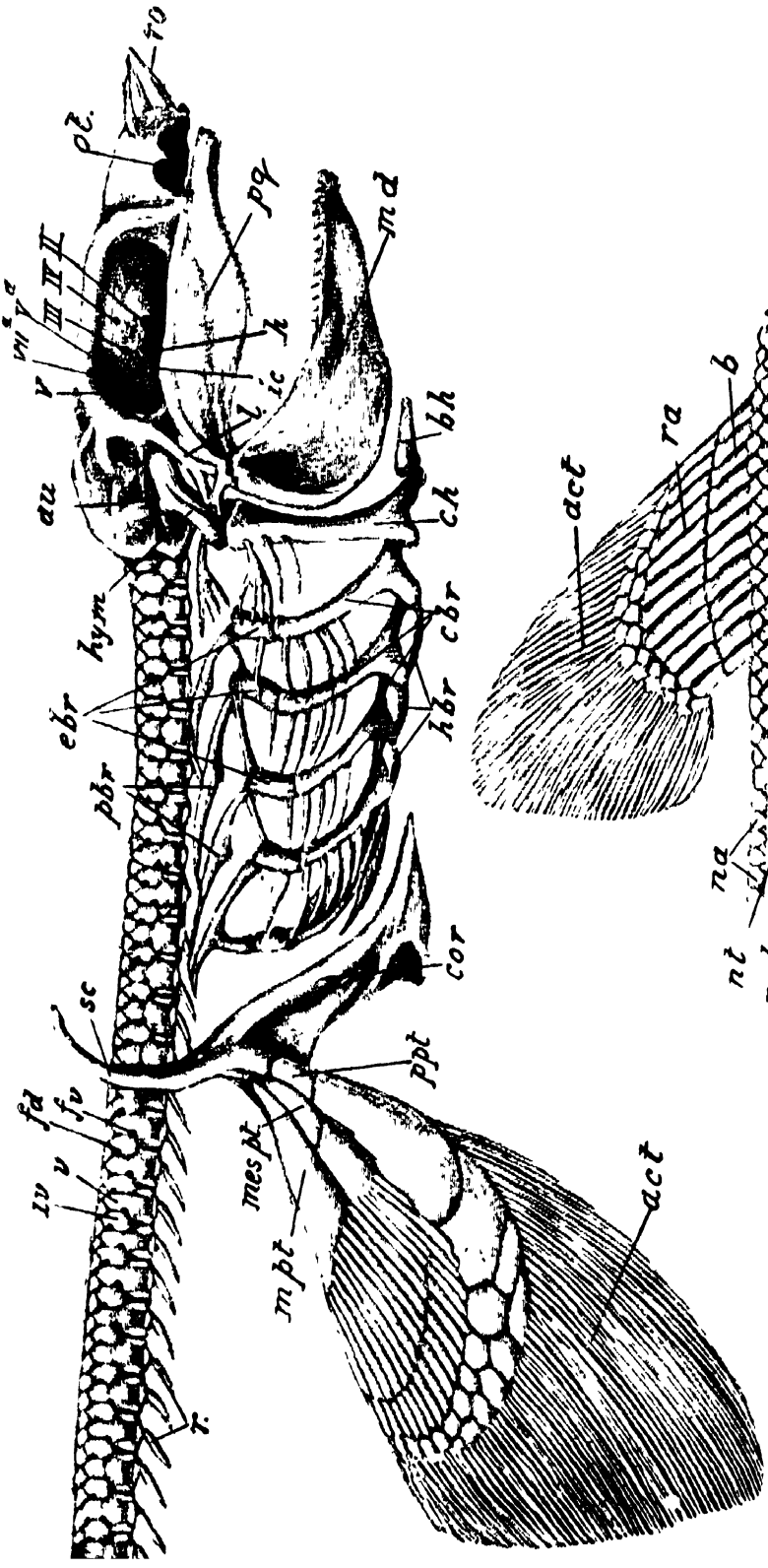


Fig. 52. Scyllium Canicula. (*See description opposite*)

The upper figure represents the skull, visceral skeleton, the anterior part of the vertebral column and the pectoral girdle and fin of *Scyllium canicula*. The lower figure shows the skeleton of the first dorsal fin attached to a section of the vertebral column; the last few vertebræ have been cut through vertically. In the skull—*au*, auditory capsule; *ol*, olfactory capsule; *ro*, rostrum; *pq*, palato-quadrate cartilage; *md*, mandibular cartilage; *l*, post-spiracular ligament; *II*, optic foramen; *III*, foramen for 3rd nerve; *IV*, foramen for 4th nerve; *V*, foramen for main branch of 5th, 6th, and main branch of 7th nerve; *V*a, *VII*a, foramina for ophthalmic divisions of the 5th and 7th nerves; *h*, foramen for hyoidean artery; *ic*, interorbital canal. In the vertebral column—*v*, vertebral plate; *iv*, intervertebral plate; *fd*, foramen for dorsal root, and *fv*, foramen for ventral root of a spinal nerve. In the visceral skeleton—*hym*, hyomandibular cartilage; *bh*, basihyal; *ch*, ceratohyal; *pbr*, pharyngobranchials; *ebr*, epibranchials; *cbr*, ceratobranchials; *hbr*, hypobranchials; the gill-rays are shown on the epi and ceratobranchials and on the hyomandibular and ceratohyal cartilages. The extra branchial cartilages are omitted. In the pectoral girdle—*sc*, scapula; *cor*, coracoid; *ppt*, propterygium; *mes.pt*, mesopterygium; *m.pt*, metapterygium; *act*, actinotrichia. In the lower figure—*b*, basals; *ra*, radials; *act*, actinotrichia; *na*, neural arches; *nt*, spinal cord; *nch*, the notochord constricted intravertebrally.

are contiguous, and are lodged in spacious orbital cavities. The orbital cavities of the dogfish are bounded by the olfactory capsules in front, the auditory capsules behind; the roof is formed by a supra-orbital ridge of cartilage projecting from the cranial roof, and the floor below is formed by a horizontal plate of cartilage continuous with the cranial floor. Between each supra-orbital ridge and the ridge of the cranial roof there is a wide shallow groove in which a bundle of mucous canals is lodged, and at the anterior end of the groove is a foramen through which the ophthalmic branches of the fifth and seventh nerves pass from the orbit to be distributed over the upper surface of the snout. The inner wall of the orbit is perforated by the following apertures or foramina, whose positions can easily be studied in fig. 52:—The **optic foramen**, through which the optic nerve passes from the brain to the orbit; the foramen for the third nerve; the foramen for the fourth nerve; the foramen for the main branches of the fifth and seventh and the sixth nerves, a large hole in the posterior corner of the orbit; the foramen for the ophthalmic branches of the fifth and seventh nerves lying close together above and rather in front of, the last named foramen. The aperture of the interorbital canal lies in front of and rather below the foramen for the fifth and seventh nerves, and admits the passage of a blood-vessel putting the venous sinus of the orbit of one side into communication with that of the other. Posteriorly there is a deep groove overhung by the projecting ridge of the horizontal semicircular canal, and leading from the orbit to the back of the skull. In life it admits the passage of

the vein which puts the orbital sinus in communication with the anterior cardinal sinus. Immediately behind and below this groove is a large foramen in the posterior wall of the auditory capsule, through which the ninth cranial nerve passes to the exterior, and further inwards, at the side of the foramen magnum, is another large foramen for the exit of the tenth cranial nerve. The flat floor of the cranium is marked just behind the middle of its length by a pair of shallow grooves running forwards and inwards from its sides. At the point where they meet in the middle line, is an aperture through which the internal carotid artery enters the skull.

The jaws and suspensory apparatus of the jaws of the dogfish are pretty firmly attached to the cranium by ligaments, but they do not belong to the cranium but to the series of visceral arches, the hinder members of which afford support to the gill-pouches. The upper jaw of either side is a stout curved bar of cartilage compressed laterally, with a prominent upper ridge for the attachment of the jaw muscles. Anteriorly it meets its fellow of the opposite side in a median symphysis, and it is attached to the cranium just behind the olfactory capsule by a stout **ethmo-palatine ligament**. The posterior extremity of the jaw stands well away from the cranium, and bears on its lower surface an articular surface for the lower jaw. The lower jaws are somewhat *S*-shaped, and laterally compressed. They are connected together anteriorly by a ligamentous symphysis, and posteriorly they articulate with the hinder ends of the upper jaws. As the upper jaw is held to represent the quadrate, pterygoid, and palatine bones of higher vertebrates, it is commonly called the quadrato-pterygo-palatine cartilage. The lower jaw may be taken to be the equivalent of Meckel's cartilage in the frog and higher vertebrates (vol. i. p. 28). The upper and lower jaws, taken together, constitute the first visceral arch. Posteriorly they are not directly attached to the cranium, but are suspended from it by the upper members of the second visceral or hyoid arch. The dorsal segment of the hyoid arch on each side is a stout somewhat flattened bar of cartilage called the **hyomandibular**, articulated by its proximal end with a concave surface below the auditory capsule. It projects outwards, backwards, and downwards from the cranium, and its distal end articulates opposite the angle of the jaw with the next segment,

or **ceratohyal**. The ceratohyal curves inward and forward, running close inside the lower jaw, and is articulated to a median crescentic plate of cartilage, known as the **basihyal**. A number of slender cartilaginous rods called **gill-rays**, some of which are branched, are borne on the posterior edges of the hyomandibular and ceratohyal. The hyomandibular cartilage not only carries the ventral segments of the hyoid arch, but also supports the jaws, being bound to the posterior edge of the upper jaw by a stout **symplectic** ligament. In rays there is a pre-spiracular ligament passing from the front of the auditory capsule, to the lower end of the hyomandibular cartilage. This ligament is strengthened by a curved piece of cartilage, stiffening the anterior wall of the spiracle. The pre-spiracular ligament is absent in *Scyllium canicula*; a dense band of fibrous tissue which passes down to the integument in front of the spiracle must not be mistaken for it. The band in question is perforated by a canal, and is connected with the mucous canal system. It has no connection with the jaws. The five remaining visceral arches form a series of cartilaginous hoops supporting the roof, walls, and floor of the pharynx. They are known as the **branchial arches**, and it should be noted that the spiracle opens in front of the hyomandibular arch, the first gill-slit (or branchial cleft) opens between the hyoid and the first branchial arch, the second gill-slit between the first and second branchial arches, and so on, so that each branchial arch lies behind the gill-slit denoted by the same number. The branchial arches are divided into four segments on each side — namely, the **pharyngobranchials** in the roof of the pharynx, the **epibranchials** and **ceratobranchials** curving round and forming the supports of the side walls of the pharynx, and the **hypobranchials** in the floor of the pharynx. The first hypobranchial is a small nodule of cartilage connecting the first ceratobranchial with the basihyal. The second, third, and fourth hypobranchials are directed backwards, and the two last are connected with a median, dagger-shaped plate of cartilage, the **basibranchial**, lying in the roof of the pericardial cavity. The fifth arch has no hypobranchials, but its ceratobranchials are large and expanded, joined to the basibranchial, and their posterior borders are notched to admit the passage of the Cuvierian

sinuses. The fourth and fifth pharyngo-branchials are joined together. The form and position of the branchial arches will be best understood by reference to fig. 52. The posterior edges of all the ceratobranchials except the last are furnished with cartilaginous gill-rays.

Under the head of the appendicular skeleton are reckoned the cartilaginous supports of the median and paired fins. The paired fins are attached to cartilaginous supports or girdles which connect them with the trunk. The pectoral girdle consists of two half-hoops of cartilages, of which the lower ends are fused together in the mid-ventral line, while the upper ends remain separate and are imbedded in the muscles of the trunk. The ventral moiety of each half-hoop is called the **coracoid**, the dorsal moiety the **scapula**, and at the point where the coracoid passes into the scapula the hoop is thickened and bears a triple facet for the articulation of the basal cartilages of the fin. The ventral conjoined ends of the coracoids are flattened and produced forward into a prominent process which strengthens the floor of the pericardial cavity. The skeleton of the pectoral fin consists of three basal cartilages known as the **propterygium**, **mesopterygium**, and **metapterygium**, the last named being the largest, and forming a considerable part of the inner border of the fin. As may be seen in fig. 52, the propterygium is succeeded distally by a single fin-ray, consisting of a plate of cartilage, the mesopterygium is similarly succeeded by a single broad ray divided into two or three distal lobes, but the metapterygium bears a number of narrower cartilaginous rays. The proximal fin-rays are succeeded by two or more rows of polygonal plates of cartilage, the outer row supporting the horny dermal fin-rays or **actinotrichia** which support the greater part of the expanse of the fin. In the posterior or pelvic limbs the girdle is reduced to a horizontal bar of cartilage lying just in front of the cloaca. The basal skeleton of the fin is a curved rod, the **basipterygium**, the front end of which articulates with the pelvic girdle. The fin-rays are slender cartilaginous segmented rods articulated to the outer border of the basipterygium, with the exception of the first, which articulates directly with the pelvic girdle. The claspers of the male are provided with stout skeletal cartilages, articulated to the hinder ends of the basipterygia.

The first dorsal may be taken as an example of the skeleton of the median fins (fig. 52). Its skeleton is composed of twelve backwardly directed basal cartilaginous rods attached by ligament to as many neural spines. These are succeeded by as many somewhat longer and stouter radial rods, and these in turn are succeeded by two rows of polygonal cartilaginous plates which support the **actinotrichia**. The second dorsal and ventral median fins are formed on much the same plan as the first dorsal, but in the caudal fin the radial and basal cartilages have disappeared, their place being taken by the elongated flattened spines of the neural and hæmal arches, which afford sufficient support to the actinotrichia. As fin-structure is of great importance in the classification of fishes, it is essential that the foregoing description should be thoroughly understood by the student of comparative anatomy.

Such ample directions for the dissection of the dogfish are given in Marshall and Hurst's "Practical Zoology" that there is no need to recapitulate them here, but attention must be directed to those features which are of importance from the point of view of comparative anatomy.

The cœlom is spacious, but is confined to the trunk. In the caudal region, behind the anus, the whole thickness of the body is made up of the myotomes surrounding the vertebral column. The only spaces are those enclosed by the neural and hæmal arches. The former is occupied by the spinal cord, the latter by the caudal artery and vein, and the narrow space surrounding these can scarcely be regarded as cœlom. Nor is there any trace of cœlomic cavities in the head or in the gill-region in the adult animal, but in the embryo dogfish at least five cœlomic pouches are discoverable in front of the auditory region, and an uncertain number in the post-auditory region of the head, and it has been shown that the ventral or splanchnocœlic moieties of some of these cavities extend down into the partitions between the gill-slits. This indicates that the visceral arches belong to the ventral part of the head, and, in the course of specialisation and modification have been shifted backwards, so that the five branchial arches lie beneath the anterior segments of the trunk, and only the jaws and hyoid arch retain their connec-

tion with the head. In the course of development the walls of the head cavities are converted into muscles, the cavities themselves disappear, and the primitive segmentation is almost wholly obscured. The paired cranial nerves, however, give evidence of the original segmental arrangement, and it is interesting to note that the muscles of the eyeball are formed from the walls of three of the embryonic head-cavities lying in front of the auditory capsule. The whole question of the segmentation of the head is still involved in obscurity, and cannot be discussed here, but it should be borne in mind that the embryo dogfish affords ample evidence of the forward extension of myotomes into the head region, and greatly strengthens the belief that the craniate vertebrates are descended from an Amphioxus-like ancestor. There is still much uncertainty as to the number of primitive myotomes that enter into the composition of the vertebrate head, but there is no doubt whatever that head-myotomes and head-cavities exist. One must insist, however, on the fact that the primitive segmentation is lost in the cranium of the adult.

The trunk cœlom is divisible into two parts, the abdominal and the pericardial cavities. The former is the large space surrounding the abdominal viscera, and it should be remembered that it communicates with the exterior by the abdominal pores situated on either side of the cloacal aperture. The pericardial cavity surrounding the heart lies in the ventral wall of the throat just in front of the pectoral fins. Its roof is stiffened by the basibranchial cartilage, its floor by the anterior prominence of the pectoral girdle. It is divided from the abdominal cavity by a membranous partition, but communicates with it by a narrow passage, the **pericardio-peritoneal canal**, running close below the œsophagus and dorsal to the hepatic sinus.

The alimentary canal is rather more than twice the length of the distance separating the mouth from the cloaca, and is divisible into buccal cavity, pharynx, œsophagus, stomach, intestine, and rectum. The teeth have already been noticed. They are borne in several concentric rows on the margins of the upper and lower jaws, and are continually replaced as they wear out by new rows developed in a fold of mucous membrane behind the jaw. The teeth are simply imbedded

in the tough fibrous dermis, and are not fused to or implanted in the jaws. The mouth leads into a wide buccal cavity of which the flat roof is formed by the floor of the cranium and the floor is supported by the basihyal cartilage. The buccal cavity passes without any diminution of its size into the pharynx, a region defined by the presence of the internal openings of the spiracles and the five pairs of gill-slits. Passing these by for the moment, we find the pharynx contracting to form an œsophagus, which shortly widens out into a sac-like stomach. The further part of the stomach is bent forwards, and lies alongside of the nearer half, so that the whole organ is U-shaped. The distal end of the stomach is separated by a slight thickening from the intestine, which runs nearly straight backwards in the abdominal cavity, is dilated in its middle portion, and narrows posteriorly to form the rectum, which, after a short course, opens into the cloaca (see fig. 51). The mucous membrane lining the stomach is thrown into longitudinal folds, and the internal surface of the intestine is increased by the **spiral valve**, a fold of the mucous membrane, one edge of which is attached to the inner wall of the intestine, and runs round it in a spiral of some seven or eight turns. The line of attachment of the spiral valve is marked externally by blood-vessels. Shortly behind the pylorus, the intestine receives the ducts of the liver and pancreas. The liver is very large, consisting of two elongate lobes lying right and left of the stomach and a much smaller median lobe lying ventral to the stomach. The three lobes are united anteriorly, and suspended from the anterior wall of the abdominal cavity by a median suspensory ligament. The gall bladder is a conspicuous oval sac imbedded in the anterior end of the left lobe of the liver. The bile duct passes back from it, receives other ducts from the lobes of the liver, and runs in the membrane connecting the liver with the stomach to the anterior end of the intestine. It runs for a short distance in the wall of the intestine, and opens into it a little in front of the commencement of the spiral valve.

The main part of the pancreas lies between the two limbs of the stomach. It is a yellowish-white organ, compressed from side to side, and produced at its anterior end into a ventral lobe which lies in the angle between the stomach and

intestine, and partly surrounds the anterior end of the latter. The pancreatic duct traverses the length of the gland, and passes from the hinder end of its ventral lobe to the intestine. It runs back for a short distance in the ventral wall of the intestine, and opens close to the commencement of the spiral valve. The rectum is provided with a small tubular **rectal gland**, which opens into its anterior dorsal wall. The spleen, a ductless gland, having no opening into the alimentary canal, may be mentioned here. It is a reddish organ, of triangular shape, attached by a membrane to the bend of the stomach. It sends forward a band-like prolongation along the distal limb of the stomach, which is often mistaken by beginners for the pancreas (fig. 51, *sp*). It should be noticed that the membranous folds suspending the alimentary tract from the roof of the abdominal cavity, are very incomplete. The stomach is suspended by a **mesogaster**; there is no mesentery suspending the intestine, but the rectum is suspended by a **mesorectum.** Membranes attaching different regions of the gut to one another, or other organs to the gut, are called **omenta**. In the dogfish the following may be distinguished: a **gastro-hepatic omentum** uniting the stomach and liver; a **gastro-intestinal omentum** uniting the stomach and intestine; and a **gastro-splenic omentum** uniting the spleen and stomach.

The **spiracles** and **gill-slits** are formed in the embryo as outgrowths of the wall of the throat which meet and break through the body-wall. The position of the internal openings of the spiracles is shown in fig. 55. They lead into short passages which pass in front of the hyomandibular cartilage and open to the exterior. The anterior wall of the spiracular passage is furnished with a rudimentary gill or **pseudo-branch**, in the form of a few small vascular folds, whose presence indicates that the spiracles are gill-slits of diminished size which have lost their respiratory function.

The internal openings of the gill-pouches are large vertical slits, considerably larger than the external openings, and curved in correspondence with the curvature of the lateral walls of the pharnyx. Each slit leads into a capacious pouch, narrow from side to side, but deep from above downwards. The first four pouches have a gill or **demi-branch** on their anterior and posterior walls; the fifth pouch has a demi-branch on its anterior wall only. The shape and arrangement of the

gills and gill-pouches can be studied in figs. 53, 54, and 55, but their exact relations can only be understood after careful dissection. Each gill-pouch or branchial cleft is formed as an outgrowth of the throat, which meets and fuses with the epidermis, and eventually opens to the exterior by an aperture formed in the line of fusion. The pouches, therefore, are

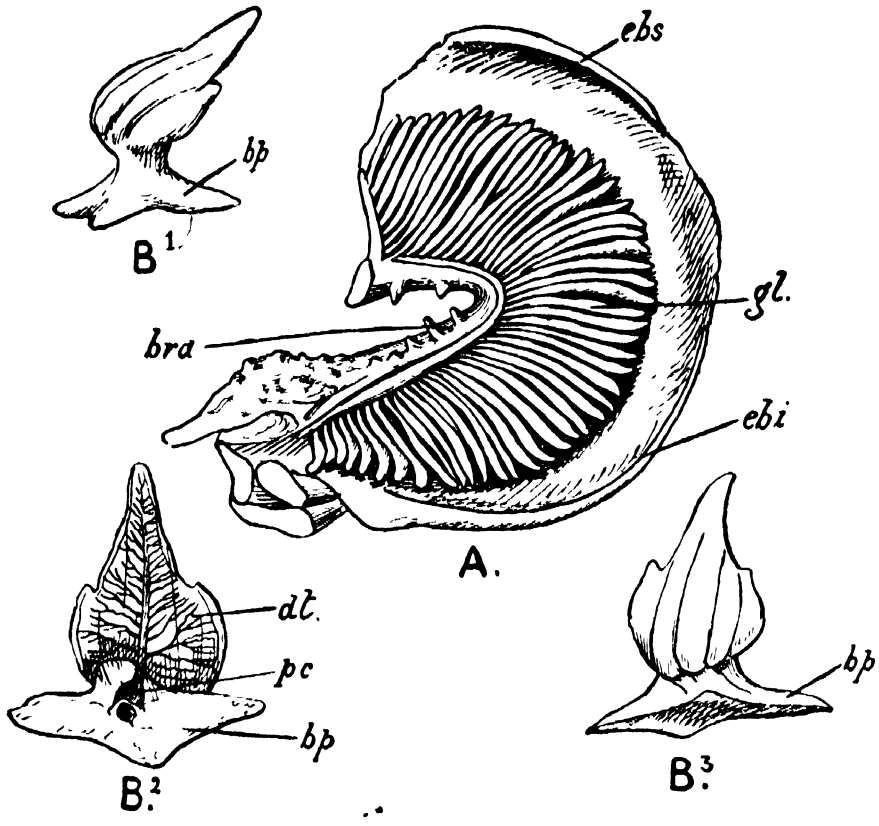


Fig. 53

A. A single gill partition from the left side of *Scyllium canicula*, seen from in front. *bra*, branchial arch; *ebi*, inferior extra-branchial cartilage; *ebs*, superior extra-branchial cartilage; *gl*, vascular folds forming the gill or demi-branch. B^1, B^2, B^3. Three views of a denticle from the skin. *bp*, basal plate; *dt*, dentinal tubes; *pc*, pulp cavity.

lined by a hypoblastic epithelium or mucous membrane continuous with that of the pharynx. The transition from this membrane to the epidermis can easily be seen when the gills are slit up, the epidermis being covered with denticles, while the mucous membrane of the gill-pouches is smooth and moist. The partition wall between any two contiguous gill-pouches is thick on the internal or pharyngeal side, owing to the presence of the cartilaginous visceral arch, but the re-

mainder of it is thin, and is only prevented from being flaccid by the cartilaginous gill-rays which support it, as the silk of an umbrella is supported by the wires. The gill-rays are covered over by a very thin sheet of interbranchial muscle, and the blood-vessels carrying blood to and from the demi-branchs run in the partition. The gill-pouches are compressed antero-posteriorly and laid back so as to overlap one another to a considerable extent, and the external apertures are of much less vertical height than the cavities of the pouches. The outer edges of the posterior walls of the first, second, and third pouches are strengthened by curved cartilaginous rods, reaching from the lower sides of the external gill-slits nearly to the mid-ventral line. These are the **inferior extra-branchial cartilages**, and the upper edges of the posterior walls of the first, second, third, and fourth pouches are similarly strengthened by **superior extra-branchial cartilages**. Each demi-branch is formed by numerous vascular folds of the mucous membrane radiating outwards from the visceral arch and extending over about two-thirds of the partition wall. A partition with its demi-branch and extra-branchial cartilages is shown in fig. 53A. The whole branchial apparatus is covered over by a superficial sheet of muscle, the **constrictor superficialis branchiarum**, lying immediately below the skin.

The gills are respiratory organs in whose capillaries the blood is separated from the water by such thin membranes that an exchange of gases is readily effected between the blood and the air dissolved in the water. It is clear, then, that the blood coming to the gills is what is called "venous" blood, rich in carbonic acid and poor in oxygen, while the blood leaving the gills is what is called "arterial" blood, richer in oxygen and poorer in carbonic acid gas after its passage through the gill capillaries. Notwithstanding this difference in their contents, the blood-vessels bringing blood to the gills are to be regarded as arteries as much as those carrying blood away from them, for, as has been explained in connection with the frog (vol. i. p. 49), arteries are vessels carrying blood from the heart, veins are vessels bringing blood back to the heart.

The heart of the dogfish lies in the triangular pericardial space already described as lying below the basi-branchial cartilage and above the forward projection of the pectoral girdle

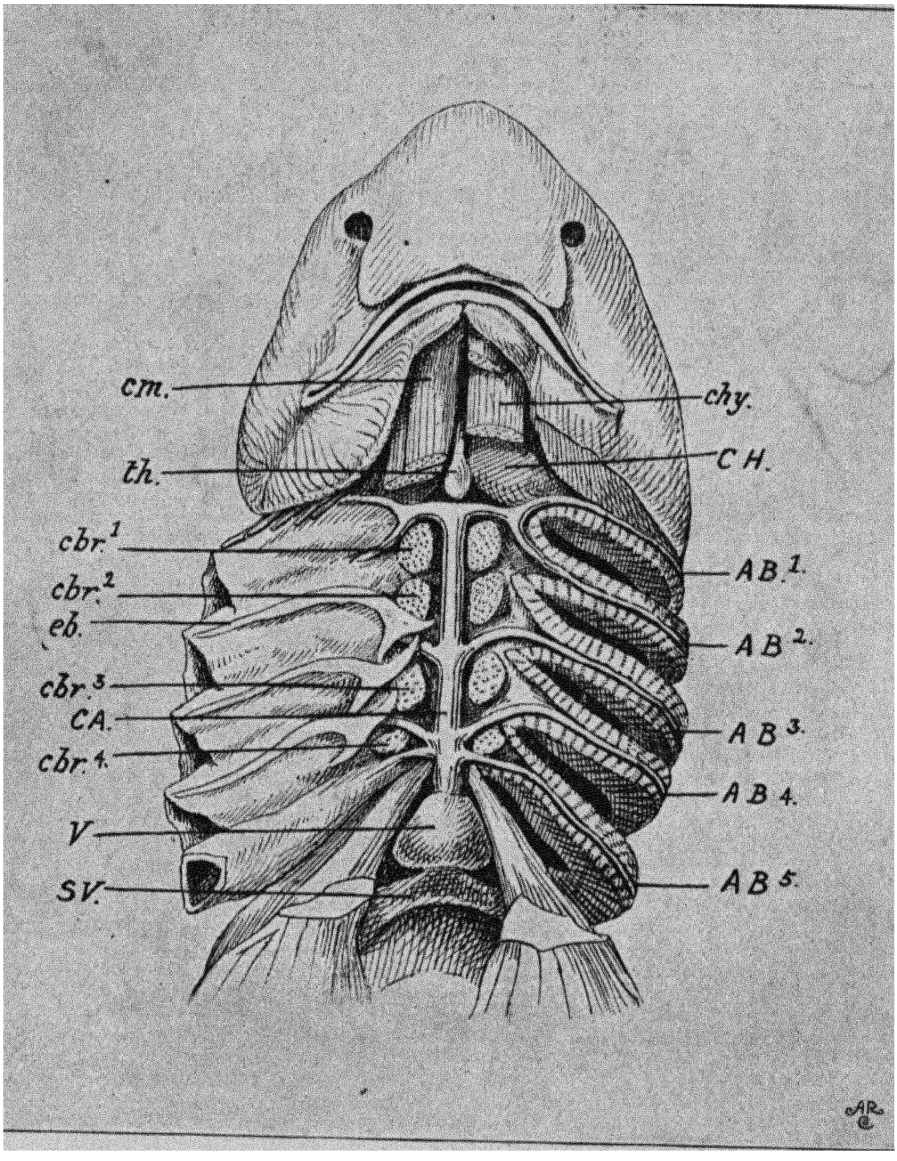


Fig. 54

A dissection of the ventral side of the throat of *Scyllium canicula*, to show the heart, cardiac aorta, and afferent branchial arteries. On the left side of the figure the constrictor superficialis branchiarum muscle has been removed; but the membranous gill-pouches have not been slit up, but have been pulled outwards to exhibit better their relations to one another. On the right side the gill-pouches have been slit up, and the gill-partitions and demi-branchs have been cut away down to the level of the afferent branchial arteries. *AB*1-*AB*5, the five afferent branchial arteries; *CA*, cardiac aorta; *cbr*1-*cbr*4, the cut ends of the first, second, third, and fourth coraco-branchiales muscles; *chy*, cut end of the coraco-hyoideus muscle; *CH*, ceratohyal cartilage; *cm*, coraco mandibularis muscle; *eb*, inferior extra-branchial cartilage of the second gill-arch; *SV*, sinus venosus; *th*, thyroid gland; *V*, ventricle.

The heart may be said to originate in two large venous vessels, the **ductus Cuvieri**, which run transversely towards the middle line in close contact with the fifth cerato-branchial cartilages. In the posterior wall of the pericardial cavity these venous trunks dilate, and, meeting in the middle line, form a transverse thin-walled tube known as the **sinus venosus**. By their union in the middle line the limbs of the sinus venosus form a single vessel which runs forward in the median ventral line below the ventral members of the branchial cartilages. The posterior end of this vessel, immediately succeeding to the sinus venosus, is dilated, bent upon itself to form a figure **S**, and its walls are thickened by muscular tissue. It is, in fact, the **heart**, and it should be remembered that the heart is, essentially, nothing more than a muscular dilatation of a ventral median blood-vessel.

The sinus venosus, then, opens by a single median aperture, guarded by a membranous valve, into the posterior division of the heart or **auricle**. The auricle of the dogfish is a single triangular sac, its apex pointing forward and its posterior angles produced into lappets or auriculæ. Its walls are muscular, but not thick, and it lies in the dorsal moiety of the pericardial cavity. The **ventricle** is an almost globular sac, with very thick muscular walls lying ventral to the auricle, with which it communicates by a single opening guarded by valves. The anterior end of the ventricle is continued forwards as a stout muscular tube, the **conus arteriosus**. This in turn passes through the anterior wall of the pericardium and runs forward on the ventral wall of the throat, as the so-called **cardiac aorta**. The interior of the conus arteriosus is provided with two rows of semilunar valves, each row consisting of three watch-pocket valves so disposed as to admit of the free passage of the blood from the heart to the cardiac aorta, but prevent any reflux in the contrary direction.

The cardiac aorta runs forward nearly as far as the lower ends of the cerato-hyal cartilages, where it divides into right and left branches, and each of these almost immediately subdivides into two branches, the anterior of which runs along the hyoid arch, supplying the anterior demi-branch of the first gill-pouch with blood, the posterior runs along the first branchial arch supplying the posterior demi-branch of the first gill-pouch, and the anterior demi-branch of the second gill-pouch.

The remaining demi-branchs are supplied by three pairs of vessels, one pair arising from the middle, and two pairs arising close together from the hind end of the cardiac aorta (fig. 54). These vessels carrying blood to the gills are known as the **afferent branchial arteries**. They break up into capillaries in the demi-branchs, and the blood is carried away from these latter structures by a system of **efferent branchial arteries**, whose arrangement is shown in fig. 55.

The blood from the capillaries of the demi-branchs is collected into vessels having the form of loops, four of which are complete, and surround the inner margins of the first, second, third, and fourth gill-slits. But as the fifth gill-slit has only one demi-branch on its anterior side, the loop belonging to this slit is incomplete—*i.e.* is a half-loop, running along its anterior face. The loops communicate with one another by short horizontal vessels placed about the middle of their lengths, and a vessel given off from the corresponding position of the anterior limb of the first loop runs dorsal to the hyomandibular cartilage, turns inwards to pass along the anterior wall of the spiracle, runs across the floor of the orbit, and enters the cranium by a foramen situated just in front of the inter-orbital canal. This vessel (*hy.a* in fig. 55) is known as the **hyoidean**, or sometimes as the anterior carotid artery.

The half-loop belonging to the fifth gill-slit has no special efferent vessel connected with it. All the blood from the demi-branch of this gill-slit passes by way of the horizontal vessel into the loop surrounding the fourth gill-slit. But the upper ends of the loops surrounding the first four gill-slits are continued into four **efferent branchial arteries** which run upwards, inwards, and backwards, in close connection with the pharyngo-branchial cartilages, to unite with their fellows of the opposite side in a large median vessel, the **dorsal aorta**. The dorsal aorta is continued both forwards and backwards from the points of union of the efferent branchial arteries. Anteriorly, it is continued along the lower side of the cranial floor as a small median vessel which bifurcates opposite the first branchial arches, and its branches curve outwards from the middle line, and unite on either side with the **common carotid artery**, a vessel springing from the inner and anterior end of the loop surrounding the first gill-cleft, and curving inwards and forwards along the under surface of the floor of

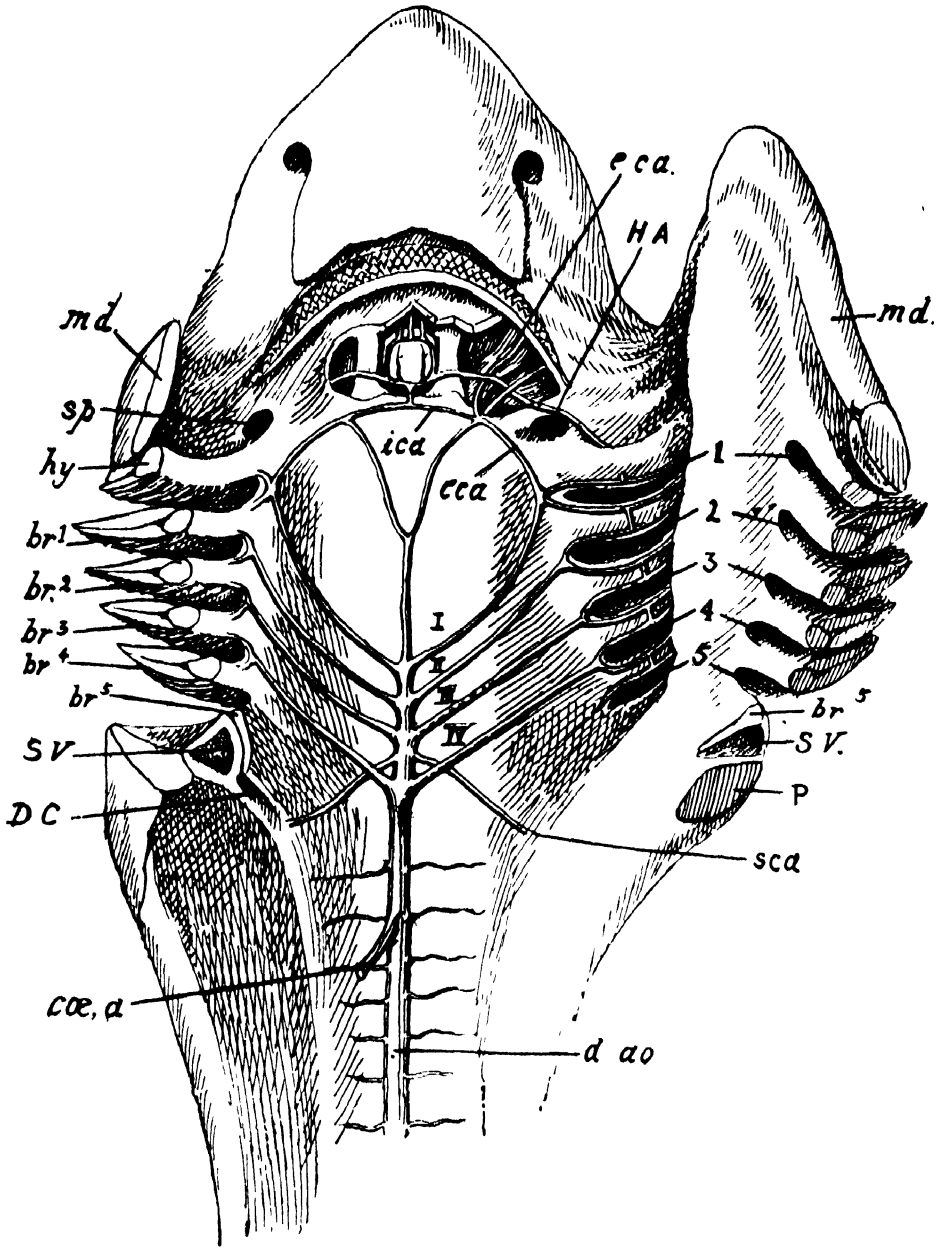


Fig. 55

A dissection of the roof of the pharynx of *Scyllium canicula* to show the efferen branchial arteries and their relation to the gill-slits. The mandible, hyoid, an branchial cartilages have been cut through on the animal's right side, and th floor of the pharynx has been forced over to the (animal's) left. The floor o the cranium and the left orbit has been removed to show the course of th carotid arteries. 1-5, the five gill-slits, the first four surrounded by the loops o the collecting vessels, but the fifth has only a half loop on its anterior margin *I-IV*, the four efferent branchial arteries; *br*1-*br*5, the five branchial arches *cca*, common carotid artery; *cœ.a*, the cœliac artery; *d.ao*, dorsal aorta; *DC* ductus Cuvieri; *eca*, external carotid artery; *H.A*, hyoidean artery; *hy*, hyoi arch; *ica*, internal carotid artery; *md*, mandible; *P*, cut end of pectora girdle; *sca*, subclavian artery; *sp*, internal opening of spiracle; *S.V*, sinu venosus.

the skull close below the posterior margin of the orbit. The common carotid artery divides into external and internal carotids. The former is given off immediately in front of the union of the common carotid with the bifurcation of the dorsal aorta. It passes through a small foramen in the hinder floor of the orbit, runs forward below the maxillary branch of the fifth nerve, and breaks up into branches, supplying the upper jaw and snout. The internal carotid is a continuation of the course of the common carotid to the middle line. Here it passes into the cranial cavity by a median foramen, crosses the internal carotid of the opposite side, unites with the opposite hyoidean artery, and breaks up into branches, supplying the brain.

Posteriorly, the dorsal aorta is continued backward as a large vessel lying close beneath the vertebral column; in the caudal region it is enclosed in the hæmal arches of the vertebræ. In its course it gives off arteries to the limbs, viscera, and myotomes, and diminishes correspondingly in size towards the tail. The most important of these arteries are: The **subclavian arteries**, arising just in front of the union of the fourth efferent branchials with the dorsal aorta; they supply the pectoral girdle and pectoral fins. **The cœliac artery** is a large median vessel arising from the ventral surface of the aorta, a short distance behind the junction of the last efferent branchial arteries. After a short course in the mesentery, it divides into two branches, one of which supplies the anterior end of the stomach and the liver, the other the anterior end of the intestine and the pancreas.

The **anterior mesenteric** and the **lieno-gastric** (fig. 51) arteries arise close together from the dorsal aorta about an inch and a half behind the cœliac artery. The former supplies the intestine, the latter, arising just behind the anterior mesenteric, crosses it in its course, and is distributed to the posterior bend of the stomach and to the spleen. The **posterior mesenteric artery** is a small median vessel which leaves the dorsal aorta some little way behind the lieno-gastric and runs in the meso-rectum to the rectal gland. The above are the more conspicuous branches of the dorsal aorta. In addition there are smaller vessels—*e.g.* the **intercostal arteries**, a pair of which are given off in each trunk segment to the myotomes; the **pelvic arteries**, supplying the

pelvic fins and the **renal arteries**, a number of small paired vessels supplying the excretory organs.

The blood which has been carried to the various organs and tissues of the body by the arteries is returned to the heart by a system of venous channels which, for the most part, have the form of wide irregular spaces rather than of definite tubes, and are therefore called sinuses. The blood from the head and branchial region is returned by a pair of large sinuses lying between the upper ends of the gill-pouches and the muscles of the body, known as the **anterior cardinal sinuses**, and these are supplemented by a pair of smaller channels running along the ventral ends of the gill-pouches, known as the **inferior jugular sinuses**. They discharge their contents on either side into a short transverse passage, the **ductus Cuvieri**, which is really a short and narrow lateral continuation of the sinus venosus lying in a notch in the posterior border of the fifth cerato-branchial cartilage. The anterior cardinal sinus of either side communicates in front with a large blood space surrounding the eyeball, the **orbital sinus**, by means of a narrow passage running in the post-orbital groove of the auditory region of the skull. It also communicates with the jugular sinus by a relatively wide **hyoidean sinus**, running in a groove on the outer side of the hyomandibular cartilage and by smaller passages running down the outer faces of the first four branchial arches. Thus the blood from the head and branchial region is returned direct to the heart by way of the ductus Cuvieri and sinus venosus.

The blood from the kidneys, the genital organs, the trunk muscles of the abdominal region, the pectoral fins, and the lateral line, is also returned direct to the heart through the **posterior cardinal sinuses**, whose position and extent is shown in fig. 51. They lie close alongside of one another in the roof of the abdominal cavity near the middle line; their dorsal walls are closely adherent to the body wall, their ventral walls are covered below by the peritoneal lining of the abdominal cavity. They take their origin from the posterior section of the kidneys, from which they receive blood through numerous **renal veins**. Thence they run forward, separated by a median partition, and expand into very wide thin-walled sacs lying right and left of the œsophagus, and communicat-

ing freely with one another above it. The posterior cardinal sinus of each side opens into the ductus Cuvieri by a relatively narrow passage situated below and behind the opening of the anterior cardinal sinus, and just behind and to the outer side of this passage it receives the **subclavian vein** bringing back blood from the pectoral fin, and a little further back is the opening of the **lateral sinus**, a vessel which runs up the side of the body close to the surface and in connection with the lateral line, and curves inwards and downwards past the scapula to enter the posterior cardinal sinus. The opening of the **genital sinus** is placed still further back, just above and to the side of the œsophagus.

The blood from the tail is collected into a **caudal** vein which lies below the caudal artery enclosed in the canal formed by the hæmal arches of the caudal vertebræ. On reaching the hinder ends of the kidneys the caudal vein divides right and left to form the veins of Jacobson, also called the **renal portal veins**. These run forward along the dorsal edges of the kidneys, are joined by the intercostal veins of that region, and give off branches to them throughout their entire length. These branches break up again into capillaries in the kidneys, and the blood is collected from these capillaries by the renal veins and passed into the posterior cardinal sinuses. Thus the dogfish, like the frog (vol. i. p. 56), has a renal portal system. The blood from the stomach, intestine, and spleen is collected by (1) the **posterior intestinal vein** (fig. 51, *i.v.*); (2) the **posterior gastric vein** (*p.g.v.*); and (3) the **splenic vein** (*s.p.v.*). These vessels unite together to form the **mesenteric vein**, which runs forwards along the dorsal border of the pancreas, and receiving an **anterior intestinal** and an **anterior gastric** vein becomes the **hepatic portal vein**, which runs forward alongside the bile duct and enters the liver, where it branches and breaks up into capillaries. The blood from the liver is collected into two large sinuses traversing the right and left lobes of the liver, and these run forwards to form a pair of wide **hepatic** sinuses separated by an incomplete partition on the ventral wall of the œsophagus. The hepatic sinuses open by two small apertures into the sinus venosus opposite the opening of the latter into the auricle. It should be noticed that a hepatic portal system is present in Amphioxus as well as in

the frog and the dogfish. This system is, in fact, highly characteristic of all chordate animals.

The excretory organs or kidneys of the dogfish differ considerably both in extent and in their relations to the generative organs in the two sexes. They occupy the same relative position as the kidneys of the frog, but are of greater extent, especially in the male dogfish, and exhibit more clearly some of the primitive characteristics of the vertebrate excretory system. It should be noticed that they are covered ventrally by the peritoneal membrane, and therefore lie outside the cœlom.

The vertebrate kidney consists essentially of a series of paired coiled glandular tubules, each of which has a ciliated funnel opening into the cœlom. In development the pairs are formed in succession from before backwards. At first each pair corresponds to a body segment, but later in development additional tubules are formed in connection with the pre-existing pairs, and the whole organ becomes surrounded with a vascular tissue and forms a solid mass. The first tubules to be formed are situated far forwards in the peritoneal cavity, close behind the pericardium, and they constitute the primary excretory organ or **pronephros**. Though it is present in the adults of most fishes, and is a conspicuous and functional organ in the tadpole, the pronephros is a very inconspicuous, functionless, and transient organ in the embryo dogfish, and disappears altogether in the adult. The pronephric tubules of either side of the body open into a longitudinal duct, the **segmental duct**, which runs backwards in the dorsal wall of the peritoneal cavity and opens behind into the cloaca. The tubules formed next in succession to the pronephros are at first independent of the segmental duct, but as development proceeds they make connection with and open into it, and so constitute a second section of the kidney known as the **mesonephros**. In the frog the mesonephros is the functional kidney of the adult, and there is no other section of the excretory system behind it, but in the dogfish a number of excretory tubules at the posterior end of the peritoneal cavity acquire separate ducts, which either unite to form a common duct, or open separately into the posterior section of the segmental duct, just before the latter opens into the cloaca. This posterior part of the excretory

system is distinguished as the **metanephros**, and it forms

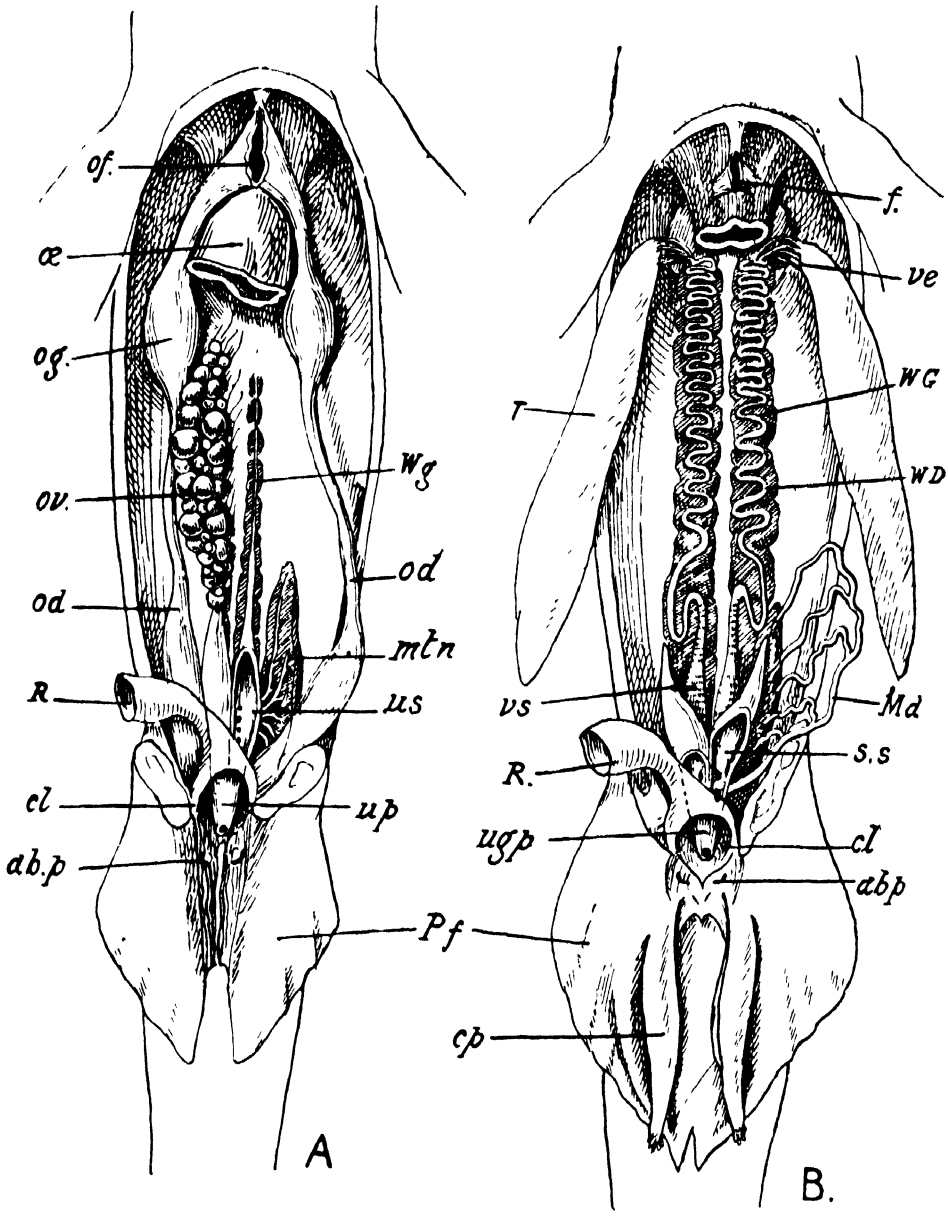


Fig. 56

A. Urogenital system of the female. *B*. Urogenital system of the male dogfish. *abp*, abdominal pores; *cl*, cloaca; *cp*, claspers of the male; *f*, rudiment of the oviducal opening in the male; *Md*, metanephric ducts; *mtn*, metanephros; *od*, oviduct; *œ*, cut end of œsophagus; *og*, oviducal gland; *ov*, ovary; *Pf*, pelvic fins; *R*, rectum; *s.s*, sperm sacs; *T*, testis; *up*, urinary papilla in the female; *ugp*, urogenital papilla in the male; *us*, urinary sinus; *ve*, vasa efferentia; *vs*, vesicula seminalis; *WD*, Wolffian duct; *WG*, Wolffian gland or mesonephros.

the chief excretory organ of the dogfish—in fact, it is the only functional excretory organ of the female.

Further than this, the segmental ducts of each side become split longitudinally in the course of development into two ducts. One of these, now known as the **Wolffian duct**, retains its connection with the mesonephric tubules and serves as the mesonephric duct; the other, now known as the **Müllerian duct**, is converted into the oviducts of the female, but is aborted and represented only by a rudiment in the male.

Let us now examine the excretory organs and their relations to the generative system in the adult male dogfish (fig. 56, *B*). The mesonephros of either side is an elongate glandular body extending far forward in the roof of the peritoneal cavity, and continuous posteriorly with the metanephros. The latter is a compact laterally-compressed glandular mass extending back into the pelvic region dorsal of and to the side of the cloaca. The mesonephros is functional in the adult, and its excretion is carried to the cloaca by the Wolffian or mesonephric duct, which is a conspicuous tube imbedded in the ventral surface of the mesonephros and thrown into a number of horizontal loops. The Wolffian duct, however, is not only an excretory duct, but serves also as the sperm duct or vas deferens. The testes are a pair of elongated bodies lying in the dorsal part of the peritoneal cavity and attached to its dorsal wall by folds of membrane, the **mesorchia**. They are united together posteriorly, but their anterior ends lie on opposite sides of the gullet, and each communicates by a number of very slender ducts, the **vasa efferentia**, with the anterior end of the mesonephros of its own side. The sperm passes through the vasa efferentia into the mesonephric tubules, and thence is carried by the Wolffian duct to the cloaca. The posterior end of each Wolffian duct dilates to form a **vesicula seminalis**, which runs straight down the ventral face of the metanephros and opens into a cavity known as the **urogenital sinus**, which in turn opens by a single median aperture situated at the end of a prominent papilla, into the cloaca. The urogenital sinus is formed by the union of the posterior ends of a pair of thin-walled conical **sperm-sacs**. The anterior ends of these sacs are adherent to the ventral surfaces of the vesiculæ seminales and taper forwards to end blindly near the front end of the latter. The urogenital sinus receives not only the openings of the Wolffian ducts, but also those of the ureters or metanephric ducts. The latter are formed by the union of five ducts on

each side which arise from the ventral and outer side of the metanephros and joining together form a single wide duct which opens into the urogenital sinus just behind and to the inside of the opening of the Wolffian duct.

The Müllerian ducts are aborted and disappear in the adult male, except for a small median pouch situated in the suspensory ligament of the liver on the ventral side of the œsophagus. This pouch represents the conjoined openings of the oviducts of the female, and in some specimens rudiments of the Müllerian ducts can be traced along the walls of the œsophagus.

In the female the mesonephros is degenerate and functionless, being represented by two streaks of brown tissue occupying the same position as the more fully developed mesonephros of the male. These streaks are traversed by the Wolffian ducts, which in the anterior part of their course are straight and narrow tubes, but posteriorly are dilated to form a pair of sacs, the **urinary sinuses**. Still further back the urinary sinuses unite together and open into the cloaca by a median aperture placed on the end of a urinary papilla. The metanephros of the female resembles that of the male, but its ducts, instead of uniting to form a single duct on each side, open separately by five or six small apertures situated on each side of the septum dividing the anterior ends of the urinary sinuses. The ovary of the female varies a good deal in size according to the age and condition of the specimen. It occupies the same relative position as the right testis of the male, and is attached to the dorsal wall of the peritoneal cavity a little to the right of the median line by a double fold of peritoneal membrane, the **mesovarium**. The left ovary appears to be aborted. The ovary is full of ova in various stages of maturity. When ripe, the ova are distended with food-yolk and form very prominent projections of the ovarian walls. There is no direct communication between the ovary and the excretory system as there is between the testes and the Wolffian ducts in the male. The ova, when ripe, escape into the peritoneal cavity by rupture of the ovarian walls, and are passed forward by contractions of the abdominal walls to its anterior end, where they pass into the capacious aperture of the oviducts. The latter, which, as has already been explained, are formed from the Müllerian ducts of the embryo, are two

conspicuous tubes of varying diameter running forwards from the cloaca, one on either side of the middle line. They are attached to the dorsal wall of the peritoneal cavity by a fold of the peritoneum known as the **mesometrium**. Anteriorly the two ducts curve inwards to the ventral side of the œsophagus and their ends unite and open by a single large slit-like opening in the same position as the rudimentary organ in the male. At no great distance from their anterior ends the oviducts are swollen and their walls thickened to form the **oviducal glands**. Behind the oviducal glands the oviducts run straight backwards as rather thick tubes. Their hinder ends are somewhat dilated, and they unite together dorsal to the rectum and open into the cloaca by a large median aperture immediately above the rectal opening.

The secretion of the oviducal gland is poured round each ovum as it passes down the oviduct and sets into a firm horny semi-transparent egg-case or shell, which has the same relation to the enclosed yolk that the egg-shell of a bird has to the yolk within. The egg-cases of Scyllium are oblong capsules, about two inches in length and rather less than an inch in width, and their angles are produced into long tapering threads or tendrils. The eggs are extruded by the female and the tendrils are twined round a seaweed or sea-fan or other branching object in shallow water, and there undergo their development. The empty egg-cases of Scyllium and the larger and blacker but similar cases of the skate are common objects on the seashore, and are familiarly known as "sea-purses." Complete eggs may be easily obtained by dredging in suitable localities, and occasionally they are cast up on the shore. In advanced eggs the embryo is seen attached to a voluminous yolk-sac by a narrow umbilical stalk. Scyllium is thus oviparous, but in Acanthias and many other dogfishes and sharks the eggs are retained in the oviducts of the mother and undergo their development there.

The central nervous system of the dogfish presents the same features as that of the frog, but the relative proportions of the parts are different. The spinal cord has the typical vertebrate structure, with a ventral and a dorsal fissure, and a central canal, and the spinal nerves are given off in pairs in each segment of the body, each member of a pair arising from a dorsal and a ventral root which unite outside the neural canal

to form a mixed nerve trunk. The brain, like that of the frog, consists of a fore-brain, mid-brain, and hind-brain. The fore-brain is divided into cerebral hemispheres (prosencephalon) and thalamencephalon, the mid-brain consists of the corpora bigemina (mesencephalon), and the hind-brain is divided into the cerebellum (metencephalon) in front and above, and the medulla oblongata (myelencephalon) behind and below. The shape and relative positions of these parts, as seen from the dorsal surface, are shown in fig. 57, and it can readily be seen that, though the general plan is the same, the details differ from those of the frog.

The **cerebral hemispheres** form the extreme anterior end of the brain, and at first sight look like a single globular mass, but closer inspection shows that the mass is divided nearly into two by a fissure extending inwards from its anterior end. From the sides of the cerebral hemispheres the **olfactory lobes** arise as a pair of stout stalks which run outwards and forwards and expand on either side into a triangular nervous mass closely applied to the posterior face of the olfactory capsule. Posteriorly, the cerebral hemispheres are continued into the narrow **thalamencephalon.** This, the posterior division of the fore-brain, contains a considerable cavity, the **third ventricle**, which is roofed in above by a very thin membrane. The hindmost part of this roof is produced in the middle line into a slender tube which runs forward over the cerebral hemispheres, and ends in a small dilatation attached to the lower side of the membrane covering the anterior fontanelle of the skull. The stalk and dilatation together constitute the **pineal outgrowth.** The floor of the thalamencephalon is also thin, and is produced into a hollow finger-shaped process, the **infundibulum**, the proximal half of which is directed backwards, while the distal half is bent forward at a sharp angle so as to underlie the proximal half. Close to their union with the thalamencephalon, the walls of the proximal moiety of the infundibulum are expanded to form a pair of conspicuous rather thick-walled sacs, known as the **lobi inferiores**, and the infundibular walls are further produced at the flexure into a pair of thin-walled lateral sacs, the **sacci vasculosi.** The **pituitary body** is a very small tube lying on the under side of the distal half of the infundibulum. It is formed in embryonic life as an outgrowth of the dorsal

wall of the stomodæum, and its posterior end, being attached to the floor of the skull, retains a trace of its origin.

The **corpora bigemina** are prominent rounded swellings on the dorsal surface of the mid-brain, and are partly overlapped by the anterior end of the cerebellum. They contain cavities which open below into the so-called Sylvian aqueduct, leading from the third to the fourth ventricle. The **cerebellum** of the dogfish is relatively of large size, and very unlike the corresponding organ in the frog. Viewed from above, it is oval in outline, and it partly overhangs the corpora bigemina in front and the medulla oblongata behind. Its dorsal surface is marked with a shallow, longitudinal furrow, dividing it into right and left lobes, but it contains a single wide cavity which communicates by a narrower passage with the fourth ventricle below. At the sides of the cerebellum are the **restiform bodies**, a pair of hollow outgrowths of the dorso-lateral walls of the hind-brain, with thin and much-folded walls. They communicate with one another below the hinder extension of the cerebellum by a band of nervous tissue bridging over the anterior part of the fourth ventricle.

The **medulla oblongata** is narrow in front and behind, where it passes into the mid-brain and the spinal cord respectively, and widest in its middle part. Its floor and sides are thick, but its roof is very thin, consisting of a transparent sheet of tissue, the **velum medullæ posterius**, covering in the wide cavity of the fourth ventricle. The last-named narrows posteriorly, and is continued into the canal of the spinal cord.

The dogfish has ten pairs of cranial nerves which in distribution and arrangement closely resemble those of the frog, but as the dogfish breathes by gills, while the adult frog breathes by lungs, we find that the more posterior pairs of cranial nerves of the former animal bear relations to the gill-arches which are worthy of the most careful study.

The **olfactory nerves** arise as a number of fine branches from the anterior ends of the olfactory lobes, and pass at once into the nasal capsules, where they are distributed to the epithelium lining the olfactory organ.

The **optic nerves** arise from the lower surface of the thalamencephalon. The nerve of each side crosses its fellow in the **optic chiasma**, and passing to the opposite side of the

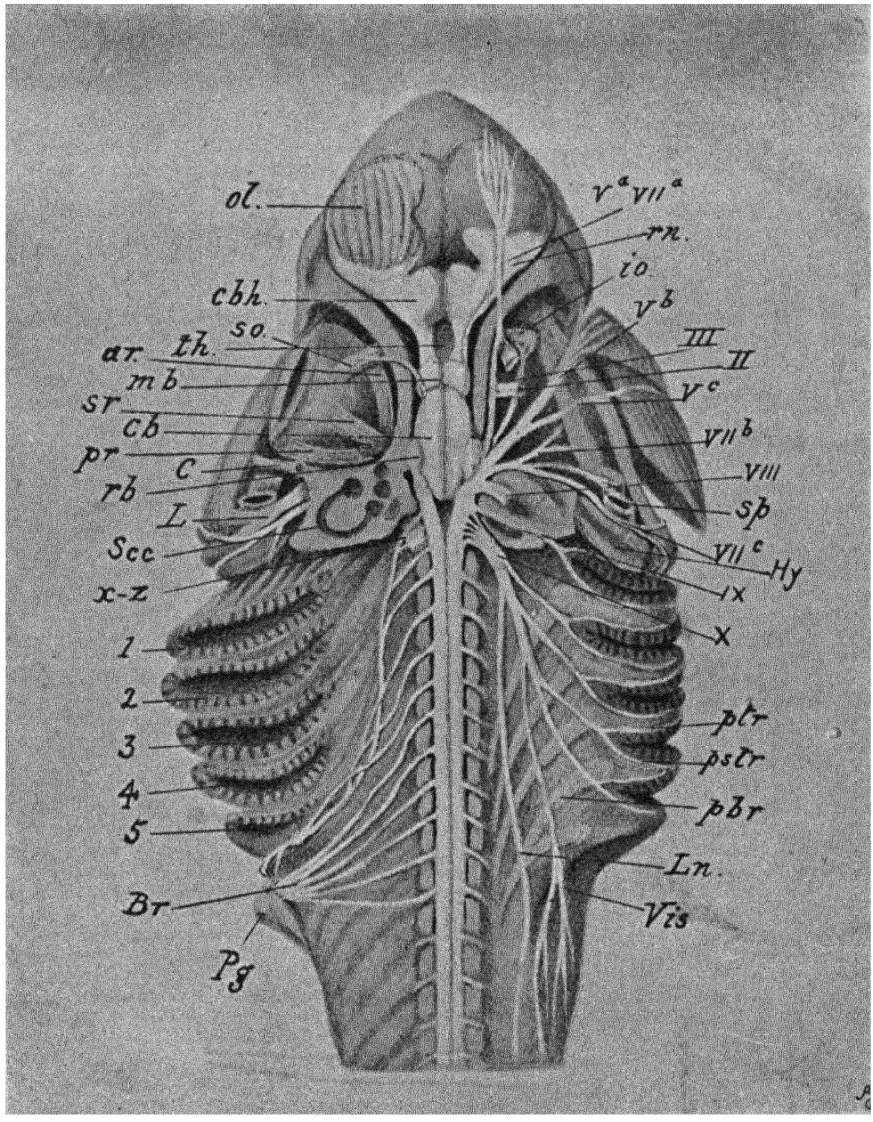


Fig. 57

A dissection of the brain, anterior part of the spinal cord, cranial, occipital, and anterior spinal nerves of *Scyllium canicula*. 1-5, the five gill-slits of the left side; *ar*, anterior rectus muscle; *Br*, brachial plexus; *C*, ligamentous band passing in front of the spiracle, and perforated by a mucous canal; *cb*, cerebellum; *cbh*, cerebral hemispheres; *Hy*, hyomandibular cartilage; *io*, inferior oblique muscle; *L*, post-spiracular ligament; *Ln*, lateral branch of the vagus nerve; *mb*, mid-brain or corpora bigemina; *ol*, olfactory capsule; *pbr*, 4th pharyngo-branchial cartilage; *Pg*, cut end of pectoral girdle; *pr*, posterior rectus muscle; *ptr*, pretrematic branch, and *pstr*, post-trematic branch of a branchia nerve; *rb*, restiform body; *rn*, olfactory lobe (rhinencephalon); *Scc*, horizontal semicircular canal; *so*, superior oblique muscle supplied by the fourth nerve; *sp*, spiracle; *sr*, superior rectus muscle; *th*, thalamencephalon; *Vis*, visceral branch of vagus nerve; *x-z*, occipital nerves; *II*, optic nerve; *III*, oculomotor nerve; *Va*, *VIIa*, ophthalmic branches of 5th and 7th nerves; *Vb*, maxillary branch of 5th nerve; *Vc*, mandibular branch of 5th nerve; *VIIb*, palatine branch of 7th nerve; *VIIc*, post-spiracular branch of 7th nerve; *VIII*, auditory nerve; *IX*, glossopharyngeal nerve; *X*, Vagus nerve.

head, passes through the optic foramen into the orbit, where it enters the eyeball.

The eyeball of the dogfish, like that of the frog and craniate vertebrates in general, is moved by six muscles —viz. the **superior**, **inferior**, **anterior**, and **posterior recti muscles**, and the **superior** and **inferior oblique muscles**. In the dogfish the four recti muscles arise close together from the hinder angle of the orbit just above the foramen for the exit of the main branches of the fifth nerve. The two oblique muscles arise, close together, from the anterior angle of the orbit.

The **third pair of nerves** arising from the ventral surface of the mid-brain pass outwards on either side through a special foramen in the orbit, and divides into three branches, of which the first goes straight to the rectus anterior, the second straight to the rectus superior, the last passes between the rectus posterior and the rectus superior, runs ventral to the rectus inferior, which it supplies with a branch, and continues with a forward course along the floor of the orbit to the obliquus inferior. The superior oblique muscles are supplied by the **fourth nerves**, which rises as very slender trunks from the dorsal surface of the brain between the optic lobes and the cerebellum. Each nerve runs forward inside the cranium to about the level of the optic nerve, then turns sharply outwards, passes through a foramen into the orbit, and is distributed to the superior oblique muscle. The posterior rectus of each side is innervated by the **sixth nerve**, a very slender trunk arising from the ventral surface of the medulla, and passing through the same foramen as the fifth nerve. Its course in the orbit is very short, but it can be seen running along the lower border of the posterior rectus.

The fifth, seventh, and eighth pairs of cranial nerves arise close together from the sides of the medulla below the restiform bodies. The fifth or **trigeminal nerve** has three main branches, of which the first, distinguished as the **ophthalmic branch**, leaves the medulla at the anterior end of the common root of the fifth nerve, runs forward for a short distance inside the skull and then passes through the lower of two foramina situated just above and in front of the origin of the recti muscles, and runs forward in a groove in the inner wall of the orbit alongside of a similar branch

of the seventh nerve. At the anterior end of the orbit the two nerves pass through the ophthalmic foramen to the surface of the snout, where they break up into branches supplying the mucous canals of that region. The main branch of the fifth nerve passes through a large foramen in the posterior angle of the orbit and runs over the orbital floor as a broad flat band. About half-way across it divides into two branches. The anterior and larger of these is the **maxillary nerve**; it passes over the edge of the upper jaw to the anterior end of the orbit, and there breaks up into branches, supplying the skin and mucous canals on the under side of the snout. The smaller posterior branch is the **mandibular nerve.** It runs outwards over the upper edge of the palato-quadrate cartilage, and turning downwards, passes between the levator labii superioris and adductor mandibuli muscles, supplying both with nerves, and is continued forward towards the mandibular symphysis. It will be noticed that the main branch of the fifth nerve forks over the mouth, one branch, the maxillary, running in front of, and the other, the mandibular, behind, the mouth opening. The significance of this relation will be better understood after consideration of the other cranial nerves.

The **seventh nerve**, like the fifth, has three branches. The anterior, or ophthalmic branch, originates from the dorsal edge of the medulla behind the cerebellum, and runs forward, leaving the skull by an aperture above and behind the aperture for the ophthalmic division of the fifth. In the orbit it joins the latter nerve and runs close alongside of it for the remainder of its course. The main branch of the seventh leaves the skull in company with the main branch of the fifth, and runs outwards and backwards along the hinder wall of the orbit and in front of the auditory capsule. Shortly after leaving the skull it gives off a **palatine branch**, which traverses the floor of the orbit behind and parallel to the main branch of the fifth. On reaching the upper jaw, the palatine nerve divides into two branches. the anterior running forward along the jaw, the posterior turning downwards and inwards between the jaw and the skull, and innervating the mucous membrane of the roof of the mouth. Just to the outside of the palatine branch the main branch of the seventh gives off one or two slender nerves to the prespiracular muscle (musculus levator

maxillæ superioris *) and to the anterior wall of the spiracle.

The main branch of the seventh nerve is continued outwards as the **hyoidean** or **post-spiracular nerve**. Running beneath the post orbital process of the auditory capsule it passes below the attachment of the post-spiracular ligament † to the wall of the auditory capsule, and lies between the posterior edge of the ligament and the hyomandibular cartilage. Emerging just behind the spiracle the nerve divides into three branches, the anterior of which is distributed to the skin and mucous canals on the side of the head, the middle branch runs in the depression between the ceratohyal and mandibular cartilages and supplies the mucous membrane of the buccal cavity, while the posterior branch supplies the anterior part of the constrictor superficialis branchiarum muscle. It should be noted that the seventh nerve forks over the spiracle just as the fifth nerve forks over the mouth opening.

The eighth nerve is the **auditory**; it passes straight into the auditory capsule and divides into two main branches, the anterior supplying the utriculus and the ampullæ of the anterior and external horizontal canals, the posterior supplying the sacculus and the ampulla of the posterior semicircular canal.

The ninth nerve originates from the ventro-lateral border of the medulla opposite the middle of the auditory capsule, and entering the latter runs through a canal which traverses it diagonally. Emerging near the posterior angle of the

* According to Vetter, this muscle is innervated by a twig from the fifth in Acanthias. In Scyllium it is supplied by two slender nerves, one of which is certainly a branch of the seventh. The other possibly runs back in the connective tissue sheath of the seventh, and joins the fifth, but I have not yet satisfied myself on this point.—G. C. B.

† The ligament which originates from the wall of the auditory capsule, and is inserted partly on the outer end of the hyomandibular cartilage, partly on the palato-quadrate cartilage is *post-spiracular*, as shown in fig. 57, *L*. I cannot find any trace in Scyllium of the *pre-spiracular* ligament so commonly figured and described. There is a stout connective tissue band passing from the post-orbital process to a thick sheet of sub-dermal connective tissue overlying the adductor mandibuli muscle. But it is not attached either to the palato-quadrate or the hyomandibular cartilage, and is hollow, being pierced by a canal connected with the mucous canal system.—G. C. B. (See also Ridewood, *Anatomischer Anzeiger*, 1896.

auditory capsule the nerve divides into a smaller anterior and a larger posterior branch; the former, called the **pre-trematic** branch, runs down in front of the first gill-cleft along the hinder border of the hyomandibular cartilage. The hinder or **post-trematic** branch runs behind the first gill-cleft, along the anterior face of the first branchial arch.

Just as the ninth nerve bears a definite relation to the first gill-cleft, so does the tenth or **vagus** nerve bear similar definite relations to the remaining gill-clefts. It arises by a number of roots close behind the ninth nerve and emerges from the skull through a foramen situated at the side of the foramen magnum, and thence runs backwards along the inner wall of the anterior cardinal sinus, where it gives off numerous branches and appears to be joined by the first five spinal nerves, and by the slender trunk formed by the so-called occipital nerves. This union, however, is only apparent; the nerve formed by the spinal and occipital nerves is bound up in the same connective tissue sheath as the vagus as far back as the ductus Cuvieri, but makes no connections with it. The four external branches of the vagus are the **branchial nerves**. They run backwards and outwards over the pharyngo-branchial cartilages, and respectively supply the second, third, fourth, and fifth gill-slits, each nerve having a pretrematic and a post-trematic branch like the ninth nerve. On its inner side the vagus, soon after its emergence from the skull, gives off a large **lateral nerve** which turns inwards and runs back to the posterior end of the body in the fascia between the dorsal and ventral sections of the musculature of the trunk. Its course is parallel to, but a good deal deeper than the lateral line. The main trunk of the vagus is continued backwards past the ductus Cuvieri to the dorsal wall of the œsophagus, where it breaks up into several branches and enters into connection with the sympathetic system. A small branch is given off to the sinus venosus, but it is difficult to trace it beyond the sinus into the heart.

We may now review the distribution of the several cranial nerves and consider what may be learned from them. It has already been pointed out that the spiracle is a rudimentary gill-cleft. The seventh nerve has the same relation to the spiracle that the ninth has to the first gill-cleft and the vagus

to the remaining gill-clefts. Thus these nerves form a series correlated with the branchial apparatus. The maxillary and mandibular divisions of the fifth nerve may be regarded as pretrematic and post-trematic branches in relation to the mouth, and there is embryological evidence, which cannot be detailed here, for regarding the mouth as a modified pair of gill-clefts, the lower jaw being the modified branchial arch supporting the hinder wall of the cleft, and the upper jaw an outgrowth of that arch. The fifth nerve, then, belongs to the same series as the seventh, ninth and tenth, and is essentially a segmental nerve related to an important segmental organ—viz. a gill-cleft. The first, second, and eighth nerves, whatever their primitive relations may have been, are now nerves of special sense related to the three pairs of sense capsules. But what of the third, fourth, and sixth nerves supplying the muscles of the eyeball? There is embryological evidence to show that they also belong to a series of segmental nerves, and the muscles which they supply are the relics of three pairs of primitive head segments or myotomes. The first embryonic myotome gives rise to the anterior, superior, and inferior rectus, and to the inferior oblique muscle; the second to the superior oblique and the third to the posterior rectus. The third, fourth, and sixth nerves, then, are the segmental nerves of the three anterior myotomes of the primitive head, but they do not represent the whole of the segmental nerves. There is evidence to show that they are the ventral or motor roots, and the ophthalmic and main divisions of the fifth and the seventh nerves are the corresponding dorsal roots proper to those segments. Similarly the ninth and tenth nerves do not appear to represent whole segmental nerves but only their dorsal roots, the vagus belonging to several segments. It is not surprising that, in a structure so complex and so far changed from its primitive condition as the vertebrate head, there should still be much uncertainty and conflict of opinion as to the amount and nature of the changes undergone, but the statements given above may be said to be so fairly established that they may legitimately find a place even in an elementary treatise. It is beyond doubt that the vertebrate head was segmented, and the head of the embryo dogfish is still segmented. Thus we are able to institute a comparison between the segmented anterior end of the headless Amphi-

oxus and the unsegmented head of the higher vertebrates, and in the latter we may point to the cranial nerves as evidence of a primitive condition of which all traces would, but for their presence, have been lost.

It should be borne in mind, however, that when we speak of the head as having been segmented, we do not mean that the skull is formed of a number of fused vertebræ, as was once supposed. The segmentation in question is a muscle segmentation like that of Amphioxus, and the head must have been evolved out of the anterior muscle segments before any vertebræ were formed. There is, however, some evidence that a certain number of vertebræ have been fused into the occipital region of the skull. This evidence partly consists in the existence of the **occipital nerves**, which in the dogfish are represented by three very slender nerves arising from the lower border of the medulla below the roots of the vagus. They pass through fine canals in the occipital region of the skull, and unite immediately outside it to form a slender trunk which is joined by the first five spinal nerves, and increasing in size with each accession, runs back in the anterior cardinal sinus bound up in the same connective tissue sheath with the trunk of the vagus. At about the level of the ductus Cuvieri this trunk separates from the vagus and runs downwards to the anterior border of the pectoral girdle. Here it divides into two branches, one of which passes through a foramen in the pectoral girdle and runs along the ventral surface of the pectoral fin, inosculating with the branches of the brachial plexus; the other turns forward to course along the anterior border of the coracoid cartilage, and is eventually distributed to the ventral muscles of the throat —viz. the coracomandibularis, the coracohyoideus, and the coracobranchiales. The brachial plexus (fig. 57, *Br.*) is formed by the union of the sixth to eleventh spinal nerves.

The sympathetic nervous system of the dogfish is somewhat diffuse, as compared with that of the frog, and the ganglia and nerves connecting them are so minute that they cannot be identified by simple dissection, special treatment with reagents being necessary to bring them into prominence. On opening the posterior cardinal sinus and carefully washing out the blood, one is able to see a number of irregularly-shaped bodies attached to the dorsal wall of the sinus. The most anterior is the largest, and has the form of an elongate lobulated body

placed obliquely in the anterior part of the sinus, not far behind the subclavian artery, from which it receives a branch. Similar but much smaller bodies of discoid shape are placed on the courses of the intercostal arteries throughout the length of the sinus. The function and significance of these bodies is problematical. Recent researches indicate that they are not homologous with the supra-renal capsules of higher vertebrates, as was once supposed, and we may call them the supra-renal bodies. Whatever may be their function and significance they are closely related to the sympathetic system. The first sympathetic ganglion is imbedded in the substance of the first supra-renal body, and the more posterior ganglia are either imbedded in or placed in proximity to the remaining supra-renal bodies. The first sympathetic ganglion is much the largest of the series, and is connected by a network of fine nerve fibres with a large plexus situated in the anterior corner of the posterior cardinal sinus, which in its turn is connected with fibres of the visceral branch of the vagus nerve. Posteriorly the first sympathetic ganglion gives off a number of nerve bundles which constitute the splanchnic plexus, closely attached to the walls of the œsophagus. The remainder of the sympathetic ganglia are minute, measuring from $\frac{2}{10}$ths to $\frac{7}{10}$ths of a millimetre in diameter. They are united in an irregular manner with one another by very slender nerves, and are connected with the spinal nerves by fine fibres representing the rami communicantes of higher forms.

The organs of special sense may be briefly described.

The olfactory organs are a pair of spacious sacs, enclosed in the cartilaginous olfactory capsules. The nostril on either side leads into the cavity of the sac, which is subdivided into a number of chambers by vertical partitions or septa, attached on either side of a median partition which runs across the cavity from its posterior and outer, to its anterior and inner wall. The walls of the septa are thrown into smaller folds and are covered by a thick epithelium, in which the olfactory cells are situated. The epithelium is richly supplied by the branches of the olfactory nerves. The eye has the same general structure as that of the frog (vol. i. p 69), and need not be described at length. Its more remarkable features are the cartilaginous condition of the sclerotic, the flatness

of the cornea, the slit-like pupil, the spherical shape of the lens, and the glistening membrane called the **tapetum**, which forms an inner lining to the choroid.

The auditory organs, being imbedded in cartilage which can easily be pared away with a knife, are particularly favourable objects for study. There is no middle ear or tympanic cavity, as in the frog, and except for the small openings of the ductus endolymphatici, the organs of hearing are completely enclosed in the cartilaginous auditory capsules, and have no communication with the exterior The general structure of the auditory organ is very similar to that of the frog (vol. i. p. 70). The essential part of the organ is the **membranous labyrinth**, filled with a fluid **endolymph**, and lodged in a corresponding cartilaginous labyrinth. Between the walls of the membranous and cartilaginous labyrinths is a space filled with a fluid **perilymph**. The membranous labyrinth is divisible into a **utriculus** above and a **sacculus** below. The latter is a simple elongated sac, produced at its posterior end into a dilatation called the **lagena**. The utriculus is larger, and is complicated by the presence of three **semicircular canals** which open into it—viz. the anterior and posterior vertical and the external horizontal canals. Each canal is swollen to form an **ampulla** at one end before opening into the utriculus. The ampullæ are at the lower ends of the anterior and posterior canals, and at the anterior end of the external horizontal canal. A remarkable feature in the auditory organ of the dogfish is the permanent opening of the **ductus endolymphaticus**. This tubular offset of the sacculus ends blindly in the frog, but in the dogfish it runs upwards and inwards towards the middle line through a canal in the skull, and on reaching the outside of the skull is slightly dilated, bends first forward and then backwards, narrows to form a very fine tube, and finally opens on the upper surface of the hinder part of the head by a minute aperture.

If we now review the anatomy of the dogfish in the light of what we already learned of the anatomy of the frog, we shall see that in almost every organ it presents a more primitive and simpler structure than the latter animal. The skeleton remains cartilaginous throughout life, and its early simplicity is not disguised by the development of bone. The component parts

of the vertebræ are distinct; the notochord is largely persistent; the jaws are so loosely connected with the cranium that their primitive relations to the skull are readily discernible. The teeth are seen to be nothing more than modifications of skin denticles. The branchial skeleton is well developed, and undergoes none of the modifications which in higher types render its origin obscure. The musculature of the body is relatively simple and retains its primitive segmentation. The excretory organs retain their segmental arrangement to a much greater degree than in the frog. The heart has only a single auricle and a single ventricle, contains only venous blood, and escapes all the complications attendant on aerial respiration. The general plan of the arterial system is simple, and is distinctly correlated to the gills and gill-slits; we shall see that in the higher vertebrates the arterial arrangement is evolved, in the course of individual development, from just such a system as is persistent in the adult dogfish. The distribution of the 7th, the 9th, and the 10th cranial nerves affords a clue to the more obscure and complex distribution of these nerves in higher forms. Lastly, the primitive character of the adult dogfish is so far shared by its embryo that we have evidence of the segmentation of the head, of the origin of the eye-muscles, and of the relation of cranial nerves to head segments, not to mention a number of other characters, such as is not to be obtained by the study of any of the higher vertebrates.

The embryology of the dogfish is, indeed, as interesting and instructive as its adult anatomy, but for various reasons it will not be considered here. For one thing, the ovum is so greatly distended with food-yolk that the segmentation and earlier phases of development are modified to an extent which renders their interpretation difficult, unless the student has already acquired a considerable familiarity with a more normal type of vertebrate embryology. Such a type is furnished by the common frog, and we will therefore consider it in some detail in the next chapter.

CHAPTER XXVII

THE DEVELOPMENT OF THE FROG

THE ova of the frog are extruded by the female in the early spring, and are fertilised upon extrusion by the spermatozoa of the male. Each ovum is about the size of a No. 3 shot, and is surrounded by a transparent gelatinous coat secreted by the walls of the oviduct. These coats swell up on contact with water, and adhere to one another, forming gelatinous masses in which the ova are imbedded, the masses being familiarly known as frog's spawn. Quantities of it may be obtained in ditches and ponds in the month of March; the ova can easily be kept in aquaria, and are particularly favourable objects for the study of segmentation. The later stages are not quite so easily studied, because the abundance of black pigment and consequent opacity of the embryos does not admit of their being studied as transparent objects, and the relatively large quantity of food-yolk makes it difficult to cut good sections of the earlier stages. With a little care, however, satisfactory sections can be made, and all the stages of development may be followed out with great thoroughness.

The segmentation and formation of the blastula have already been described (vol. i. p. 126). The subsequent events may be briefly sketched as follows:—The blastula, by a modified process of invagination, becomes a gastrula with an outer layer or **epiblast** and an internal cavity or archenteron lined by **hypoblast.** During the formation of the gastrula a portion of the inner cells is separated off as a sheet of **mesoblast** lying between the other two layers. The epiblast of the dorsal surface is raised to form a pair of longitudinal folds enclosing a groove, and the folds meet and unite in the middle line, converting the groove into a tube, the cavity of which becomes the canal of the spinal cord and the ventricles of the brain, the walls of the folds being converted into the cerebro-spinal nervous

system. The notochord is formed as a median rod of tissue underlying the neural groove, and in the frog is apparently derived from the continuous sheet of mesoblast, and not from the hypoblast. The lateral sheets of mesoblast, after the formation of the notochord, are divided into mesoblastic somites. Meanwhile the embryo has elongated, the anterior end of the neural tube is dilated and divided by constrictions into a fore, a mid, and a hind brain. The limits of the gut become defined, and the liver is formed as an outgrowth from its lower side. The heart is formed in the mesoblast on the ventral side of the anterior end of the gut. The gills are formed from thickenings on the sides of the head, known as the gill-plates, and the sense organs are developed from thickenings known as sense-plates, situated in front of the gill-plates. After these and other changes are completed, the embryo escapes from its gelatinous capsule as an elongate free swimming larval form, destitute of limbs, but provided with a long tail. This larva is the well-known tadpole.

The tadpole, when hatched, has no mouth, but lives for some days on the still abundant remains of the food-yolk stored in the floor of the gut. It has a sucker on the lower side of the head, by which it attaches itself to weeds and other objects, and it breathes by three pairs of tuft-like external gills situated on the sides of the neck. It is interesting to note, in this connection, that the embryo dog-fish is similarly furnished with tufted external gills. In the space of a few days a mouth is formed; it is provided with a fringe-like upper and lower lip, and is furnished with a pair of horny jaws, which are eventually cast off, and are not to be confounded with the jaws of the adult. On the establishment of the mouth, the tadpole begins to feed on a purely vegetable diet, and the gut, which was previously short and wide, becomes very long, and is coiled up inside the abdomen like a watch-spring. Posteriorly it opens by the anus, which was established somewhat early in embryonic life. The liver becomes histologically differentiated and the pancreas is formed.

While these changes are in progress the gill-plates on either side of the neck are perforated by four slit-like openings, the gill-slits, leading from the pharynx to the exterior. The original external gills shrivel up and are replaced by a new series formed

lower down on the branchial arches: these new gill filaments are external like the first. Shortly after the formation of the gill-slits a fold of skin grows out from each side of the head and extends backwards, forming a cover or operculum to the gills. The folds unite ventrally and continue to grow backwards so as to form a gill-chamber, and at a later period their hinder edges fuse with the body-wall along the right side and on the ventral surface, but the fusion does not extend to the left side, so an opening is left there, the margins of which are produced into a spout-like process. Through this aperture the water taken in by the mouth and passed through the gill-slits into the gill-chamber is discharged. The tadpole has now attained its maximum development as such. Its body and head are broad and depressed, and it has a large muscular tail provided with a dorsal and a ventral fin-like expansion, used in swimming, but there are no limbs. At this stage of its existence the larval frog or tadpole is a fish, not only in habit but in many important structural features. It has a cartilaginous cranium, an unconstricted notochord (in this respect it is in a more primitive condition than the dogfish), gill-slits leading from the œsophagus to the opercular chamber, a bilocular venous heart, afferent and efferent branchial arteries, and the gill-arches are supported by cartilaginous bars, and there is no trace of pentadactyle limbs. But from this point onwards it gradually loses its piscine characters and takes on the structure of an amphibian. Lungs are formed as outgrowths of the gullet, and the arterial system is modified in connection with the new mode of respiration; the gills after a time atrophy and the gill-slits are closed up. The hind limbs are developed on either side of the base of the tail and the fore-limbs beneath the opercular folds, and both pairs gradually assume pentadactyle characters. The tail gradually atrophies and eventually is completely absorbed. The permanent jaws are formed, the frilled lips shrivel up and the horny jaws are cast off. Finally, in the course of a rapid metamorphosis, the herbivorous tadpole becomes a carnivorous frog, the intestine becomes shorter, the cartilage of the skeleton is largely replaced by bone, and the animal assumes its adult characteristics. We may now consider some of these remarkable changes in detail.

The segmentation has already been described (vol. i. p. 122),

and we left the ovum as a sphere whose walls are composed of several layers of cells enclosing an excentric cavity. One half of the sphere is composed of small and deeply pigmented cells, the other half is composed of much larger white cells filled with granules of food-yolk. Thus we may speak of a pigmented hemisphere and a white hemisphere, and it is important to observe that the former always turns uppermost in whatever position the egg may be placed. The cavity is the segmentation cavity or **blastocœle**. Close inspection shows that all the cells of the pigmented hemisphere are not alike, but some of them on one side are smaller and lighter in colour than the others. When the pigmented cells reach down to the equator, or a little below the equator of the egg, a short streak or furrow, rendered conspicuous by the deeply pigmented cells bounding it, makes its appearance just below the equator of the egg on the side occupied by the smaller cells. The groove soon becomes a crescent with the concavity turned towards the white hemisphere, and the limbs of the crescent gradually extend along the lower sides of the white hemisphere. The groove which becomes crescentic is the first indication of the formation of the enteron, and will be referred to as the dorsal lip of the blastopore. The changes which follow on its appearance and accompany its extension require the most careful attention. The eggs, as has been said, float with the pigmented side uppermost. In order to see what is going on on the lower side one must place them on a strip of looking-glass, cover them with a just sufficient depth of water and study the reflections of the lower or white hemispheres.* The external changes are represented in the series of drawings, fig. 58, *A* to *J*. In *A* we see the lower white hemisphere slightly tilted towards the bottom of the page, so that part of the pigmented hemisphere is seen at the top of the figure. The small transverse groove forming the dorsal lip of the blastopore is seen at *dl.*, just below the equator of the egg. In *B* the pigmented cells of the upper hemisphere have grown downwards over the cells of the white hemisphere at all points, but most rapidly in the upper part of the picture. The dorsal lip of the blastopore is now a crescentic groove, the horns of the crescent forming the anterior boundary of the white area

* I am indebted to Mr J. W. Jenkinson, M.A., for the following details corroborative of Pflüger's account of the closure of the blastopore.

not yet covered by the overgrowth of the pigmented cells.

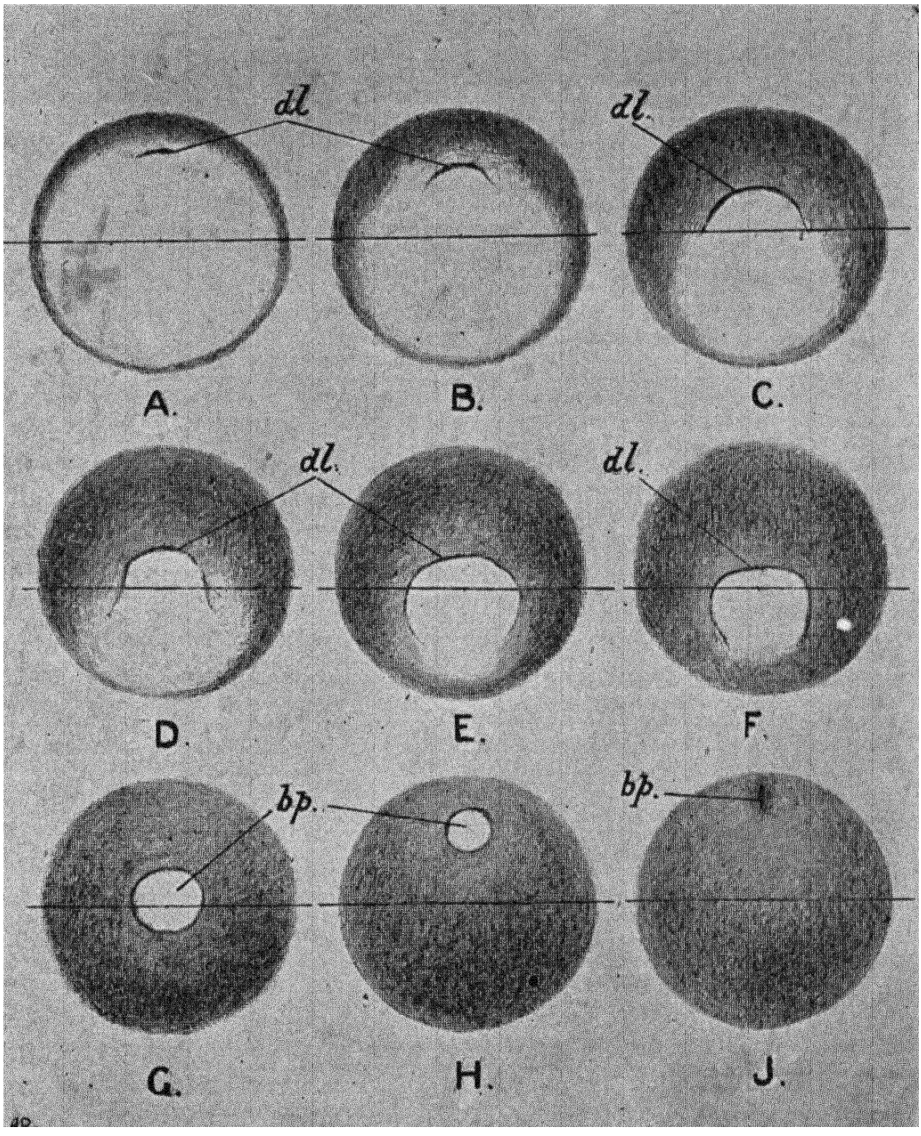


Fig. 58

A to *J*. A series of views of the lower pole of the Frog's ovum, illustrating the overgrowth of the white hemisphere by the pigmented cells and the formation and changes of position of the blastopore. For full description see text. *dl*, dorsal lip of blastopore; *bp*, blastopore. The horizontal lines are drawn through the lower pole of the ovum, but in *D*, *I*, *J* they have inadvertently been placed too low down in the figures.

The dorsal lip has not only increased in size, but it has

travelled a certain distance downwards from the equator towards the lower pole of the egg. In *C* the lip of the blastopore forms a larger and wider crescent, and has travelled still further down towards the lower pole. The pigmented cells have grown still further over the white cells, leaving a relatively small white area at the lower pole. In *D* the process has continued further, and the dorsal lip of the blastopore nearly coincides with the lower pole of the egg. In *E* the horns of the blastoporic crescent have turned inwards, and embrace the rapidly diminishing white area. In *F* the horns of the crescent have nearly met; the whole ovum is covered with pigmented cells except for a small oval area circumscribed by the rim of the blastopore. The dorsal lip of the last named is now coincident with or a little below the lower pole of the egg. These changes occupy some thirteen hours, and during this time the egg, as a whole, has remained quite still and has not undergone any rotation. It is clear then that the dorsal lip of the blastopore has travelled from above downwards through an angle of about 90°. During the next six hours the egg, as a whole, slowly rotates about a horizontal axis in the direction of the point at which the dorsal lip of the blastopore first made its appearance. Consequently in *G* we find that the dorsal lip has returned some way back along the path by which it moved downward, but this time its change of position is not due to its own movement but to the rotation of the egg as a whole. In point of fact, while the egg is rotating backwards, the dorsal lip of the blastopore is still moving slowly along its original path, and at the same time its sides are contracting towards the centre, so that the white area is restricted to a small patch of yolk-cells circumscribed by the now circular rim of the blastopore. This area is still further diminished in size by the contraction of the blastoporic rim, and in *H* the yolk-cells form a projecting mass known as the blastoporic or **yolk-plug**. Finally in *J* the yolk-cells are entirely covered in by pigmented cells, and the blastopore forms a minute orifice at the bottom of a slight depression. It should be noted that in consequence of the rotation of the whole egg in a direction the reverse of that along which the dorsal lip of the blastopore travelled, the blastopore in *J* is slightly above the point occupied by the dorsal lip in *A*.

We must now study the internal changes that have been

going on in the egg by means of a series of sagittal sections—

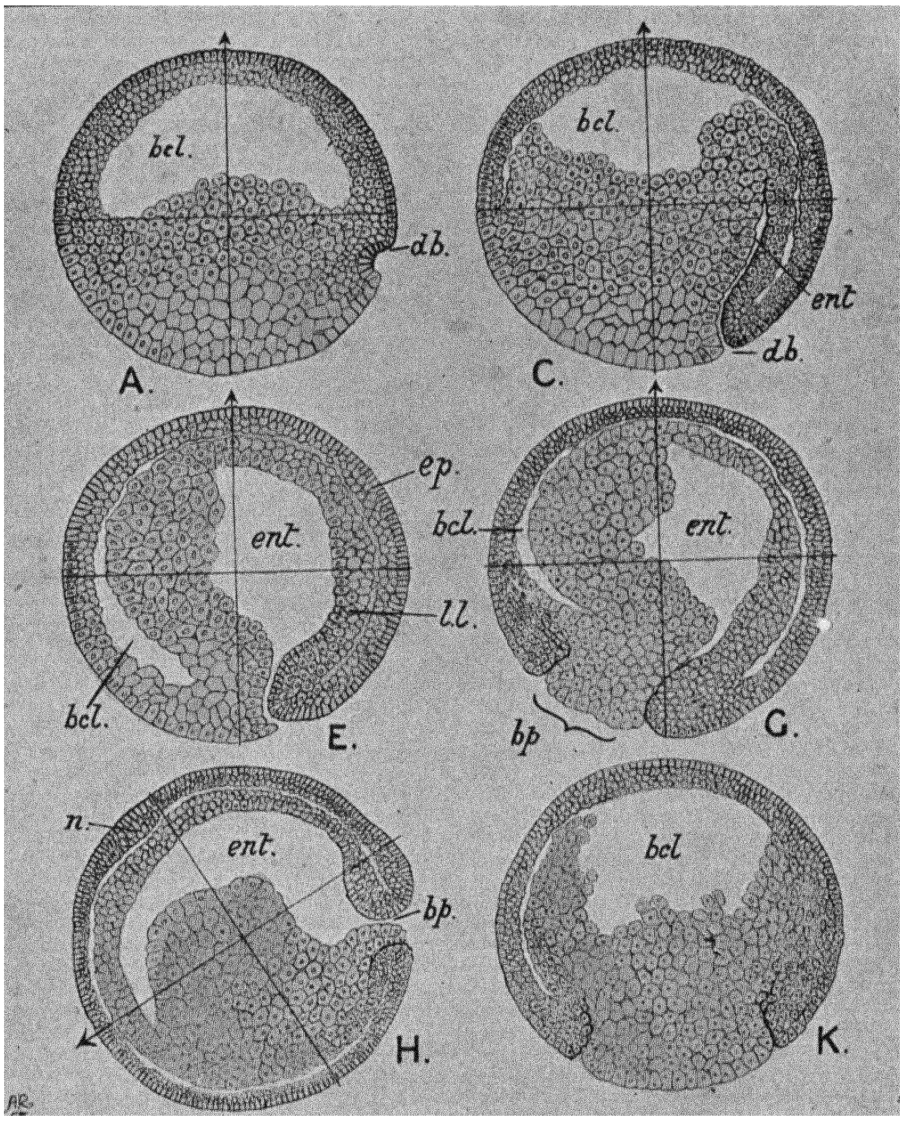


Fig. 59

A, *C*, *E*, *G*, and *H*. Sagittal sections through the stages indicated by the corresponding letters in fig 58. The vertical lines in *A*, *C*, *E*, *G*, are drawn through the poles of the eggs; the horizontal lines indicate the equators. In *H* the egg has rotated through an angle of 120 degrees. *K* is a transverse section taken through the horizontal line in stage *E*, fig 58, to show the infolding of the lateral lips of the blastopore. *bcl*, blastocœle; *bp*, blastopore; *db*, dorsal lip of blastopore; *ent*, mesenteron; *ep*, epiblast; *ll*, lower layer; *n*, epiblastic thickening marking the anterior end of the neural plate.

that is, by sections of the principal stages depicted in fig. 58,

taken through the middle of the ovum at right angles to the plane of the paper. Fig. 59, *A*, is such a section of the stage shown in fig. 58, *A*. The egg is just beginning to advance beyond the blastula stage, and has a large segmentation-cavity or blastocœle roofed in above by several layers of small cells; the outermost layer, covering the upper hemisphere of the egg, having the form of a deeply pigmented columnar epithelium. The floor of the blastocœle is formed by a mass of large yolk-cells occupying the whole of the lower or white hemisphere of the egg. At *db*. the dorsal lip of the blastopore is seen in section, and it appears that it is formed by the tucking in of some of the small pigmented cells along a short horizontal line just below the equator of the egg. Fig. 59, *C*, corresponds with the similarly lettered stage in fig. 58. It shows that the dorsal lip of the blastopore has travelled through an arc of some 45° towards the lower pole of the egg, and that this movement has been accompanied by a continuous infolding of the dorsal lip of the blastopore. The process can best be understood by fixing one end of a strip of cloth to some curved surface, and folding back the free end of the strip over the attached end. If a piece of chequered cloth be used and the chequers are taken to represent cells, then, as one pulls down the folded edge, one can see how the chequers on the outer surface are continually rolling inwards over the edge of the fold and are forming the roof of a narrow space enclosed between the inner limb of the fold and the curved surface. Fig. 59, *C*, shows that the dorsal lip of the blastopore has advanced in this manner, that the pigmented cells actually roll in over the advancing lip of the blastopore, and that the result is the formation of a double fold of tissue covering in a narrow slit-like space which is the first indication of the gut or enteron. Between the limbs of the fold there is a yet narrower slit-like space which communicates above with the blastocœle and is evidently a continuation of the latter.

Fig. 59, *E*, shows a more advanced stage of the process. The dorsal lip of the blastopore has now travelled nearly as far as the lower pole of the egg, and the double fold formed by its advancement is longer, and has extended upwards, forming the boundary of a relatively spacious cavity which is evidently an extension of the slit-like enteron of

the previous figure. The great increase of the size of the enteron has resulted in a corresponding diminution of the blastocœle, which is now displaced to the left-hand side of the picture, but can be traced between the outer and inner limbs of the fold right round to the dorsal lip of the blastopore.

It must be borne in mind that while the blastopore is advancing it is also elongating and becoming crescentic in shape, and that the horns of the crescent bend inwards and eventually meet together. The same process of infolding that is observed at the dorsal lip is also in progress, but at a slower rate, along the horns of the crescent, and eventually, when the horns meet and unite, the infolding extends all round a ring and we get the condition represented in fig. 59, *G* (corresponding to stage *G* in fig. 58), where the ventral lip of the blastopore is also seen to be infolded and has advanced from the equator towards the lower pole of the egg to meet the dorsal lip, the two being separated by the yolk-plug—*i.e.* by the circular space where the white cells still project on the surface. It can be seen that the enteron has increased in size and that the blastocœle is reduced to very narrow dimensions.

The result of this complex process of overgrowth and enfolding is the obliteration of the blastocœle and the formation of a new cavity, the enteron, whose roof and side walls are formed by two layers, each several cells deep, and whose floor is formed by a compact mass of yolk-cells. The external layer of cells is the epiblast, differing only from that of the embryonic Amphioxus in being more than one cell thick. The internal layer forming the roof and side walls of the enteron may be called the lower layer or primitive hypoblast, and is to be compared with the interior layer of the gastrula of Amphioxus. The mass of yolk-cells has no exact counterpart in Amphioxus, but a little consideration will make it clear that the stage which we are now considering in the frog is really a gastrula stage, and that the changes that have led up to it are really a process of invagination, modified by the presence of a mass of inert yolk-cells, which have prevented a complete tucking in of one hemisphere within the other. Further differences may be noted between the two forms. In Amphioxus the process of invagination is relatively rapid, in the frog it is slow, being

retarded by the presence of yolk-cells, and we find accordingly that parts of the embryo, which in Amphioxus do not make their appearance till invagination is completed, are formed in the frog while invagination is still in progress. Thus the mesoblast, which in Amphioxus arose from outgrowths of the archenteron, is formed in the frog at an early stage by a splitting of the lower layer into a hypoblastic and a mesoblastic sheet, and the mesoblast sheet is extended in the region of the yolk-cells by the additon to its edges of a number of irregular branched cells derived from the sides and ventral lip of the blastopore, as is shown in fig. 59, *K*. The neural folds have also made their appearance at and even before the stage represented in fig. 58, *J*. It is important that the situation of the neural folds should be clearly understood. At one time they were supposed to be formed on the upper or pigmented hemisphere of the egg, but they may more correctly be described as being formed on the lower or white hemisphere on either side of the line along which the dorsal lip of the blastopore has travelled, and this in spite of the fact that the neural folds are always uppermost in the developing egg. Let us see how this has come about. In stage *G*, fig. 58, the egg has already begun to rotate in a reverse direction to the path of the dorsal lip of the blastopore, and in stage *H* fig. 58, this rotational movement has continued further, so that the whole egg has moved about a horizontal axis through an angle of 110° more or less. The reason of this rotation is obvious. The blastocœle is a cavity situated excentrically in the egg, and as long as it was spacious the hemisphere in which it was contained was the lighter and floated uppermost. As the enteron is formed, the blastocœlic cavity is pushed to one side and eventually obliterated, and the new enteric cavity being also excentric, the hemisphere in which it lies is the lighter, so the egg rotates until that hemisphere floats uppermost, bringing the blastopore back to the equator. This final position of the blastopore marks the hind end of the embryo. A meridian drawn from this point through the upper pole indicates the longitudinal axis of the embryo, and this is the path along which the dorsal lip of the blastopore travelled. The epiblast on either side of this meridian is thickened, but becomes thinner along the meridian itself. These changes are expressed in an external view of the embryo by a flattening of the dorsal

urface, and the appearance of a broad but shallow median groove, the so-called primitive groove. The flattened surface s the **neural plate.** Its edges soon become thicker, and

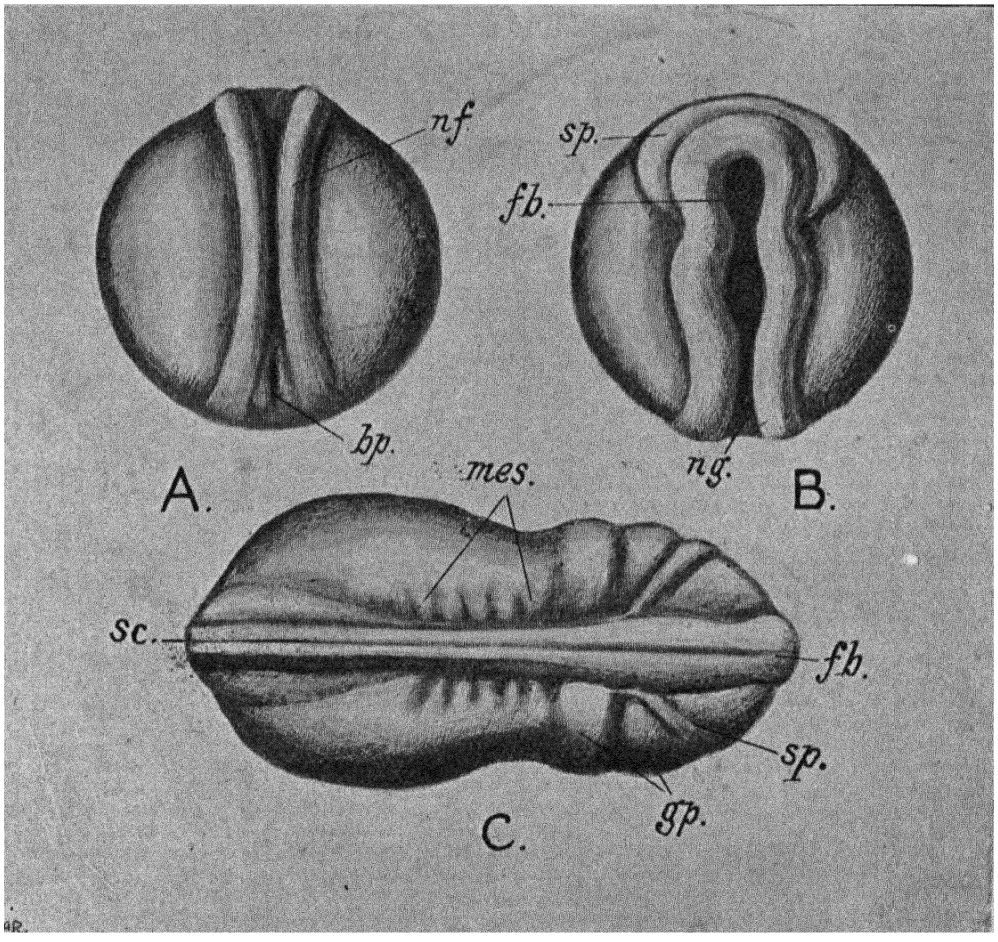


Fig. 60

A. Dorsal view of a frog's egg, showing the neural folds and the blastopore lying between their posterior ends. *B.* A somewhat later stage seen from in front and above, showing the sense plate and the anterior ends of the neural folds dilated to form the brain. *C.* Dorsal view of a later embryo in which the neural folds are completely closed, and five mesoblastic somites are indicated externally. *bp*, blastopore; *fb*, fore-brain; *gp*, gill-plates; *mes*, mesoblastic somites; *nf*, neural folds; *sc*, spinal cord; *sp*, sense plate.

re raised up to form the **neural folds,** which are continued nto each other anteriorly in front of the primitive groove, but posteriorly diverge somewhat so as to embrace the

blastopore. A thickening is formed on either side of the anterior end of the neural folds, and each thickening after a time is divided into two by a transverse furrow. The part lying behind the furrow is then known as the **gill-plate**, the part lying in front of it as the **sense-plate**. The sense-plates eventually grow downwards and forwards, and meet in front of the neural folds. The latter increase in height, and begin to fold in towards the median line, forming the walls of a deep **neural groove**, which extends posteriorly to the blastopore. The embryo now begins to elongate; the neural folds become longer and deeper, and turn inwards towards the middle line, while posteriorly they overlap and begin to enclose the blastopore. The elongation of the embryo continues, the neural folds meet and fuse in the middle line, their union being first effected about the middle of their length, and extending forwards and backwards. Thus they convert the neural groove into a tube, which becomes the central canal of the spinal cord and the ventricles of the brain. Before the folds have united in front, the anterior end of the neural groove is enlarged, and even before they have met and fused this bulb-like enlargement is divided by slight constrictions into a **fore-brain**, a **mid-brain**, and a **hind-brain**. Posteriorly the neural folds envelop and fuse together over the blastopore, and as the latter opens into the enteron a **neurenteric canal** is established, having the same relations as in Amphioxus. It is a transitory structure, and soon closes up. At this time the gut is completely closed, neither mouth nor anus being present; but the latter is soon formed as a small depression situated a little way behind the blastopore, and connected with it by a groove. The depression grows deeper, and meets an outgrowth from the floor of the hinder end of the enteron, their walls fuse and are perforated to form the anus. At first the anus is nearly on the dorsal side of the embryo, but soon after its formation the region above grows out to form the commencement of the tail, and the anus is then shifted to a ventral position. Meanwhile important changes have been going on inside the ovum. We have already seen that the internal layer of cells forming the roof and walls of the enteron becomes split at an early stage into a thin sheet of hypoblast, forming the actual roof and side walls of the enteron, and a thicker sheet

of mesoblast lying between the hypoblast and epiblast. This

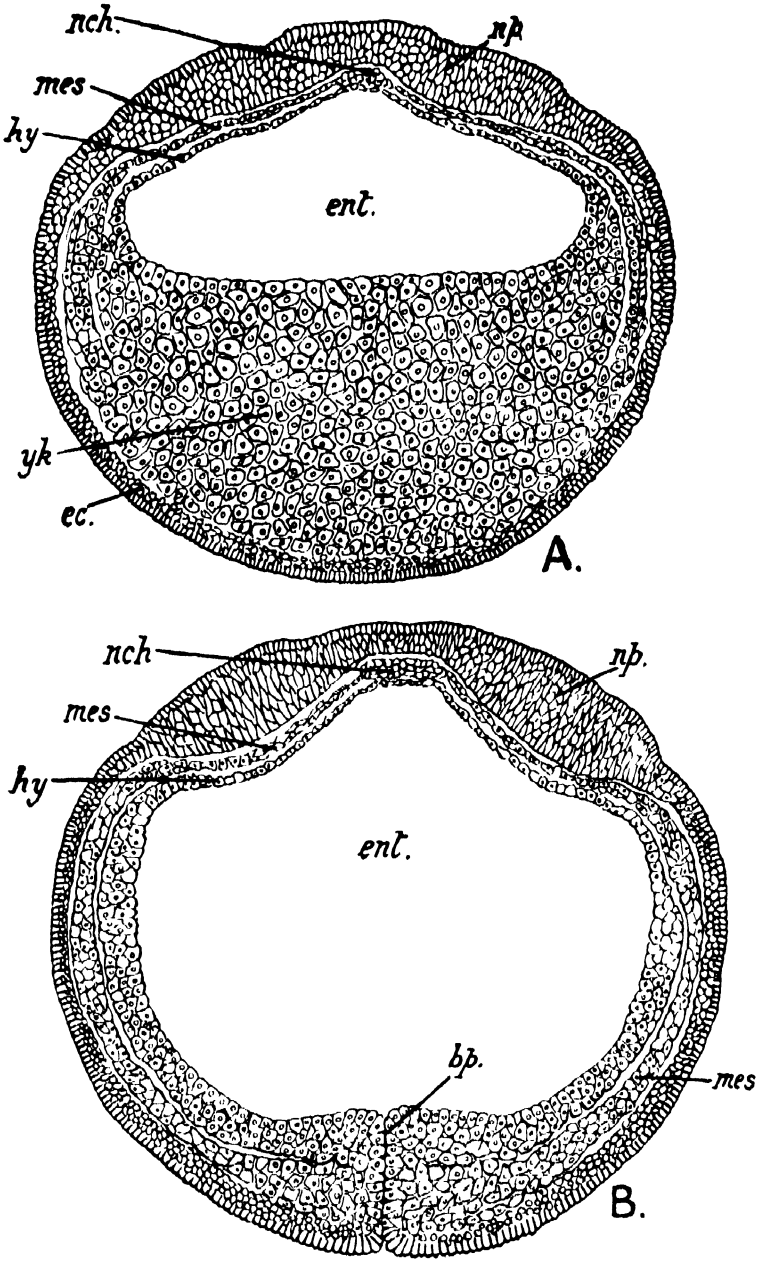


Fig. 61

A. Transverse section through the anterior part of a young embryo of the frog, showing the formation of the notochord, mesoblast, and hypoblast. *B*. A horizontal section through the blastopore of an embryo of the same stage as *A*, to show the mesoblast extending round to the lips of the blastopore. *bp* blastopore; *ec*, epiblast; *ent*, enteron; *hy*, hypoblast; *mes*, mesoblast; *nch*, notochord; *np* neural plate; *yk*, yolk.

splitting does not at first extend to the tract of lower layer

cells lying immediately under the neural groove; so there is a stage, represented in transverse section in fig. 61, *A*, in which the hypoblast and mesoblast are fused in the mid-dorsal line, but are separated laterally where they form the roof and walls of the enteron. The floor of the enteron is formed by the yolk-cells, into which the hypoblast passes insensibly, but the mesoblast continues to spread round the embryo between the epiblast and the yolk till it completely encloses the latter. The ventral extension of the mesoblast differs in different regions of the embryo. It is obvious, from an examination of fig. 59, *G*, that in the neighbourhood of the blastopore—that is, at the hinder end of the embryo—the mesoblast forms a complete investment to the yolk, for it grows inwards all round the lips of the blastopore. Further forward the mesoblast extends some way down on either side of the yolk-cells, and at the extreme anterior end it forms only the roof and side walls of the enteron, and does not extend down the sides of the yolk. At the stage when the neural folds have become distinct, the median tract of cells, which in the preceding stage was continuous with the mesoblast sheets at the side and the hypoblast below, becomes separated from both layers and forms a solid rod of cells, the notochord, lying beneath the neural groove. The notochord is first differentiated in the hinder half of the embryo, and extends gradually forward. Posteriorly it does not reach the blastopore, but ends in a mass of cells lying in front of the dorsal lip, in which mesoblast and hypoblast are indistinguishably blended together. In the frog the notochord appears to be formed from a tract of cells in which mesoblast and hypoblast are blended together, and at the time of its appearance as a separate structure it has the appearance of being formed as a differentiation of the median tract of the mesoblast. In the newt, and some other long-tailed Amphibia (*e.g.* the Axolotl), the notochord is distinctly formed from a groove in the dorsal median line of the hypoblast, which is pinched off and converted into a solid rod, just as is the case in Amphioxus. In the frog the origin of the notochord from the hypoblast is obscured. The hypoblast and mesoblast are first differentiated out of the lower layer cells, and then the notochord separates out from the mesoblast, and its ancestral origin from hypoblast would not be recognised if

it were not for the comparison afforded by other Amphibia.

When the notochord has been established, the mesoblast forms two lateral sheets lying between epiblast and hypoblast, and extending right round or nearly round the yolk, as the

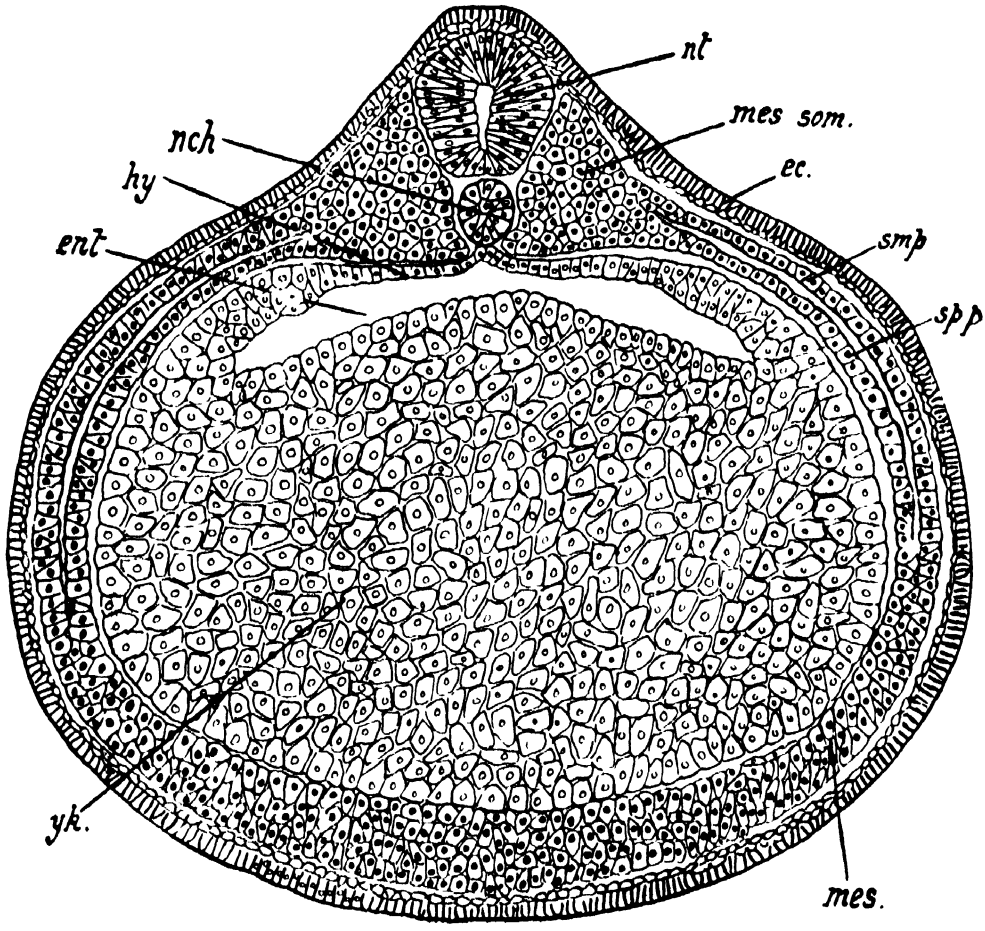


Fig. 62

Transverse section through the middle of the body of an embryo of about the age depicted in fig. 60, C. *ec*, epiblast; *ent*, enteron; *hy*, hypoblast; *mes*, unsplit mesoblast on the ventral side; *mes.som*, mesoblastic somite; *nch*, notochord; *nt*, neural tube; *smp*, somatic layer of mesoblast (somatopleur); *sp.p*, splanchnic layer of mesoblast (splanchnopleur). The space between these two layers is the cœlom; *yk*, yolk.

case may be, in different regions of the embryo. The edges of these sheets abutting on the notochord now become thickened (fig. 62) to form the so-called segmental plates, and shortly afterwards the lateral parts of the sheets are divided into an outer or somatic layer adjacent to the epiblast,

and an inner or splanchnic layer adjacent to the hypoblast. The narrow cavity between these two layers is the body-cavity or cœlom. At the time of its first appearance it extends some way into the segmental plates, but the latter soon become solid, and the cœlom is confined to the lateral plates.

As soon as the neural folds begin to turn inwards to form the nerve-tube, the segmental plates begin to be divided by transverse lines into a series of paired blocks or mesoblastic somites, and shortly after their appearance the somites are divided off from the lateral plates of mesoblast, into which the segmentation does not extend. The first somite is formed at some little distance from the anterior end of the body, and new somites are formed successively from before backwards. The head region lies in front of the first somite, and here the mesoblast is not segmented, but breaks up into a mass of scattered branched cells, united to one another by protoplasmic processes. Such scattered branched mesoblastic cells are commonly called **mesenchyme**, and it should be noted that the head of the frog is never segmented, even in the embryonic condition, whereas, as we have learned (p. 218), the head of the embryo dogfish is definitely segmented, the segmentation disappearing in later life. It is worthy of remark that there are traces of a pair of mesoblastic somites in front of the first pair of body somites in the embryo-frog, but these soon break up to form mesenchyme. We have here an instance of abbreviation in development. The frog's head, instead of passing through a segmented condition which is subsequently lost, passes at once to the unsegmented condition of the adult, though there are just traces enough to remind us of a primitive segmentation.

The embryo has now reached the stage shown in sagittal section in fig. 63, which has been so fully lettered that a lengthy description is unnecessary, and a dorsal view of the same stage is shown in fig. 60. Only the ventral part of the mesoblast appears in the sagittal section, as the somites and lateral plates of the mesoblast lie to the sides of the median plane cut by the section. It should be noted that there is an anus, but no mouth, and that the notochord only extends as far forward as the floor of the mid-brain, the fore-brain being bent down over its anterior end to form the **neural flexure**, which is afterwards straightened out. The embryo

is formed from three germinal layers, which are already in part differentiated. The central nervous system has clearly been formed from the outer layer or epiblast, the rest of the layer forming the external covering of the body. The mesoblast and hypoblast were formed in close connection with the blastopore, and at first were blended together, but soon separated out, and the notochord was formed in the mid-dorsal line, where the two layers remained longest in contact. There is still a large mass of yolk occupying the posterior end of the enteron; it must be regarded as belonging to the inner layer or hypoblast. All these relations, and the growth

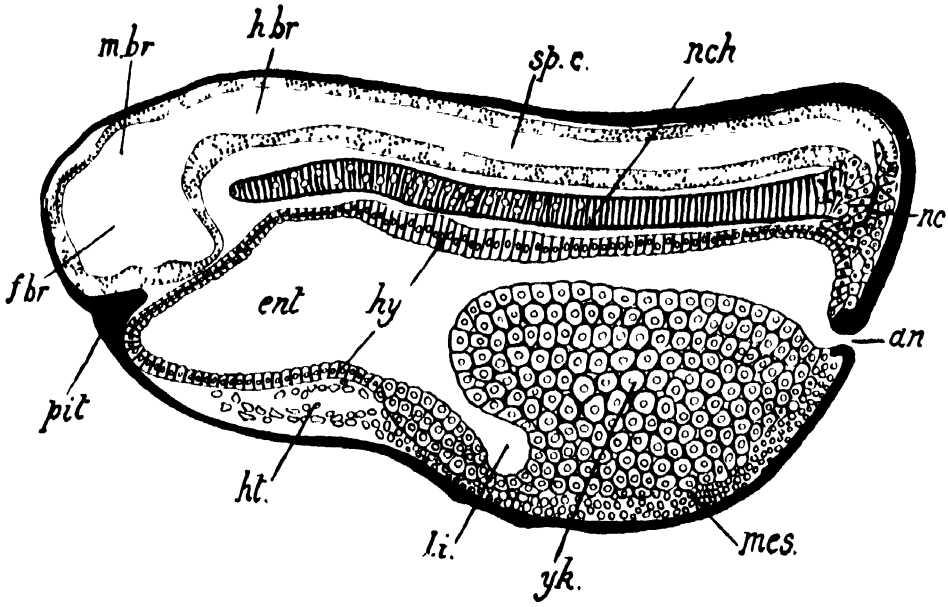


Fig. 63

Diagrammatic longitudinal section through an embryo of about the same age as that drawn in fig 60, *C*. *an*, anus; *ent*, enteron; *fbr*, fore-brain; *hbr*, hind-brain; *ht*, heart; *hy*, hypoblast; *li*, liver diverticulum; *mbr*, mid-brain; *mes*, ventral mesoblast; *nc*, remains of the neurenteric canal; *nch*, notochord; *pit*, epiblastic ingrowth which will form the pituitary body; *spc*, points to the canal of the spinal cord; *yk*, yolk. The external epiblast is represented by a thick black line, the nervous system is shaded with dots.

processes that led up to them, should be compared with the stages in the development of Amphioxus.

The further development of the embryo is too complex to follow as a whole, and it is necessary to deal with it organ by organ. It would be beyond the limits of this work to attempt a detailed account of the organogeny of the frog, and in the following sketch of the course of events, only

such points will be enlarged upon as are of special importance in the study of comparative anatomy.

The inner germinal layer or hypoblast gives rise to the epithelium lining the mid-gut, or enteron, to the liver, pancreas, cloacal bladder, lungs, and gill-slits.

The enteron, in the stage represented in fig. 63, has no anterior opening or mouth. Its anterior end is wide, but its posterior end is narrow, owing to the large mass of yolk-cells forming its floor. For some time after hatching the tadpole is incapable of feeding, and subsists on the reserve material stored up in the yolk-cells. By the time it has reached a length of 8 mm., a deep depression of the ectoderm is formed on the lower side of the fore-part of the head, and this meets and fuses with the anterior end of the enteron. Soon afterwards, the wall dividing stomodæum from enteron is perforated, and the mouth is thus established. The epiblastic invagination is the **stomodæum**; it forms the lining epithelium of the buccal cavity, and an outgrowth from its roof forms the **pituitary body**. At the hind end of the body the anus was formed at an earlier stage by a smaller epiblastic invagination, the **proctodæum**.

The liver is formed at an early stage as a hollow outgrowth of the ventral wall of the enteron, reaching back into the mass of yolk-cells (fig. 63, *li*). The walls of the outgrowth are thickened and thrown into numerous folds, the whole organ is surrounded and its folds penetrated by a vascular connective tissue, and is converted into the glandular substance of the liver; the proximal end of the hollow outgrowth persists as the bile-duct.

The pancreas is formed as a pair of diverticula of the gut close behind the liver. At first its duct opens directly into the gut, but later it is shifted to open into the bile-duct.

The cloacal bladder is formed, late in larval life, as a ventral outgrowth from the hind end of the enteron.

The gill-slits are indicated, just before the larva is hatched, by a series of paired lateral outgrowths of the hypoblastic epithelium lining the anterior part of the enteron, or, as we may now call this region, the pharynx. Three anterior pairs are first formed, and two posterior pairs appear successively after short intervals of time, making five pairs in all. These outgrowths are shown in fig. 64. Each outgrowth is

a vertical fold of hypoblast, which extends from the pharynx

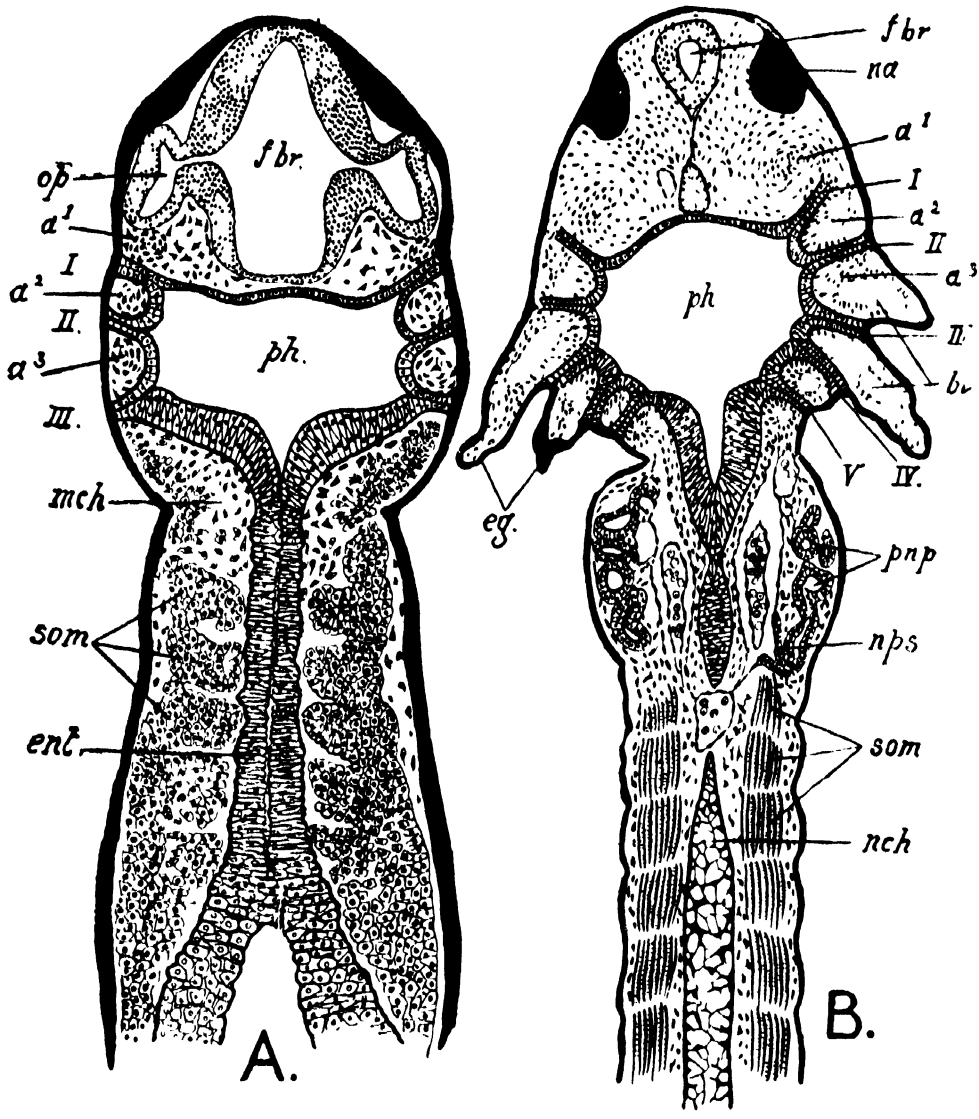


Fig. 64

A. Horizontal section through an embryo frog some time before hatching, showing the optic vesicles springing from the sides of the fore-brain, the three anterior pairs of gill-slits, and five pairs of mesoblastic somites. *B*. A similar section through a tadpole shortly after hatching. The head is cut in a lower plane than in *A*, so only a small part of the anterior end of the brain appears in the section. a^1, the mandibular arch; a^2, the hyoid arch; a^3, the first branchial arch; *bv*, blood-vessel in first and second branchial arch; *eg*, external gills; *ent*, enteron; *fbr*, fore-brain; *mch*, branching mesenchyme cells; *na*, nasal pits; *nch*, notochord; *nps*, peritoneal funnel *op*, optic vesicle; *ph*, pharynx; *pnp*, pronephros; *som*, mesoblastic somites which in *B* are converted into muscle. *I*, mandibulo-hyoid slit; *II*, hyo-branchial slit; *III-V*, branchial slits.

to the surface epiblast, and meets and fuses with the deeper

layer of the latter. At first the two layers of the folds are in close contact with one another. The result of the outgrowth of the five pairs of gill-pouches is the formation of four pairs of visceral or gill-arches lying between them. The external wall of each arch is covered by epiblast, its internal, anterior, and posterior walls by hypoblast. An arch is also formed as a thickening in front of the first gill-slit, and a similar but imperfectly defined arch behind the fifth gill-slit, making six arches in all on each side of the throat. The first is the **mandibular arch**. Subsequently a bar of cartilage is developed in it, which undergoes peculiar changes, and gives rise to the jaws. The second arch is the **hyoid**, the remainder are the first, second, third, and fourth **branchial arches**, respectively. The first gill outgrowth is the hyomandibular cleft. Lying between the mandibular and hyoid arches, it corresponds to the spiracular cleft of the dogfish, but it never acquires an opening to the exterior in the frog. In the succeeding stages it recedes from the epiblast, acquires a wide lumen, and eventually gives rise to the tympanic cavity and Eustachian passages of the adult. Thus we learn that the last-named structures are the homologues of the spiracle of the dogfish. The remaining outgrowths are the branchial clefts, and they all acquire openings to the exterior. The second and third clefts open first, the first somewhat later, and the fourth last of all.

At the time of hatching, the first and second pairs of branchial arches bear each a branched and richly ciliated process or external gill, and somewhat later, similar gills are developed on the third branchial arches. After the gill-slits have opened to the exterior, these external gills shrivel up and are replaced by new external gills formed lower down on the branchial arches.

The lungs are formed from the ventral wall of the enteron, immediately behind the pharynx. They appear quite early in larval life, at about the time of hatching, but for some time are very small and functionless. In later larval life they extend as a pair of thin-walled sacs into the cœlomic cavity, receive a special blood supply and function as respiratory organs.

The mesoblast gives rise to the musculature, the cœlomic epithelium, the skeleton, and the reproductive, vascular, and

excretory systems. The formation of the mesoblastic somites, or myotomes, has already been described. When some fourteen of them are formed, the cells of the most anterior myotomes begin to elongate in a longitudinal direction, each cell becoming cylindrical in shape, and extending for the whole length of the myotome. The process of differentiation continues, and the myotomes are eventually transformed into the trunk muscles. In the tail of the tadpole, the myotomes are very conspicuous, and are bent, like those of Amphioxus, into a V shape, with the angle directed towards the head (fig. 65).

The lateral plates of mesoblast, as has been seen, are

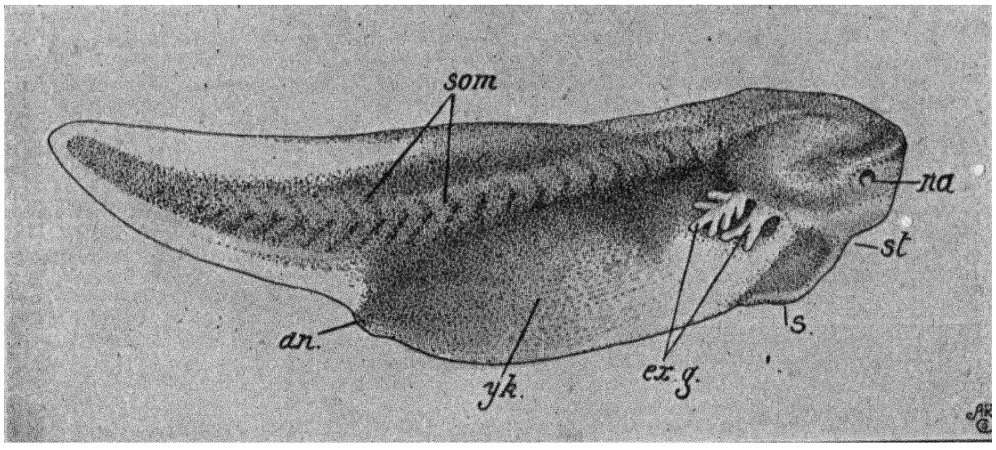


Fig. 65

A tadpole of the frog at the time of hatching. *an*, anus; *ex.g*, external gills *na*, nasal pit; *s*, sucker; *som*, somites, *st*, stomodæum; *yk*, yolk-sac.

divided, at an early stage, into a somatopleuric and a splanchnopleuric layer. The former becomes closely attached to the epiblast, and forms with it the body-wall. The latter becomes attached to the wall of the gut, and forms the musculature of the wall of the gut. The outermost cells of the splanchnopleur, and the inner cells of the somatopleur—*i.e.* those lining the cœlomic cavity—are converted into the cœlomic epithelium, and in tadpoles of about 10 mm. length, the first rudiments of the generative organs are formed as two tracts of modified cœlomic epithelium, lying one on either side of the mesentery, on the dorsal wall

of the peritoneal cavity. At first the genital ridges, as the primordia of the generative organs are called, are nothing more than modified tracts of the cœlomic epithelium which, elsewhere flattened, here becomes a columnar epithelium. Presently the columnar cells increase by division, and become several cells thick; a mesoblastic thickening is formed below each ridge, and they project into the cœlomic cavity, but it is not till the time of the metamorphosis of the tadpole into the frog that any distinction of sex can be detected. The further development of the ovaries and testes has been described in vol. i. p. 116.

In the tadpole, up to the time of the appearance of the limbs, the axial skeleton is only represented by the notochord, which consists, as in Amphioxus and the dogfish, of an elastic rod composed of vacuolated cells. At about the time that the rudiments of the hind limbs make their appearance the notochord is invested by a continuous cellular sheath, and a series of cartilaginous arches, the rudiments of the neural arches of the vertebræ, are formed in the mesoblastic tissue investing the spinal cord and rest upon the vertebral regions of the notochordal sheath, which has meanwhile become segmented into a series of nine rings followed by a posterior unsegmented portion, the urostyle. Shortly after the metamorphosis the nine rings in question are surrounded by as many thin bony rings, each of which is slightly constricted in its centre like a napkin ring. These are the true vertebral centra, and at the time of their first appearance they are amphicœlous, like the centra of a fish. But this condition does not persist long. An annular thickening of cartilage is formed from the notochordal sheath, in each intervertebral region, and this thickening extends inwards till it finally obliterates the notochord intervertebrally. The intervertebral thickenings are then divided into anterior and posterior portions which unite with and form the articular surfaces of two contiguous vertebral centra. The articular surfaces are subsequently ossified, and the original ring-shaped bone forming each centrum is greatly thickened, but a portion of the notochord remains and persists throughout life in the middle of each centrum.

The cranium is formed in the tadpole at an earlier stage than the vertebræ. It is at first entirely cartilaginous and

composed of a pair of curved longitudinal bars, the **trabeculæ cranii**, lying below the fore-brain, which are soon continued backwards into a pair of narrow **parachordal plates** lying on either side of the anterior end of the notochord. The middle and hinder parts of the trabeculæ diverge from one another, leaving between them a space through which the pituitary body passes. The parachordals unite with one another above and below the notochord, and their hinder margins grow up round the hind brain and eventually meet and fuse above to complete the occipital region of the cranium. The trabeculæ unite in front of the pituitary fossa to form the floor of the fore-brain,

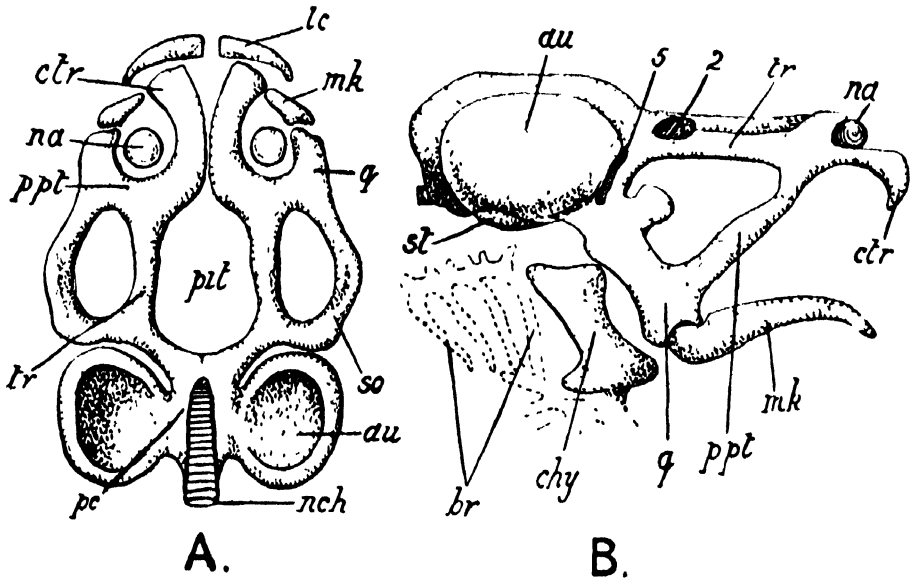


Fig. 66

A. The cranial and mandibular cartilages of a tadpole seen from above (semi-diagrammatic) *B*. The skull and branchial arches of an older tadpole seen from the side. *au*, auditory capsule; *br*, branchial arches; *chy*, ceratohyal cartilage; *ctr*, horns of the trabeculæ; *lc*, labial cartilage; *mk*, Meckel's cartilage; *na*, olfactory chamber; *nch*, notochord; *pc*, parachordal; *pit*, pituitary fossa; *ppt*, palato-pterygoid bar. *q*, quadrate; *so*, subocular arch; *st*, stapes; *tr*, trabeculæ; *2*, optic foramen; *5*, foramen for fifth nerve. (*B*, after Parker.)

and their margins, and those of the anterior part of the parachordals grow up to form the side walls of the cranium, but do not meet above, so that the roof of this region is imperfect. The pituitary fossa is eventually closed and the anterior ends of the trabeculæ are fused with the cartilaginous capsules of the olfactory organs, while the capsules of the auditory organs are fused with the upgrowths of the parachordals in the posterior region of the cranium. The various bones of the

skull are formed during the metamorphosis, except the sphenethmoid, which does not appear till the frog is nearly full grown. The parasphenoid is the first bone to be formed, and it is worth noting that the frontals and parietals, which are separate bones in many Amphibia, are formed as separate bones in the frog, and afterwards fuse together. The jaws are formed from the mandibular bar of the visceral series which, at first vertical, comes to lie beneath and parallel to the trabeculæ. It unites with the trabeculæ in front of and behind the eyeball, forming the so-called subocular bar, and its anterior end is segmented off as Meckel's cartilage, which is the basis of the lower jaw, while the subocular bar forms the basis of the upper jaw and the quadrate cartilage of the adult. During the metamorphosis these parts undergo rather complex changes of position which will not be detailed here. The upper jaw is completed by the formation of the premaxillæ and maxillæ in the membrane lying outside the subocular bar, and the palatine and pterygoid are formed, also in membrane, in close connection with the anterior attachment of the bar to the trabecula.

The hyoid and branchial bars undergo complex changes in connection with their primary functions as supports to the gill-arches. Eventually they degenerate and form the hyoid apparatus of the adult, the anterior end of the hyoid bar becoming attached to the skull and forming the so-called anterior cornu of the hyoid.

The history of the vascular and excretory systems, though important and capable of being treated at great length, can only be briefly described in this place. Their development is very clearly explained in Marshall's book on the frog.

The heart appears early in development, after the neural folds are closed, but some time before hatching. It is at first a straight tube, but soon becomes twisted to form a single turn of a spiral, and divided by constrictions into chambers which form the auricles and ventricle. The auricle is at first single, and later is divided into two by a septum which grows down from its dorsal wall. The formation of the heart is closely connected with the formation of the pericardial cavity.

In the region of the pharynx the lateral sheets of mesoblast, prior to the time we are considering, have not extended to the mid-ventral line and have not split into somatopleur and

splanchnopleur. They now grow down and unite below, and at the same time their lower borders are split so that two cavities are formed separated in the middle line by a partition. These cavities are a part of the general cœlom and are continuous with it posteriorly. A space is left between the splanchnopleur and the ventral wall of the throat in which a few scattered irregular cells, derived from the mesoblast, make their appearance.* After a time these cells unite to form a

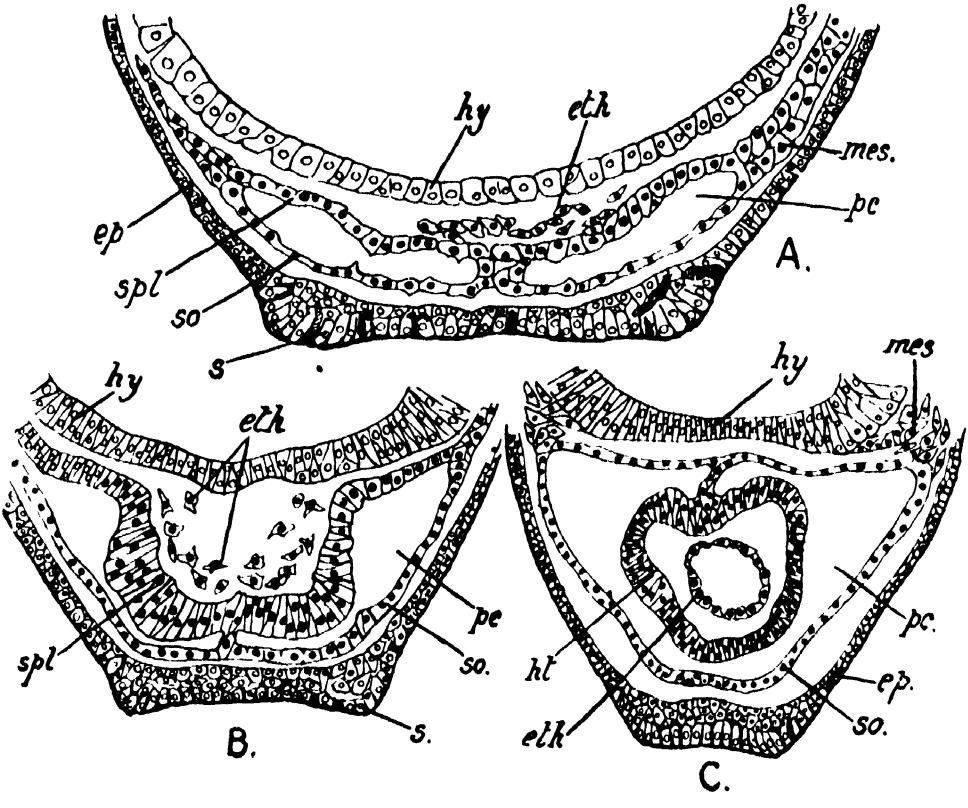


Fig. 67

A, *B*, and *C*. Transverse sections through the ventral wall of the throat of embryos of different ages, showing successive stages in the development of the heart. *ep*, epiblast; *hy*, hypoblast; *mes*, mesoblast; *eth*, endothelial lining of heart; *ht*, heart; *pc*, pericardial cavity; *s*, sucker; *so*, somatic layer of mesoblast; *spl*, splanchnic layer of mesoblast, eventually forming the wall of the heart.

tube, and become the endothelial lining of the heart. Meanwhile the inner or splanchnopleuric layer becomes thickened, and its sides are folded in towards the centre so as to enclose the scattered cells. As the endothelial tube is formed, the folds meet and unite above it, as is shown in fig. 67, so that

* I am unable to find any support for the view, maintained by some authors, that these cells are formed from the hypoblast.

we have a cœlomic cavity lying on either side of a median double tube, the heart. The layer of splanchnopleur surrounding the endothelial tube gives rise to the muscular tissue of the heart and to that part of the endothelial lining of the pericardial cavity which invests the heart. The two cœlomic cavities become the pericardial cavity. They are at first separated from one another by the vertical partitions attached to both the dorsal and the ventral side of the heart, but after a time the ventral partition disappears and the heart is suspended only by the dorsal partition or mesocardium, and the two pericardial cavities coalesce ventrally. The communication between the pericardial cavity and the general cœlom behind is obliterated on the formation of the great veins bringing blood to the heart. These are two large **vitelline veins** running along the sides of the liver and bringing blood from the yolk-mass, and the **ductus Cuvieri** bringing blood from the dorso-lateral regions of the body. These veins, uniting just before they reach the heart, form the sinus venosus. The ductus Cuvieri of each side receives an anterior and a posterior cardinal vein. The former persist in the adult as the superior venæ cavæ, but the posterior cardinals undergo great modifications, their anterior ends atrophy on the formation of the inferior vena cava, and their posterior ends share in the formation of the renal portal veins. Thus the tadpole passes through a stage in which its venous system is arranged on the same plan as that of the dogfish.

The arterial system during the time that the tadpole is breathing by gills, is even more remarkably piscine in its arrangement. The heart is continued forwards beneath the pharynx as the cardiac aorta—the future truncus arteriosus. After a short course this vessel divides into right and left branches, and these immediately subdivide into vessels running up the gill-arches. By the time that the three pairs of external gills are established, we find the arrangement shown in fig. 68, *A*. The truncus has divided into three pairs of afferent branchial arteries. One pair passing up the first branchial arch, supplies the first pair of external gills. The second and third pairs similarly pass up the second and third branchial arches, and supply the second and third pairs of external gills. There are no afferent arteries for the mandibular and hyoid arches, and as yet there is no afferent artery

for the fourth branchial arch. (Prior to this, there was a stage when only two external gills were present, and only two pairs of afferent arteries running in the first and second branchial arches.)

The blood passes through capillary loops in the external gills, and is collected and brought back to the right and left branches of the dorsal aorta by three pairs of efferent branchial vessels. Though there are no afferent arteries in the mandibular and hyoid, each of these arches is furnished with a small efferent artery, and there is also an efferent artery in the fourth branchial arch, which, even at this early stage, sends out a branch towards the lungs.

When the gill-slits open to the exterior, and a new series of external gills is formed, the afferent arteries send out vessels to them, and the blood is returned from them to the efferent arteries. The fourth pair of branchial arteries supplies the fourth gill-slit, and its corresponding efferent vessel becomes functional. Less and less blood passes into the external gills, and eventually they shrivel up and disappear. The circulation is now very like that of the dogfish, except that there are four afferent branchial vessels instead of five. There is a very important difference, however, in the fact that the lungs of the tadpole are by this time fairly well-developed, and are supplied with blood from branches of the fourth pair of efferent arteries, this, of course, being oxygenated blood which has passed through the gills. From the lungs the blood is returned to the heart by two pulmonary veins, which unite and open into the left division of the auricle, cut off from the originally single auricular cavity by the downgrowth of a vertical septum from its dorsal wall.

Soon after the secondary gills are established, and the circulation has assumed the arrangement just described, a direct communication, shown at *i* in fig. 68, is established between each afferent artery and the ventral end of its corresponding efferent vessel. Thus a certain amount of blood that has not passed through the gills, and therefore is not oxygenated, passes into the general circulation and to the lungs. At first the amount is very small, but at the time of the metamorphosis these communicating vessels are enlarged, and an increasing amount of blood flows through them without having first passed through the gills. The

last named, receiving an ever-diminishing quantity of blood, shrivel up, the gill-slits are closed, the lungs increase in size and importance, and more blood passes to them through the pulmonary arteries, and also to the skin through the

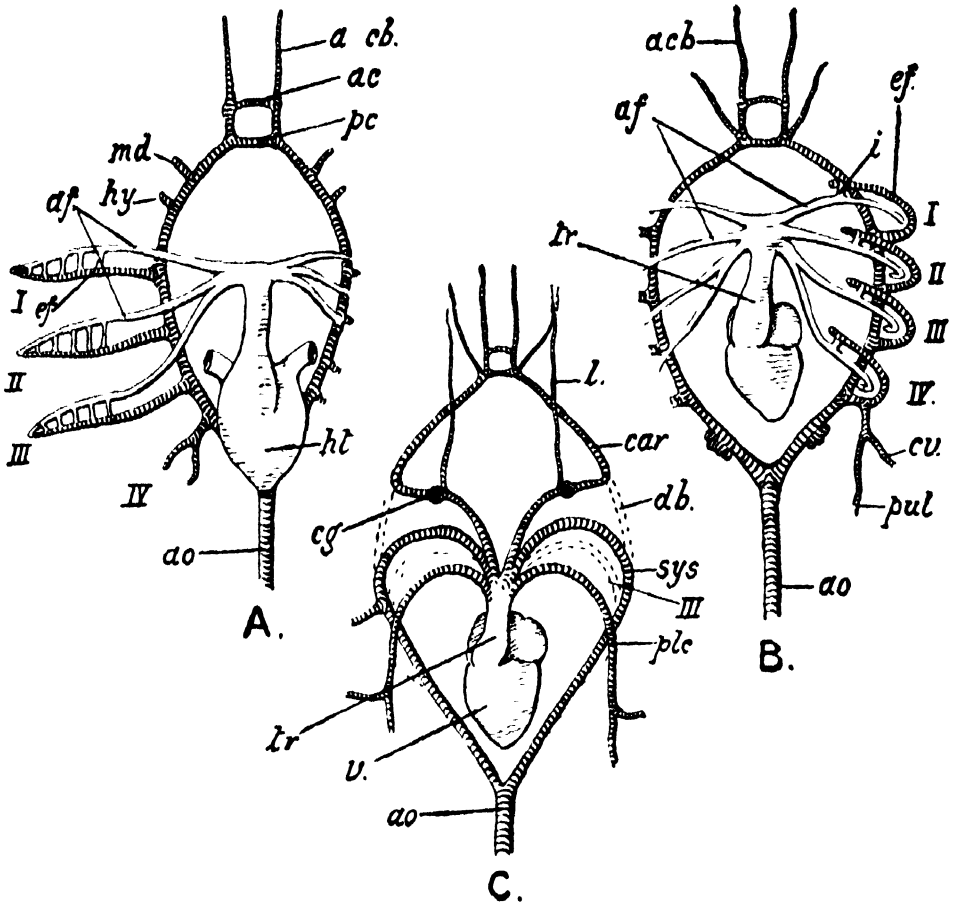


Fig. 68

A. Diagram of the heart and chief arteries of a tadpole when three external gills are present. *B*. Diagram showing the arrangement of the vessels when the tadpole is breathing by secondary gills. *C*. Diagram showing the derivation of the adult circulation from *C*. *ac*, anterior commissural vessel; *a.cb*, anterior cerebral artery; *af*, afferent branchial arteries; *ao*, dorsal aorta; *car*, carotid artery; *cg*, carotid gland; *cu*, cutaneous artery; *db*, ductus Botalli; *ef*, efferent branchial arteries; *ht*, heart; *hy*, efferent hyoidean artery; *i*, connecting vessel; *l*, lingual artery; *md*, efferent mandibular artery; *pc*, posterior commissural vessel; *plc*, pulmo-cutaneous arterial arch; *pul*, pulmonary artery; *sys*, systemic arch; *tr*, truncus arteriosus; *v*, ventricle. *I-IV*, branchial aortic arches.

cutaneous branches of the pulmonary arteries. The changes that lead to the adult condition are as follows:—

The first aortic arch, as we may now call it, becomes the carotid arch of the adult, the carotid gland being formed

from a **rete mirabile** or plexus of blood-vessels in connection with its communicating vessel. The connection between the first and second aortic arches persists in the adult as the ductus Botalli.

The second aortic arch retains its connection with the aorta, and becomes the systemic arch of the adult.

The third aortic arch loses its connection with the aorta, and disappears altogether.

The fourth aortic arch becomes the pulmo-cutaneous artery of the adult, after losing its connection with the aorta.

Thus the arrangement of the arteries in the adult frog is brought about by the modification of an arrangement characteristic of fishes—is due, in fact, to a branchial respiration having preceded a pulmonary respiration. The same may be said of the arterial system of all higher vertebrates, though in them the changes are greater, and a branchial respiration is not established at any period of their existence, the gill-slits developed in their embryos being functionless.

The excretory system of the tadpole makes its appearance at the time when the neural folds are closing in, some considerable time before hatching. It is formed as a thickening of the somatic layer of the lateral mesoblast opposite the second mesoblastic somite. The thickening is continued backwards in the substance of the somatopleur as far as the seventh somite, and its anterior end becomes enlarged. Both the enlargement and its posterior continuation become hollow, the former becoming the **pronephros** or head kidney, the latter the **segmental duct**. The pronephros is divided into three tubes, which grow towards and open into the cœlom by ciliated funnels or **nephrostomes**. These tubes, and the portion of the segmental duct immediately behind them, grow in length, become much convoluted, and are invested by a capsule of somatic mesoblast. At the same time the splanchnopleur opposite the pronephric funnels forms an irregular sacculated outgrowth, the **glomerulus**, which becomes connected with and filled with blood from the dorsal aorta. At the time of hatching, the segmental duct becomes attached to the wall of the cloaca, and opens into it.

Some time after this, when the tadpole is about 12 mm. in length, the middle kidney, **mesonephros**, or Wolffian body, is

formed as a series of paired solid thickenings of the somatic mesoblast to the inner sides of the segmental ducts. The solid thickenings are converted into coiled tubules which grow towards and acquire openings into the segmental ducts. Their distal ends dilate to form hollow vesicles, each of which is invaginated by the ingrowth of a small plexus of blood-vessels, and gives rise to the structure known as a Malpighian

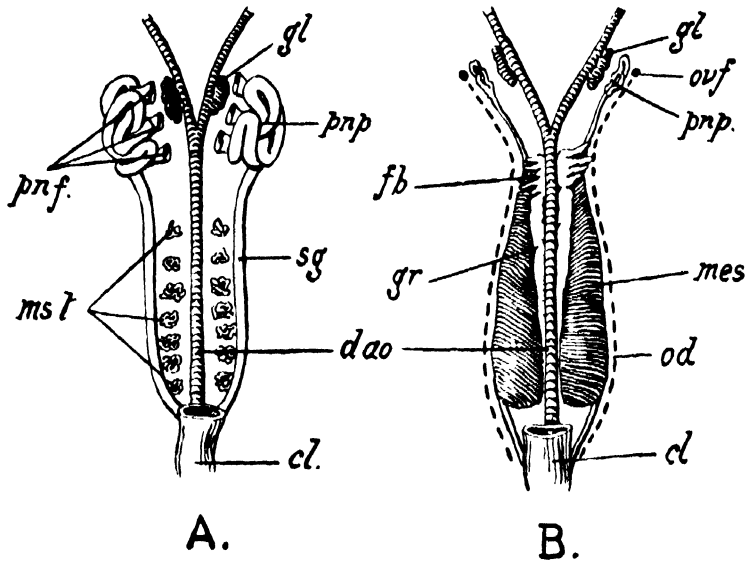


Fig. 69

A. Diagram of the excretory system of a tadpole about 12 mm. long, showing the pronephros and origin of the mesonephric (Wolffian) tubules. *B*. Diagram showing the kidneys and reproductive organs of a frog at the end of the metamorphosis. The broken line represents approximately the position of the strip of peritoneal epithelium which gives rise to the oviduct. *cl*. cloaca; *d.ao*, dorsal aorta; *fb*, fat-body; *gl*, glomerulus; *gr*, genital ridge; *mes*, mesonephros; *ms.t*, mesonephric tubules; *od*, oviduct; *ovf*, position of oviducal opening; *pnf*, pronephric funnels; *pnp*, pronephros; *sg*, segmental duct.

body. The tubule grows out beyond the Malpighian body towards the peritoneal epithelium, fuses with it and opens into the cœlom by a ciliated funnel or nephrostome. According to Marshall, the nephrostomes afterwards lose their connection with the mesonephric tubules and open into the renal veins. The whole organ is compacted by the ingrowth of abundant vascular tissue, the mesonephric tubules increase in number and branch freely, and a solid glandular mass, the kidney or mesonephros of the adult frog, is formed on either side. Thus before and nearly up to the time of metamorphosis the

excretory organs of the tadpole consist of a pronephros with its duct, the segmental duct, on either side of the body, and a compact mesonephros whose numerous tubules open into the lower ends of the segmental duct. Towards the time of the metamorphosis the pronephros is aborted, and both it and the anterior part of the segmental duct eventually disappear. The posterior end of the segmental duct persists in both sexes as the mesonephric or Wolffian duct, which in the female functions as the ureter, but in the male serves also as the genital duct, the testes being connected with the kidneys by the formation of the vasa efferentia.

In the dogfish the segmental duct has been described as splitting longitudinally to form the Wolffian and Mullerian ducts on either side, the latter persisting to form the oviducts of the female, but disappearing, except for a small anterior rudiment, in the male. In the frog the oviducts are not formed till the end of the metamorphosis, when all four limbs are well developed and the tail is being absorbed. They are not split off from the Wolffian ducts, but arise independently as differentiated tracts of the peritoneal epithelium, which are converted first into grooves and eventually into canals. The anterior end of each oviduct, which becomes the oviducal funnel of the adult female, is formed as a groove of peritoneal epithelium on the ventral side of the degenerating pronephros. The groove is lined by a well-marked columnar epithelium, which is a modification of the elsewhere flattened peritoneal epithelium. In a frog which has nearly lost its tail, the groove may be traced backwards for some little distance, and then it becomes a canal ending in a solid thickening of the peritoneum. This thickening is continued backwards towards the cloaca as a strip of columnar epithelium lying on the outer border of the kidney. The strip is gradually converted into a thickening, a lumen is formed in it, continuous with the lumen of the short canal of the anterior end, and the whole structure becomes a tube, the hinder end of which acquires an opening into the cloaca at a much later date. The groove at the anterior end of the tube persists as the oviducal funnel, after undergoing a considerable change of position due to the growth of adjacent organs. The oviduct is formed as above, both in male and female frogs, but it never reaches a higher degree of development in the male. It persists, however, and may be

recognised in the adult as a linear thickening of the peritoneum lying at a little distance from the outer border of the kidney and extending some way in front of it. In the female the posterior part of the oviduct grows very much in length, is thrown into many convolutions, and its walls in the middle part of its course become thick and glandular. In the hinder part of its course the walls remain thin, but the diameter is greatly enlarged to form the so-called uterus.

The epiblast of the embryo gives rise to the external epithelium (continued at the mouth and anus into the stomodæum and proctodæum), the central nervous system, and the organs of special sense. The infolding of the neural folds to form the neural tube, the enlargement of the anterior end of the latter, and its division into fore, mid, and hind brain has already been described. The fore-brain becomes the thalamencephalon of the adult. Its sides are thickened, but its roof and floor remain thin, and in consequence its cavity, the third ventricle, is narrowed from side to side, but has considerable vertical depth. The roof grows out to form the pineal body, the floor is produced into the infundibulum which meets and becomes attached to the pituitary body. The cerebral hemispheres are formed as a pair of hollow outgrowths of the anterior end of the primitive fore-brain or thalamencephalon, and the olfactory lobes are in turn formed as outgrowths from the cerebral hemispheres.

The floor of the mid-brain becomes very thick from the development of two diverging tracts of nerve fibres, leading from the hind-brain to the fore-brain; these are the crura cerebri. The roof of the mid-brain grows out into a pair of hollow ovoid projections, the corpora bigemina, and its cavity, reduced by the thickening of the floor and sides, remains as the Sylvian aqueduct or "iter."

The floor and sides of the hind-brain are much thickened, but the roof becomes very thin except for a strip in front, which is thickened to form the cerebellum. The thin hinder part of the roof, covering in the wide cavity of the fourth ventricle, is thrown into numerous folds, into which a vascular membrane penetrates, forming the choroid plexus of the fourth ventricle.

The walls of the spinal cord are much thickened, and undergo histological and other changes which cannot be

detailed here. The lumen of the canal is much reduced, but persists as the central canal of the spinal cord.

The cranial and spinal nerves are formed in close connection with the neural tube. The dorsal roots of the spinal nerves, and the roots of the vagus, auditory, facial, and trigeminal nerves are formed from the deeper or nervous layer of the epiblast at a very early stage before the neural folds have closed in. They are first recognisable as outgrowths of the lateral edges of the neural plate, and after the neural canal has closed they appear to arise from a ridge-like thickening along the dorsal side of the neural tube, known as the neural crest. The ventral roots of the spinal nerves arise later as ventro-lateral outgrowths of the spinal cord which soon become connected with the dorsal roots.

The organs of special sense are formed wholly or in part as paired involutions of the deeper or nervous layer of the epiblast. Their development is rather complicated, and can only be touched upon here.

The olfactory organs are formed as a pair of pits at the anterior end of the head, in which both layers of the epiblast are involved. The deeper parts of these pits expand to form the olfactory chambers, their walls are thrown into numerous folds, and their openings persist as the anterior nares. The posterior nares are formed as downgrowths or diverticula of the olfactory chambers, which grow towards and fuse with the roof of the pharynx and presently open into it.

The auditory organs are formed as a pair of invaginations of the nervous layer of the epiblast at the sides of the hind part of the head. In this case the outer or epidermic layer of the epiblast does not share in the invagination, so the auditory organs never open to the surface. Each invagination becomes a pit, which is converted into a closed vesicle and loses its connection with the epiblast. The vesicles become surrounded by mesoblast, from which the cartilaginous auditory capsules are developed. The walls of the epiblastic vesicles are converted into the membranous labyrinth, and after the metamorphosis the hyomandibular cleft enters into relations with the auditory organ, and forms the middle ear or tympanic cavity and the Eustachian passages. In the case of the organs of sight, only a part of the eye—viz. the lens—is formed from the surface epiblast. The retina and the pigmented coat of

the choroid are formed from paired outgrowths of the fore-brain known as the optic-vesicles. These vesicles appear early in development, soon after the closure of the neural folds, as tubular evaginations of the fore-brain. The evaginations grow out towards the sides of the head, their distal ends become swollen and their proximal ends constricted, so that each has the form of a hollow bulb attached to the fore-brain by an obliquely directed hollow stalk. The outer half of the bulb—*i.e.* the half nearest to the surface epiblast—then becomes thickened, and is first flattened and then folded back within the inner thin-walled hemisphere, so that the original cavity of the vesicle is nearly obliterated (fig. 64, *A*). In this way a two-layered cup, the **optic cup**, is produced. Meanwhile the nervous layer of the epiblast opposite the optic cup has become thickened, so as to form a solid mass of cells projecting into the mouth of the cup. The thickening separates from the epiblast, acquires a central cavity, and lies in the mouth of the optic cup. At first a hollow vesicle, it becomes converted into the transparent lens by subsequent thickening and histological differentiation of the cells forming its posterior wall (fig. 70, *L*).

The optic cup is surrounded by a mesoblastic investment, the inner layers of which become the choroid and the outer layers form the sclerotic. At the mouth of the cup the mesoblastic investment pushes its way as a double layer between the lens and the surface epiblast. The inner of these two layers forms the iris, the outer gives rise to the cornea, while the epiblast remains as the anterior corneal epithelium. The thinner outer wall of the optic cup becomes the pigmented epithelium of the choroid, and the thicker inner wall lining the cavity of the cup becomes the retina. The vitreous humour filling the cavity of the cup between the retina and the lens is formed by an ingrowth of mesoblast through a gap produced on the under side of the optic cup by the peculiar way in which the primary optic vesicle is infolded to form a two-layered cup. The stalk of the optic cup is at first hollow, but its lumen is afterwards obliterated by the outgrowth of the fibres of the optic nerve from the brain to the retina. The full development of the eyes is not attained till the close of the metamorphosis, these organs remaining in an imperfect condition throughout the larval stage of existence.

A comparison of the development of the frog with that of Amphioxus shows many points of resemblance in the earlier stages, but in the later stages there are numerous differences, attributable to the different grade of organisation and greater complexity of structure of the mature frog. In a comparison of the development of the frog with that of higher vertebrates the resemblances would be more obvious in later stages, in some

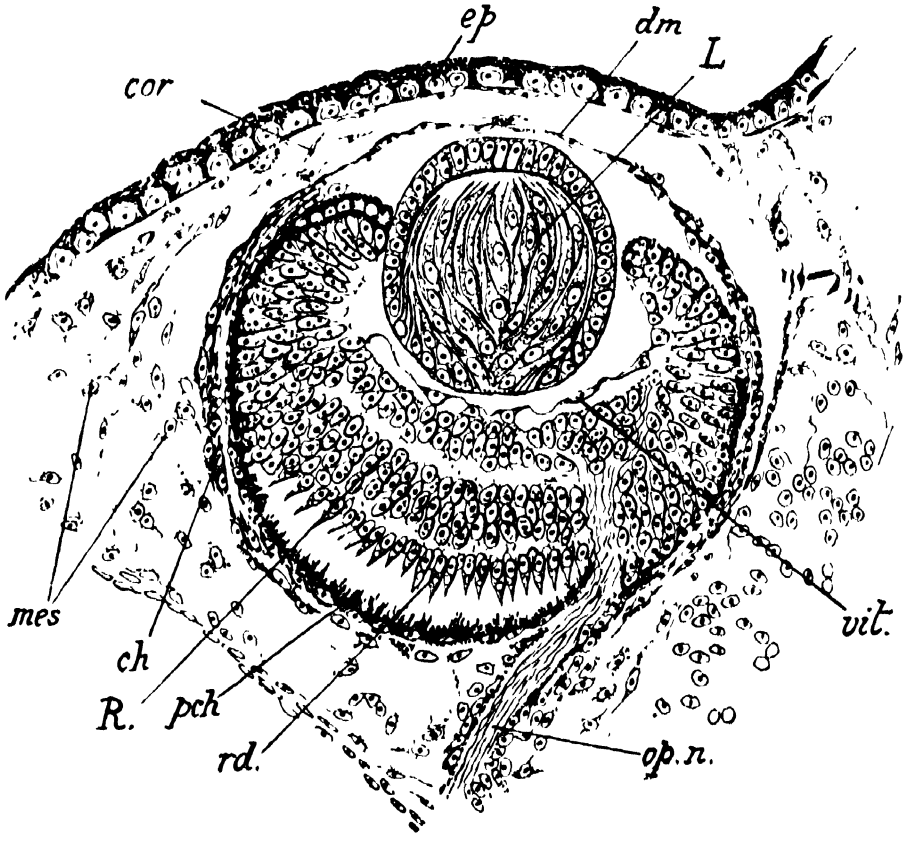


Fig. 70

Section through the eye of a tadpole at the time when the operculum is forming, much magnified. *ch*, choroid; *cor*, mesoblast cells which will give rise to the cornea; *dm*, Descemet's membrane; *ep*, pigmented external epithelium; *L*, lens; *mes*, branched mesoblast cells; *op.n*, optic nerve; *pch*, pigmented epithelium of the choroid; *R*, retina; *rd*, rods and cones pulled away from the pigmented epithelium of the choroid by contraction of the preparation; *vit*, cells of the vitreous humour.

organs, such as the eye, amounting almost to identity. Thus we should find throughout the vertebrate series that the axial skeleton is first formed as a notochord, which subsequently becomes surrounded with a cartilaginous sheath, and this in turn is supplanted by bony rings or vertebræ. In the skull we should find a cartilaginous cranium, formed from

parachordals and trabeculæ cranii, which is afterwards strengthened and replaced to a greater or less degree by membrane and cartilage bones. We should find gill-slits separated by gill-arches in every embryo, and though the gill-slits no longer function as respiratory organs, we should find that the blood-vessels were first correlated to the gill-slits, and therefore had a piscine arrangement, which was gradually altered and modified into the adult condition. Similarly, the history of the brain and spinal cord, and of the excretory and generative organs, would show a close correspondence to the history of the same organs in the frog, but in every case the greater complexity and higher grade of organisation would manifest itself at an earlier or later developmental stage, and would involve some departure from the more simple course of events observed in the frog. This close correspondence between the developmental histories or ontogenies of the members of different classes of vertebrates affords one of the strongest arguments in support of the doctrine of evolution. The fact that a frog, a lizard, a bird, and a mammal, even man himself, passes through a stage in which there are gill-slits, with heart and arteries bearing the same relation to them that they do in a fish, is not, perhaps, proof positive, but is very strong evidence of the descent of each from a fish-like ancestor. In the frog, the fish-like ancestor seems to be revealed to us in the shape of the tadpole. The more we reflect upon it, the more we are convinced that, broadly speaking, ontogeny is a recapitulation of phylogeny, the history of the individual is a synopsis of the history of the race. But though it is true in the main, this principle must not be pushed too far. It would be an error to suppose, for instance, that the tadpole represents, with any degree of exactitude, the fish-like ancestor of the Amphibia. It only represents its general plan and degree of organisation. It would be idle to suppose that changes which have occupied ages could be faithfully represented in a development occupying a few weeks of time, or to ignore the fact that embryos, and even larval forms like the tadpole, exist under very different conditions of life to those under which an ancestor, of a corresponding degree of organisation, lived, and must be modified in many ways to enable them to exist under those conditions. Every individual ontogeny is ab-

breviated, and profoundly modified. Organs which appeared late in the history of the species may appear precociously in the embryo; many of the steps of evolution are dropped altogether out of ontogeny, and many new structures and adaptations are intercalated, which can have no phylogenetic significance. At the best, then, embryology is only an aid to the interpretation of the history of animal organisation, but taken in conjunction with the comparative anatomy of adult forms, it is a very powerful aid indeed. And the student should bear in mind that the life-history of every animal is, in the strictest sense of the word, an *evolution*, a gradual becoming of the evidently complex and heterogeneous from the apparently simple and homogeneous fertilised ovum. Nor should it be forgotten that, simple and homogeneous as the ovum appears to us, it contains within itself the potentiality of the future animal. Many ingenious theories have been framed which, by attributing a great complexity of structure to the germ-cell, undertake to explain the manner of its development into an adult animal. But they are necessarily extremely hypothetical and speculative, for observation shows no complexity beyond that of an ordinary undifferentiated cell, a corpuscle of protoplasm containing a nucleus. None the less, we cannot escape the conviction that the constitution of the germ-cell cannot be so simple as it appears to us, but must be of a kind adequate to produce the observed phenomena of development.

CHAPTER XXVIII

THE MAMMALIA

After studying the anatomy of Amphioxus, the dogfish and the frog, in some detail, we have gained a good general idea of vertebrate organisation. In studying a higher vertebrate, a reptile, a bird, or a mammal, we should find the same general plan of structure as in the frog. The same organs are present having the same general relations to one another, but differing often to a considerable extent in detail, and in each case there are certain features characteristic of the class to which the animal belongs.

Space forbids any reference to reptiles and birds, and for the same reason nothing more than enumeration of the most characteristic features of a mammal can be attempted here.

Any mammal of convenient size for dissection may be taken as a type. A rabbit is commonly chosen because it is easy to obtain, but a rat, or a small carnivore, such as a cat, would serve equally well.

The following external features are characteristic of a mammal :—

The body is furnished with an external covering of **hair.** In some mammals—*e.g.* the porpoise—the hairy covering may be so much reduced as to be practically absent, but even in such cases a few scattered hairs are always discoverable. True hair must be distinguished from the chætæ and bristles so commonly found in invertebrates. A hair is an epidermic structure implanted in an invagination of the skin known as the **hair-follicle.** The projecting part of the hair is covered by a so-called cuticle formed of a layer of imbricated scales. Within this is a fibrous or cortical layer formed of very elongated epidermic cells, and the centre is occupied by a cellular medulla or pith. The root of a young hair is bulbous and has a small vascular core derived from the mesoblast, but the shaft of the hair is non-vascular. The general structure

of a hair and its relation to the hair-follicle is shown in fig. 71. The sebaceous glands near the upper end of the follicle should be noted. They secrete a fatty substance which lubricates the hair and prevents it from becoming dry and brittle.

The sweat glands, the tiny mouths of which are scattered over the skin, are as characteristic of mammals as the hairy covering. They are formed as downgrowths of the Malpighian layer of the epidermis which extend into the vascular corium

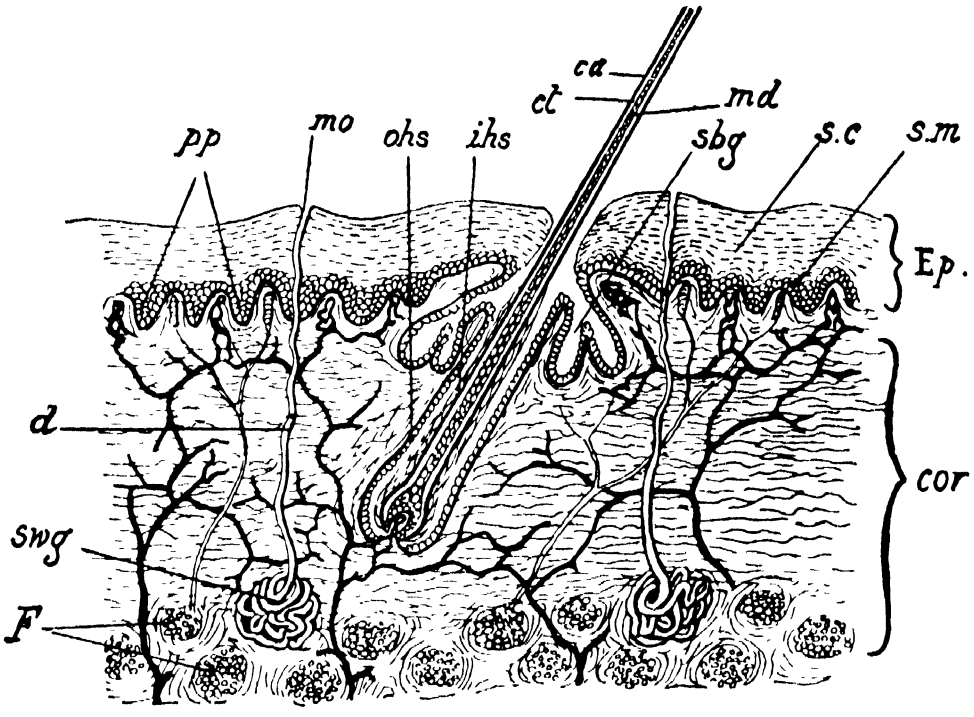


Fig. 71

Diagrammatic section through the skin of a mammal, showing a hair in its follicle, and two sweat glands. *ca*, cuticle; *cor*, corium; *ct*, cortex of hair; *d*, duct of sweat gland; *Ep*, epidermis; *F*, fat lobules; *ihs*, inner hair sheath; *md* medulla of hair; *mo*, mouth of sweat gland; *ohs*, outer hair sheath; *pp*, papillæ of Malpighian layer; *sbg*, sebaceous gland; *sc* stratum corneum of epidermis; *sm*, stratum Malpighii of epidermis, *swg*, sweat gland.

underlying the epidermis. Their inner ends are thrown into many convolutions, and form a tightly coiled knot; the distal ends retain their connection with the surface; a lumen is developed, and the epithelium lining the coiled end forms the glandular part; the straight tube leading to the exterior, the duct of the sweat gland.

The mammary glands, from which the class Mammalia

derives its name, are situated upon elevations of the skin known as teats. The number and position of the teats differ very much in different orders of mammals, their number bearing a pretty constant relation to the number of young produced at a birth.

Typically the teats are numerous, and arranged in pairs along the ventral surface of the thorax and abdomen, and in those cases where few are present, the reduction takes place at one or the other end of the series. In the rabbit there are five pairs of teats, the first pair opposite the elbow, the last pair in the inguinal region, between the thighs. In man and apes only one pair of thoracic mammæ are present, in sheep and oxen only the posterior pairs of inguinal teats are developed. The mammary glands are formed, like the sebaceous and sweat glands, as ingrowths of the Malpighian layer, which penetrate the corium, acquire a lumen, and open to the exterior. There are good grounds for regarding the mammary glands as specially modified skin glands, like those already mentioned. The tubules of the mammary glands are branched and differentiated into terminal secretory lobules or acini, ducts, milk reservoirs, etc. In the male, the teats and mammary glands are rudimentary and functionless.

The newly-born offspring would be unable to suck milk if they were not furnished with freely movable lips ; this feature is preserved in adult life, and is of great advantage in many species, as anyone will realise who watches a herbivorous animal cropping grass.

The external nares and eyes of mammals occupy the same relative positions as in lower vertebrates, and the eyes have the same essential structure and the same arrangement of eye-muscles. The ears offer characteristic features. The tympanum or drum of the ear is not situated on the surface, as in the frog, but is placed at the bottom of a tube-like depression, the **external auditory meatus**, and the entrance to the meatus is guarded by a more or less considerable fold of tissue, the external ear or **pinna**. The external ears of the rabbit are of remarkable size, and, as is the case in most mammals, are freely movable by means of special muscles. In man the external ears are reduced, and have lost their mobility, but in a few individual cases a small amount of movement is possible.

With the exception of the lowest forms, mammals have no cloaca. The urogenital and rectal orifices are completely separated by a partition known as the **perinæum.**

An examination of the buccal cavity reveals several characteristic features.

The posterior nares do not open close behind the premaxillæ as in the frog, but are carried back by the development of a horizontal platform of bone formed from the maxillæ and palatines. This partition, the **hard palate**, is continued behind into a horizontal curtain of soft tissue, the **soft palate**, and thus the opening of the posterior nares is carried back to the throat.

The teeth are confined to the premaxillæ and maxillæ in the upper jaw, and in both jaws are ranged in a single series. They vary very much in shape and in number in different mammals, and their characters afford one of the surest guides in classification. In some forms—*e.g.* the armadillos and the dolphins—the teeth are approximately of the same shape; such a dentition is called **homodont.** But in most mammals the dentition is **heterodont**—*i.e.* the teeth are of different shapes in different parts of the jaw. Thus in the dog we find on each side of the upper jaw three chisel-shaped teeth or **incisors**, in the premaxilla; a large conical tooth, the **canine**, situated between the premaxilla and the maxilla; and six **premolar** and **molar** teeth, with prominent cusped crowns, in the maxilla. The teeth in the lower jaw correspond to those in the upper jaw, but there is an additional molar at the back of the series. All these teeth are implanted in bony sockets, from which they can easily be withdrawn in the dry skull. It can then be seen that they have fangs, which are single, and taper to a point in the incisors, canines, and first premolar, but are double in the second and third premolars, and triple in the fourth premolar and two molars. In the dog, as in the great majority of mammals, the permanent dentition just described is preceded by a temporary or **milk dentition**, in which the teeth are in pattern similar to, but in number fewer, than those of the permanent dentition. As a general rule, the incisors, canines, and premolars have milk predecessors; but the molars only appear in the permanent dentition. In the dog there is a slight exception to this rule, for the first premolar has no milk predecessor.

If we now examine the teeth of the cat, we find that they are not unlike those of the dog in shape, but are fewer in number. There are only three premolars and one molar in the upper jaw, and two premolars and one molar in the lower jaw on each side. The molar tooth of the upper jaw is small and rudimentary, but the third premolar is very large, has a sharp trenchant edge, and works against the similarly modified molar of the lower jaw. The arrangement of the teeth of a mammal may be represented by a dental formula, that of the dog being

$$I\frac{3}{3}\ C\frac{1}{1}\ PM\frac{4}{4}\ M\frac{2}{3},$$

in which the letters I., C., P.M., M., stand for incisors, canines, premolars, and molars. The upper row of figures shows the number of each kind of tooth in the upper jaw, the lower row the number in the lower jaw. As the teeth of the two sides of the mouth are similar, those of one side only are represented in the formula.

The dental formula of the cat is therefore

$$I\frac{3}{3}\ C\frac{1}{1}\ PM\frac{3}{2}\ M\frac{1}{1}.$$

The teeth of the rabbit differ a good deal in appearance from those of the cat and dog. They are implanted in sockets; but their bases do not taper off to form fangs, and their pulp-cavities are widely open below. The pulp remains active throughout life, and the teeth, as they wear away above, are constantly replaced from below.

The dental formula is

$$I\frac{2}{1}\ C\frac{0}{0}\ PM\frac{3}{2}\ M\frac{3}{3}.$$

The second incisors of the upper jaw are rudimentary, and are lodged in sockets immediately behind the large curved anterior incisors. The canines are absent, and the incisors are separated from the premolars by a wide space known as a **diastema**. The premolars and molars have flat grinding crowns, marked by transverse ridges, formed by the infolding of the enamel of their outer surfaces.

In the alimentary canal of mammals the stomach very rarely retains the primitive tubular shape seen in the dogfish and frog, but is generally transversely elongated, and it may be complicated by sub-division into several chambers, more especially in ruminating animals such as oxen. The large

intestine is also of considerable size and length, and in herbivorous animals a large diverticulum, the **cæcum**, is given off at the junction of the small with the large intestine.

The skeleton is well ossified throughout and presents many characteristic features. The vertebral column is divisible into distinct regions—viz. the cervical, dorsal or thoracic, lumbar, sacral, and caudal. The **cervical** vertebræ are seven in number in all Mammalia, with the following exceptions: sloths of the genus *Bradypus*, in which there are nine, *Cholepus Haufmanni*, also a sloth, in which there are six, and the *Manatee*, in which there are also six. This constancy is the more remarkable when the great differences in the length of neck of different mammals is considered. Even the long-necked giraffe and the whale, in which the neck is practically obsolete, have each seven cervical vertebræ. The cervical vertebræ have no free ribs attached to them, but a rib element is present fused to transverse processes springing from the centrum and the neural arch and forming with them the vertebral arterial canal.

The **dorsal** or thoracic vertebræ bear movably articulated double-headed ribs. Their number varies in different groups and even in closely-allied species, but commonly twelve or thirteen are present, as in the rabbit.

The **lumbar** vertebræ are those free vertebræ in front of the sacrum which do not bear ribs. They are generally to be distinguished by their size and their large flattened horizontal transverse processes. Under the name **sacral** are commonly included all those vertebræ which are fused together in the pelvic region. Properly speaking, only those vertebræ should be called sacral which are attached to the pelvis by the intervention of an expanded rib element. Of these there are, at the most, two in mammalia, and the fused vertebræ behind them belong, strictly speaking, to the caudal series.

The **caudal** vertebræ vary in number according to the length of the tail. When many are present they decrease in size and complexity from before backwards, and the hindmost of the series are represented only by elongated centra.

It is highly characteristic of the vertebræ of mammals that the vertebral centra, as well as the long bones, have separate terminal ossifications called **epiphyses** (this, however, is not the case in the lowest group of mammals, the *Prototheria*); that

the articulating surfaces of the centra are nearly flat, and that they are united to one another by a tough fibrous and elastic material forming the **intervertebral discs**. The notochord disappears entirely within the vertebral bodies, but remnants of it may be found in the intervertebral discs forming the so-called **nucleus pulposus**.

The dog's skull, of which a full description is given in "Flower's Osteology of the Mammalia," is the most convenient example for practical study.

The following characteristic points should be specially noted.

The floor, roof, and walls of the cranium are completely ossified, and the bones connecting them are united by sutures having serrated edges which dovetail into one another. There is no parasphenoid bone, but the basis cranii is formed by three ossifications in the floor of the primitive cartilaginous cranium—viz. the **basi-occipital**, the **basi-sphenoid**, and the **pre-sphenoid**. The occipital region of the skull is completed by the **ex-occipitals** at the sides and the **supra-occipital** above the foramen magnum. There are two occipital condyles formed by the ex-occipitals. The cranial cavity is shut off from the nasal cavities in front by the **cribriform plate**, a bony partition perforated by numerous holes through which the fibres of the olfactory nerve pass. The cribriform plate is the laterally expanded posterior part of the **mesethmoid**, a vertical plate of bone and cartilage dividing the right and left nasal chambers from one another. Each nasal passage contains two characteristic scroll-like bones, of which the upper and posterior is united with the mesethmoid and called the **ethmo-turbinal**, the lower and anterior is united with the maxilla and called the **maxillo-turbinal** bone. These bones are formed by the ossification of the rolls of cartilage over the surface of which the olfactory epithelium is spread. The membrane covering the ethmo-turbinal is supplied by the olfactory nerve, but that covering the maxillo-turbinal is supplied by a branch of the fifth nerve. The bones of the upper jaw, forming the face, are firmly united to one another and to the cranium. There is a hard palate formed by horizontal plates given off from the inner sides of the maxillæ and palatines. The pterygoids are very small and confined to the base of the skull. The orbit is bounded below by a zygomatic arch formed by the jugal and

processes of the maxillary and squamosal bones. The lower jaw consists of a single piece on each side, is articulated directly with the squamosal, and is not suspended from the skull, as is the case in lower vertebrates, by the intervention of a hyomandibular or a quadrate. The homologues of the latter bones in mammals are to be found in the chain of minute auditory ossicles which stretch across the middle ear from the tympanum to the fenestra ovalis of the inner ear. There are four of these ossicles, the **malleus, incus, orbiculare,**

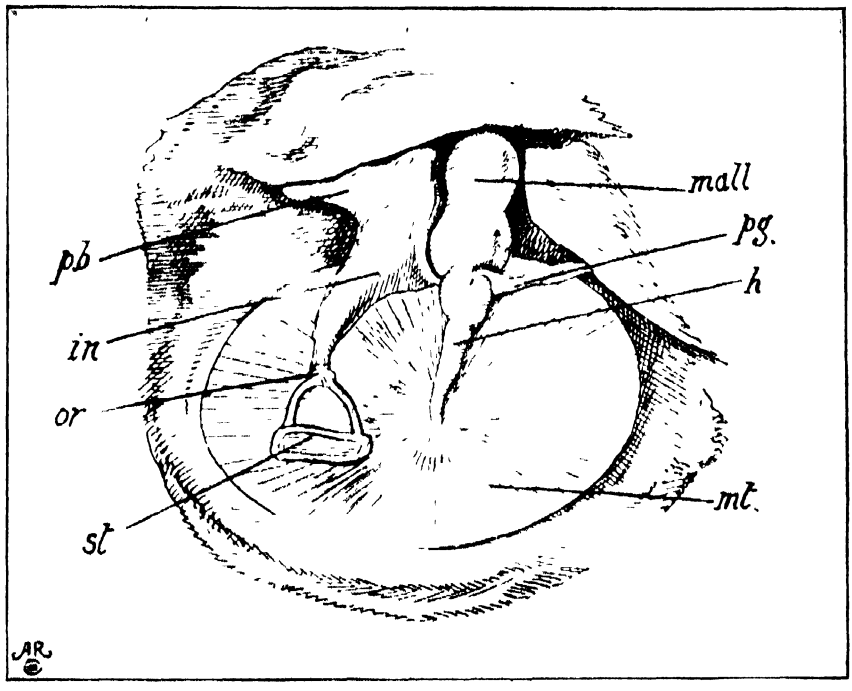


Fig. 72

The tympanic membrane and auditory ossicles of the human ear, seen from within. *h*, handle of malleus; *in*, incus; *mall*, head of malleus; *mt*, membrana tympani; *or*, os orbiculare; *pb*, processus brevis of incus; *pg*, processus gracilis of malleus; *st*, stapes. (From Quain's Anatomy, slightly modified.)

and **stapes**. The malleus is a small irregularly-shaped bone consisting of a rounded head or capitulum bearing two processes. The larger process, called the manubrium, is attached to the tympanic membrane, the smaller, processus gracilis, is attached to the walls of the tympanic cavity. The posterior face of the capitulum bears a concave surface for articulation with the incus. The incus has a body and two processes. Anteriorly the body has a saddle-shaped articular surface,

which fits against the capitulum of the malleus. The shorter of the two processes is directed backwards, and is attached to the wall of the tympanic cavity; the longer process is directed downwards and inwards, and bears at its extremity a small nodule of bone, the orbiculare. The stapes is a stirrup-shaped bone, the base of which is attached to the membrane covering the fenestra ovalis, or aperture leading into the inner ear, and its arch is articulated with the orbiculare. The study of the development of the auditory ossicles shows that the malleus and incus are formed from the upper end of the mandibular arch, and that the incus is the equivalent of the quadrate bone or cartilage of lower vertebrates. The malleus is derived from the upper end of Meckel's cartilage, which in birds and reptiles is ossified, and forms the **os articulare** of the lower jaw. The malleus of mammals, then, represents a part of the lower jaw of lower vertebrates. The homology of the stapes is more doubtful, but it appears to be formed in connection with the upper end of the hyoid arch, and therefore may be in some degree representative of the hyomandibular of fishes.

With the exception of the lowest forms, the sternum of mammals is characteristically formed of a number of segments or **sternebræ**. The first pair of ribs articulate with the body of the first sternebra, but the remaining ribs that reach the sternum articulate with the interspaces between the sternebræ. The last segment of the sternum has no ribs attached to it, and is called the **xiphisternum**. The hindmost ribs do not reach the sternum, and are described as free or floating ribs.

The shoulder-girdle of the higher mammals is characteristic. The scapula is a flattened, more or less triangular plate of bone, the outer surface of which is divided into two by a stout ridge running from the upper border to the glenoid cavity. This ridge is called the spine of the scapula, and its lower extremity is produced into a process called the **acromion**, with which the outer end of the clavicle, when present, articulates. The coracoid is reduced to a blunt, hook-like process, which overhangs the anterior border of the glenoid fossa, but does not extend to the sternum. In the lowest group of Mammalia, the Prototheria, comprising the genera *Ornithorhyncus* and *Echidna*, the shoulder-girdle

has a remarkably reptilian appearance, as the coracoids are well developed, and extend to and articulate with the sternum.

The chief characteristic of the pelvic girdle of mammals is the fact that its long axis is nearly parallel to the vertebral column. The ilia are generally large and expanded, and usually the pubes, less frequently the ischia, meet in ventral symphyses.

The fore and hind limbs are formed on the pentadactyle type, which has already been fully described for the frog (vol. i. p. 35). The fourth and fifth carpals and the corresponding tarsals in mammals are commonly fused to form the **unciform** and **cuboid** bones respectively. The digits both of the manus and pes are commonly reduced in number, this reduction being most conspicuous in the horse, whose hoof is the modified nail or claw of the ungual phalanx of the third digit, the second and fourth digits being reduced to rudimentary splint-bones, and the first and fifth altogether absent. In the rabbit the hand has five fingers, of which the first, or pollex, is much shorter than the others, while in the foot there are only four toes, the hallux or great toe having disappeared.

If we now examine the internal organs, we find that in mammals the abdominal part of the cœlom is completely shut off from the thoracic portion by a muscular partition called the **diaphragm**. The diaphragm consists of a central tendinous portion, the **centrum tendineum**, from which flat bands of muscle radiate in all directions, and are attached to the vertebral column, the floating ribs and the xiphisternum. When its muscles are relaxed, the diaphragm is arched up towards the thoracic cavity; when its muscles contract, it is flattened and the thoracic cavity is enlarged. The œsophagus, the inferior vena cava, and the dorsal aorta pass through special holes in the diaphragm, but there is no communication by way of these holes between the thoracic and abdominal cavities. The œsophagus and blood-vessels are fastened by connective tissue to the edges of the holes, and the thorax is an air-tight box, enclosed by the ribs and diaphragm. The thoracic cavity contains the heart and lungs, the bases of the great arteries and veins, and a large glandular mass of doubtful function, the thymus. The heart is enclosed in a double membranous sac, the **pericardium**, and the lungs are similarly enclosed in double membranous sacs called **pleura**. The

diaphragm of mammals is an important organ in respiration. As long as the thoracic walls are intact, the lungs, which have very elastic and distensible walls, are partly filled with air, and are closely pressed against the thoracic walls. When the diaphragm contracts and the thoracic cavity is enlarged, air rushes down the windpipe and enters the lungs which expand to fill the increased space. When the diaphragm is relaxed, this additional air is expelled. The alternate enlargement and reduction of the cavity of the thorax is further assisted by the movement of the ribs. The breathing movements of birds and reptiles are also effected by the ribs, but the diaphragm is a characteristic mammalian structure.

The heart of a mammal is quadrilocular, containing two auricles and two ventricles. The right auricle receives the blood brought back by the superior and inferior venæ cavæ, and on contraction sends it into the right ventricle. On contraction of the right ventricle the blood is forced through the pulmonary artery to the lungs, whence it is returned by the pulmonary veins to the left auricle. The left auricle empties its contents into the left ventricle, and this, by its contraction, forces the blood through the aorta to the whole body. Thus the right and left sides of the heart are (in the adult) completely separated from one another; the right side contains venous blood, the left side contains the oxygenated blood returned from the lungs. The presence of a four-chambered heart in which the venous blood is kept separate from arterial or oxygenated blood is not characteristic of mammalia, for the same arrangement is found in birds, and among the reptilia in crocodiles. But the arrangement of the aortic arches in mammals is characteristic. In the embryo the walls of the pharynx are pierced by gill-slits. Five are developed on each side—viz. the hyomandibular and four branchial clefts—but only three are in place at a time, the anterior slits closing up before the posterior ones are formed. After the heart is formed, the truncus arteriosus is continued forwards on the ventral wall of the pharynx, and divides into six arches on each side; the first runs in the mandibular arch, the second in the hyoid, the third, fourth, fifth, and sixth in the corresponding branchial arches. As the gill-slits are never functional, the arterial arches do not enter gill-capillaries but simply curve round the œsophagus and unite to form

the dorsal aorta. The subsequent fate of these arches is shown in fig. 73. The truncus arteriosus bifurcates in front

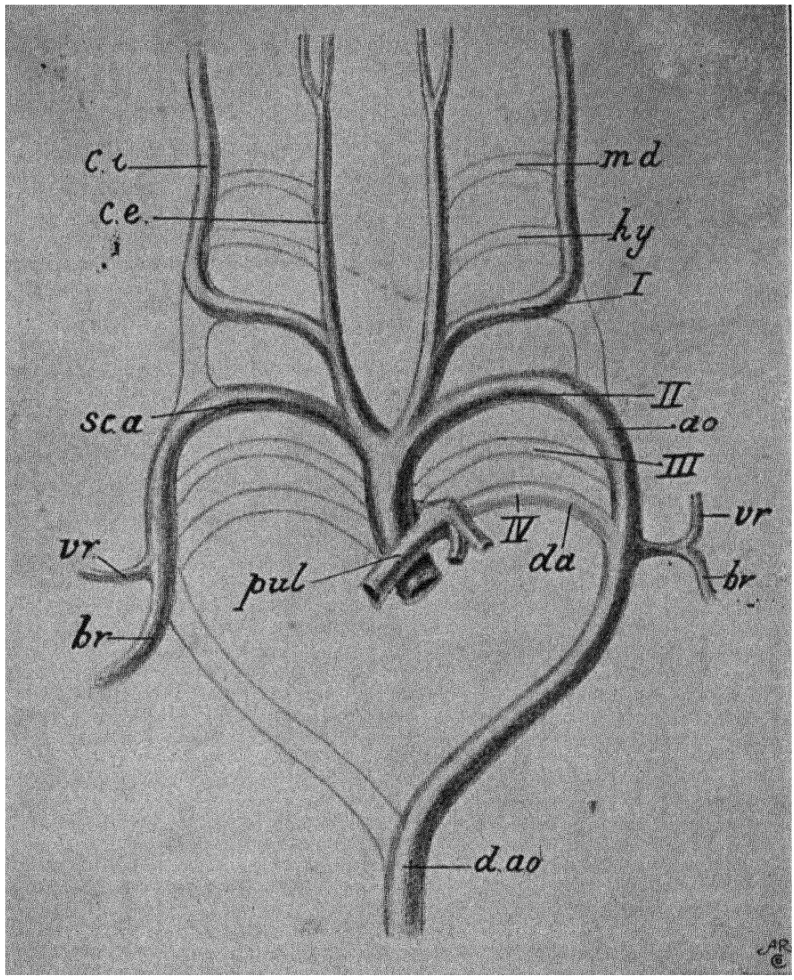


Fig. 73

Diagram illustrating the derivation of the arterial trunks of the adult from the embryonic aortic arches in a mammal. The transient embryonic vessels are drawn in outline. *md*, mandibular arch; *hy*, hyoid arch; *I-IV*, the four branchial arches. *ao*, the aortic arch formed from the second branchial arch of the left side; *br*, brachial artery; *ce*, external carotid; *ci*, internal carotid; *d.a*, ductus arteriosus, connecting the pulmonary and aortic arches; *d.ao*, dorsal aorta; *pul*, pulmonary artery; *sca*, right subclavian artery, formed by the upper part of the second branchial arch of the right side; *vr*, vertebral artery.

of the second branchial arch, and each bifurcation is continued forwards as the external carotid artery. The internal carotids

are formed as forward continuations of the collecting vessels into which the first three arterial arches open on the dorsal side. The middle parts of the mandibular and hyoid arches disappear as shown in the diagram. The first branchial arches persist to form the proximal parts of the carotid arteries, but their dorsal connections with the second branchial arches are lost. The second branchial arch of the left side becomes the aortic arch curving round to the left to pass into the dorsal aorta. The arch of the right side loses all connection with the dorsal aorta, but its proximal portion persists to form the subclavian artery. The third branchial arches disappear altogether, and so does the fourth arch of the right side. The pulmonary artery is formed as an outgrowth of the proximal side of the left fourth arch, and the remainder of the arch is aborted or persists as a solid ligamentous cord passing from the pulmonary artery to the aorta, forming the so-called **ductus arteriosus** of human anatomy. In connection with these changes, and the division of the primitively single ventricle into right and left halves, the proximal part of the truncus arteriosus is divided into two. The right division retains its connection with the right ventricle, and becomes the base of the pulmonary artery, the left division forms the base of the aorta.

In the venous system of mammals, the most characteristic thing is the entire absence of a renal-portal system. The inferior vena cava reaches to the hind end of the abdominal cavity and is formed by the union of the external and internal iliac veins bringing back blood from the hind limbs, with the ilio-lumbar veins bringing back blood from the walls of the posterior part of the trunk. The blood from the kidneys is returned to the inferior vena cava by a pair of renal veins, and the kidneys are supplied with blood only by the renal arteries. In the mammalian embryo, the venous system consists of a pair of anterior and a pair of posterior cardinal veins, and is therefore fish-like. The anterior cardinals form the superior venæ cavæ of the adult. The posterior cardinals are replaced by the inferior vena cava, but the anterior part of the right posterior cardinal persists as the **azygos** vein, and in man the left posterior cardinal is represented by the **hemi-azygos**, which discharges into the azygos by a transverse connection. (The absence of a renal-portal system is not

quite diagnostic of mammals, for there is no true renal-portal system in birds, but in this class the inferior vena cava originates in front of the kidneys, and not behind them, as in mammals, and there is a pair of so-called renal portal veins which traverse the substance of the kidneys without breaking up into capillaries within it.)

In connection with the circulatory system, the non-nucleated red corpuscles of mammals should be noticed. They are highly characteristic, and may easily be studied in a drop of human blood drawn from the finger. They are circular bi-concave discs, with swollen margins, and consist of a minimal quantity of a protoplasmic network, the stroma, holding a relatively very large quantity of hæmoglobin in its meshes. Human red corpuscles measure 7μ in diameter; those of the elephant, 9μ, of the dog and rat, 7μ, of the cat, 6μ, of the sheep, 5μ ($\mu = \frac{1}{1000}$ of a millimetre).

Before passing on to the urogenital system and the development of the embryo, we may briefly consider the more characteristic features of the central nervous system of mammals. The spinal cord does not require special mention, but the brain is well developed, and remarkable for the great relative size of the cerebral hemispheres, which in the rabbit overlap the thalamencephalon and mid-brain behind it, and in higher forms show a progressive increase in size, till in man they cover and conceal the cerebellum and medulla oblongata. With the increasing size of the hemispheres, we find an increasing complexity due to infoldings of a more or less complicated character, which are expressed by a number of tortuous grooves on their surfaces. These grooves are called **sulci**, and the raised areas between them are known as **gyri**. In a low type of placental mammal, such as the rabbit, the sulci are few in number, and shallow. In a higher form, such as the dog, they are much more numerous, and in man their complexity is remarkable. It is further characteristic of the mammalian brain, that the cerebral hemispheres are united by a broad transverse band of commissural nerve fibres called the **corpus callosum**, and that the dorsal surface of the mid-brain is produced into two pairs of swellings, or **corpora quadrigemina**, instead of one pair, or corpora bigemina, as in lower vertebrates.

In the organs of special sense, the most remarkable feature

is the development of the **cochlea** of the ear. This structure, which in the frog is represented only by a small dilatation of the sacculus (vol. i. fig. 12, *pbc.*), is produced in the mammal into a long tubular offset twisted into a spiral of from $1\frac{1}{2}$ to four turns, and lodged in a corresponding spiral chamber of the periotic bone. The epithelium lining the cochlea is differentiated to form a complicated sensory organ called the **organ of Corti.**

The urogenital organs of mammalia (excepting the Prototheria) offer many special features. The complete separation of the urogenital from the the rectal aperture has already been noted. The kidneys are formed by the metanephros, and their ducts, the ureters, open into the bladder. In the male the Wolffian ducts become the sperm ducts or vasa deferentia. The upper end of each is thrown into many convolutions, and forms a structure known as the **epididymis**, which lies close to the testis and is connected with it by the vasa efferentia. The mesonephros is represented by a small mass of coiled tubules, the **caput epididymis,** lying at the anterior end of the epididymis. The Wolffian ducts open below into the narrow stalk of the bladder, or urethra. The so-called Müllerian duct (which is formed independently of the Wolffian duct, as in the frog, and is not split off from it as in the dogfish) disappears almost entirely in the adult male, but the lower ends persist as a pouch, the **uterus masculinus**, which opens into the urethra in close connection with the openings of the Wolffian ducts.

In the female the Wolffian ducts are completely aborted in most mammals, but traces of them are to be found in the structures known as **Gaertner's canals** in the pig and a few other forms. The mesonephros is represented only by some functionless coiled tubes which bear the same relation to the ovaries as the epididymes bear to the testes. They are known as the **parovarium.** The Müllerian ducts form the oviducts. The lower ends of the oviducts always coalesce to form a single tube, the **vagina,** and the upper ends are differentiated into the uteri and the oviducts or **Fallopian tubes,** the latter opening by funnel-shaped mouths into the abdominal division of the cœlom in close proximity to the ovaries. In the rabbit the uteri are separate from one another and open independently into the vagina, but in many mammals the right and left uteri are partially or wholly fused together.

The lowest mammalia, the Prototheria, are oviparous, and lay eggs furnished with a large quantity of food-yolk. In all other mammalia the ova are very small, are practically devoid of food-yolk, and undergo a total segmentation. The embryo is retained for a longer or shorter time in the uterus of the mother, is attached to the uterine walls, and is nourished by the agency of the maternal blood-vessels. The embryonic organ by which the embryo is attached to the uterine walls is

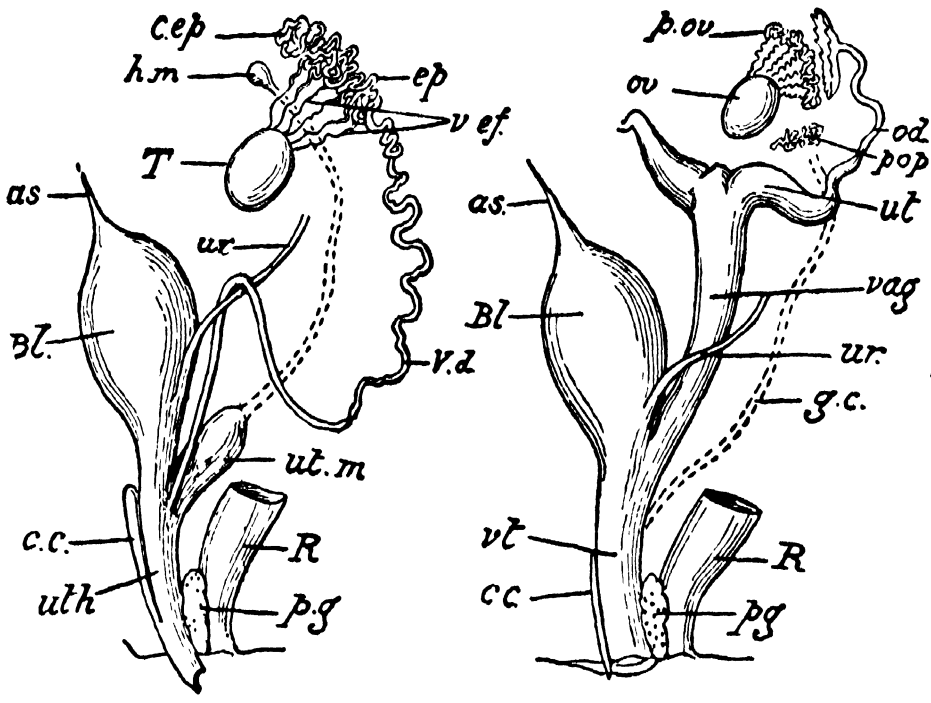


Fig. 74

Diagrams of the urogenital system of mammals, that of the male on the left, of the female on the right. The prostate and Cowper's glands are omitted. *as*, allantoic stalk; *Bl*, bladder; *cc*, corpus cavernosum; *c.ep*, caput epididymis; *ep*, epididymis; *gc*, Gartner's canal; *hm*, hydatid of Morgagni, representing the upper end of the oviduct; *od*, Fallopian tube or oviduct; *ov*, ovary; *pg*, perineal gland; *pop*, paro-ophoron; *p.ov*, paro-varium, these two representing the Wolffian body in the female; *R*, rectum; *T*, testis; *ur*, ureter; *ut*, uterus; *uth*, urethra; *utm*, uterus masculinus; *vag*, vagina; *V.d*, vas deferens; *v.ef*, vasa efferentia; *vt*, vestibule.

known as the **placenta**. In the **Metatheria** or Marsupials, including the kangaroos, wombats, opossums, etc., the young are born very early, and are carried while in a helpless state in a special pouch or marsupium situate on the abdomen of the mother. Nevertheless, a more or less intimate placental attachment is effected between the embryo and the uterine

wall in Marsupials, and although our knowledge of the different forms of placentation in this order is far from being complete, we can no longer make a distinction between the Marsupials as non-placental and the Eutheria as placental mammals.

Our knowledge of the structure of the placenta in the highest mammals or **Eutheria** is, however, far more complete, and in this group the embryos are retained for a considerable time in the uterus of the mother, and during that time are attached to the uterine wall and nourished by the maternal blood. The nature of this attachment may be briefly described as follows:—

The ovum is fertilised in the oviduct, and the segmentation is total and equal, resulting in the formation of a solid mass of cells called the **blastocyst**, which soon becomes differentiated into an outer layer and an inner mass, as shown in fig. 75, *A*. The outer layer is called the **trophoblast**, and it does not give rise to any part of the embryo, but is solely concerned with the nutrition of the embryo. The inner mass gives rise to the embryo, the yolk-sac, and the amnion.

In the next stage (fig. 75, *B*) a cavity, the **blastocystic cavity**, is formed between the trophoblast and the inner mass, so that the latter comes to lie at one pole of the now elongated blastocyst. At the same time the cells of the inner mass are differentiated into an **embryonic knob** above, and a flattened epithelium below. The latter, henceforth known as the epithelium of the yolk-sac, now begins to spread around the blastocystic cavity, forming a lining to its walls.

In the next stage (fig. 75, *C*) the upper pole of the trophoblast, above the embryonic knob, becomes enormously thickened to form a very important organ generally known by the German name "träger," literally the "carrier." The epithelium of the yolk-sac has spread further round the cavity of the blastocyst, and the embryonic knob has increased greatly in size, pushing down the yolk epithelium and forming a large projection into the blastocystic cavity. A considerable space is shortly afterwards formed in the middle of the embryonic knob.

In the next stage (fig, 75, *D*) the träger has increased very much in size and has become channelled by numerous lacunæ. The yolk epithelium forms a complete lining to the blasto-

cystic cavity, and the latter is nearly filled by the downward projection due to the increasing size of the embryonic knob and the cavity contained in it.

During these changes the walls of the uterus have been greatly thickened, the uterine epithelium has disintegrated and has nearly completely disappeared, and the blastocyst has come to lie in a deep pit in the uterine walls (fig. 75, *F*).

The embryo is now formed at the bottom of the downwardly projecting embryonic knob. Differentiation sets in over an area known as the embryonic area; the cells become several layers deep, and are divided into an epiblast above and a mesoblast below; the yolk epithelium of this region forms the hypoblast (fig. 75, *D*). Both notochord and mesoblast are formed largely from a linear proliferation of cells in the middle of the embryonic area known as the primitive streak. At first the mesoblast forms two lateral sheets a the sides of the notochord and these sheets bend upwards in conformity with the folds of the yolk epithelium Presently the inner edges of the mesoblast sheets abutting on the notochord are divided into mesoblastic somites, and the lateral parts of the sheets are split into somatopleuric and splanchnopleuric layers. in the same manner as in the frog. Meanwhile two neural folds enclosing a neural groove have been formed from the epiblast, and the folds shortly grow up and unite to form the neural tube. In these and all other details of organogeny the development of the mammalian embryo so far resembles that of the frog that it is unnecessary to describe it further. But special attention should be paid to the fate of the somatopleur and splanchnopleur. Both epiblast and mesoblast extend right round the space lying above the embryo—that is, round the cavity formed at a previous stage in the embryonic knob. When the mesoblast is split the somatopleur is adherent to the epiblast, and outside the embryonic area the two layers become widely separate from the splanchnopleur, which latter, in the embryonic area and laterally, is closely applied to the yolk epithelium, but above is in contact with the lower layer of the träger (fig. 75, *E*). The somatopleur with its lining of epiblast forms a hood, called the **amnion**, over the embryonic area, and the space between the amnion and the embryo is the amniotic cavity. This cavity is clearly the same

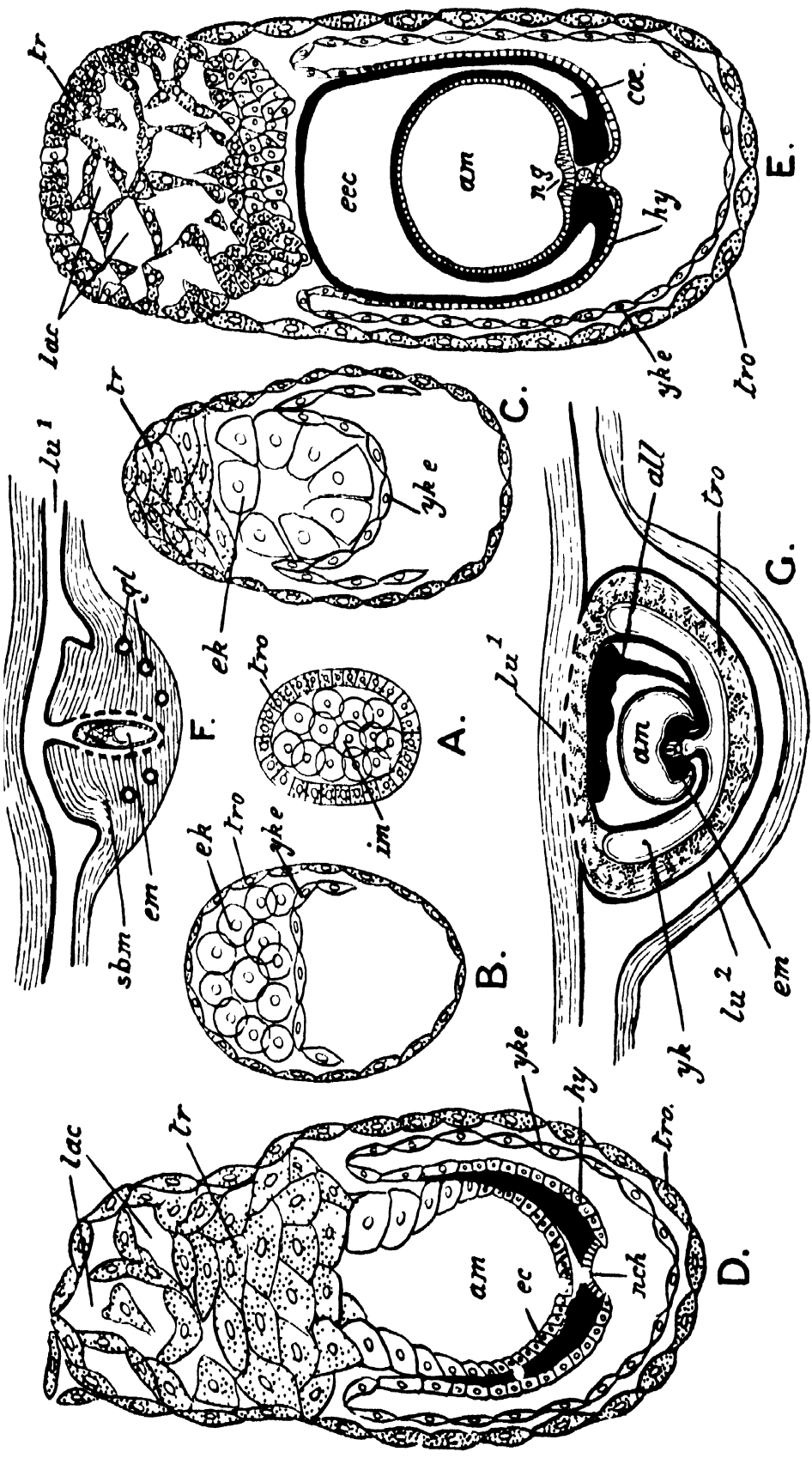

tr
lac
ecc
am
ng
cœ
hy
E.
yke
tro
lu¹
gl
sbm
em
F.
ek
tro
yke
im
A.
B.
C.
tr
yke
ek
lu¹
all
tro
am
G.
yk
lu²
em
lac
tr
yke
hy
tro
am
ec
nch
D.

Fig. 75

Diagrams illustrating the development of the blastocyst and formation of the placenta in Mammalia. *A*, a blastocyst at the end of segmentation; *B*, an older blastocyst, in which a cavity has appeared to one side of the inner mass of cells; *C*, a later stage, showing the formation of the trager and growth of the yolk epithelium round the yolk cavity; *D*, formation of lacunæ in the träger and commencement of the embryo; *E*, further development of the trager, the mesoblast has split and the amnion and extra-embryonic cœlom are formed; *F*, longitudinal section of uterus, showing the position of the embryo in a pit in the uterine wall. *G*, longitudinal section of a later stage, showing the obliteration of the old lumen and formation of a new lumen in the uterus. *all*, allantois; *am*, amniotic cavity; *ca*, embryonic cœlom; *ec*, epiblast; *eec*, extra embryonic cœlom; *ek*, embryonic knob; *em*, embryo; *gl*, uterine glands; *hy*, hypoblast; *im*, inner mass of cells; *lac*, lacunæ in träger; lu^1, original lumen of uterus; lu^2, secondary lumen of uterus; *nch*, notochord; *ng*, neural groove; *sbm*, thickened sub-mucous layer of uterus; *tr*, träger; *tro*, trophoblast; *yk*, yolk-sac; *yk.e*, yolk epithelium. In all the figures the trophoblast is shaded with dots, and the embryonic mesoblast is represented in black.

as that which appeared at an earlier stage in the embryonic knob. The space between the somatopleur and splanchnopleur is of course the cœlomic cavity, and it is evident that the cœlom is continued outside the embryo as a wide space extending all round the amnion. As development proceeds, the splanchnopleur with hypoblast, and in a lesser degree the somatopleur with epiblast, are folded inwards in front, behind, and at the sides of the embryonic area, so that the embryo is raised up above the yolk-sac and projects into the amniotic cavity, as shown in fig. 75, *G*. While these changes are in progress great changes have also taken place in the maternal tissues. The uterine wall is greatly thickened, chiefly by the growth of the submucous layer, which becomes very vascular. The uterine epithelium is entirely disintegrated and the walls of the maternal blood-vessels in the neighbourhood of the embryo break down, allowing the maternal blood to escape into the now spacious lacunæ in the träger. The last named organ has become closely adherent to the walls of the uterine pit in which the embryo lies, and thus we arrive at a stage in which the embryo is nourished by the maternal blood circulating freely in an embryonic organ—viz. the träger.

In the next stage the embryo is folded off from the yolk-sac, and many of its more important organs have made their appearance. The gut has been established by the infolding of the spanchnopleur with its lining of hypoblast, but is still, and for a long time remains, in free communication with the cavity of the yolk-sac by a hollow stalk. As soon as the hind-gut is established, a ventral outgrowth is formed from it, corresponding in position to the cloacal bladder of

the frog. This outgrowth is solid, is covered with splanchnopleuric mesoblast which soon becomes highly vascular, and is an important embryonic organ known as the **allantois**. Pushing its way between splanchnopleur and somatopleur, the allantois grows up into the extra-embryonic cœlomic space in the direction of the träger, and presently meets and becomes attached to this organ. It then gives off numerous branching upgrowths, the **allantoic villi**, which penetrate into the träger, and are surrounded by the trophoblastic tissue of which that organ is composed. The allantoic villi are highly vascular, being supplied with embryonic blood-vessels by the allantoic artery. The lacunæ of the träger are filled with maternal blood, and thus an exchange of material is readily effected between the maternal and embryonic blood, whereby the embryo obtains nourishment and gets rid of waste products.

During this time the uterus undergoes remarkable changes, represented in fig. 75, *F* and *G*. In *F* the young embryo is seen lying in a pit in the lower or anti-mesometric side of the uterus, and the uterine lumen is continued above the pit. In consequence of the loss of the uterine epithelium and adhesion of the träger to the uterine wall, the original lumen above the embryo is obliterated, and a new lumen is formed by outgrowths which pass through the thickened uterine wall and meet *below* the embryo in the manner shown in *G*. It can be seen that on the establishment of the new lumen a part of the uterine tissue adjacent to the yolk-sac is cut off from the rest, and forms a thick layer or envelope below the embryo. This layer is lined by trophoblastic tissue, and lacunar spaces containing maternal blood are formed in it. At this time the yolk-sac is highly vascular, being supplied by the omphaloidean artery, and thus the embryo is receiving nourishment both by the agency of the allantois and the yolk-sac. The name placenta is given to all trophoblastic structures in which there are lacunæ containing maternal blood, so at this stage (fig. 76) there are two placentæ present; the one connected with the allantois is the **allantoidean placenta**, the one connected with the yolk-sac is the **omphaloidean placenta**.

As development proceeds the allantoidean placenta gains in size and importance, the omphaloidean diminishes and

eventually disappears. Fig. 77 shows the final condition. The allantoic villi have increased to an immense extent, and their ramifications, covered by trophoblastic tissue, penetrate

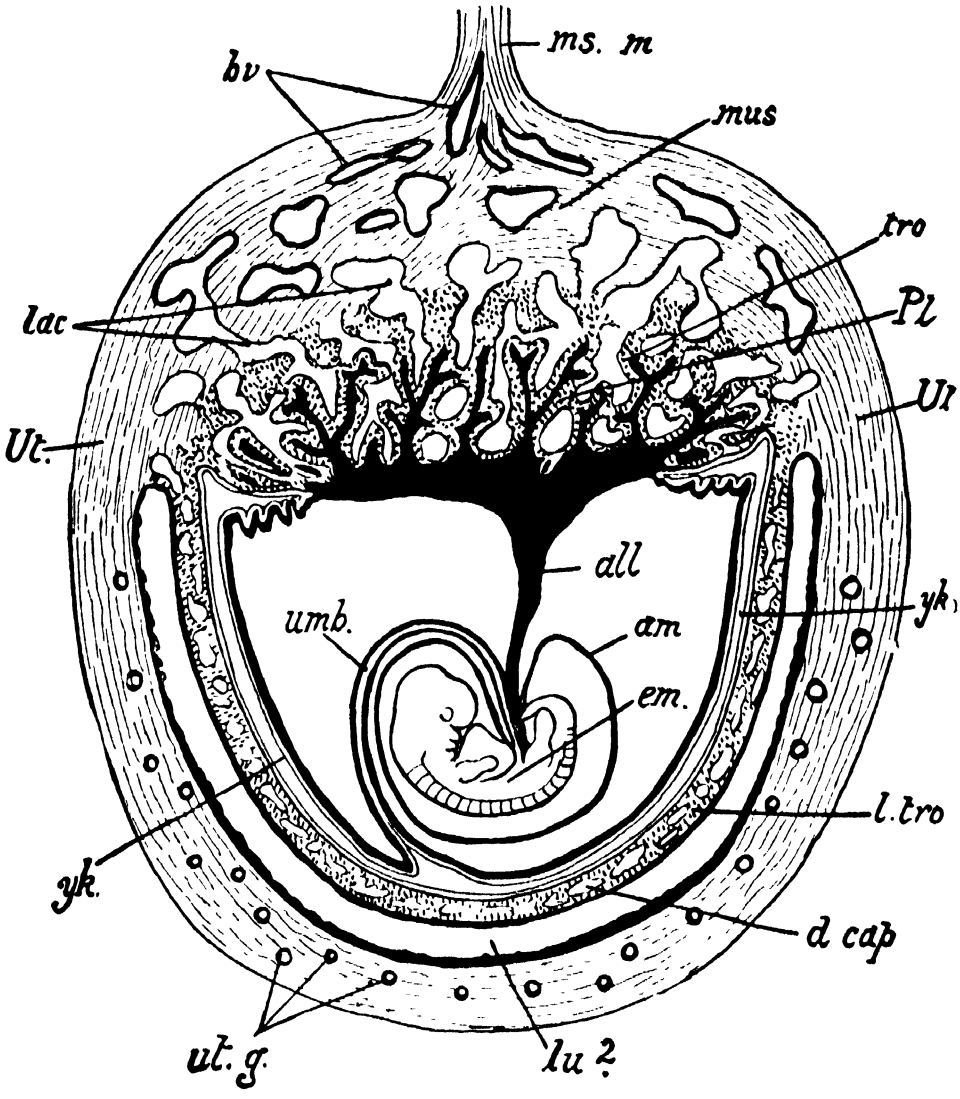


Fig. 76

Diagrammatic transverse section of a pregnant uterus, illustrating an early stage of placentation. *all*, allantois; *am*, amnion; *bv*, uterine blood-vessels; *d.cap*, decidua capsularis; *em*, embryo; *lac*, lacunæ; *l.tro*, lateral or omphaloidean trophoblast; lu^2, secondary lumen of uterus; *ms.m*, mesometrium; *mus*, muscular wall of uterus; *Pl*, placenta; *tro*, trophoblastic tissue surrounding the allantoic villi; *umb*, stalk of the yolk-sac; *Ut*, uterus; *ut.g*, uterine glands; *yk*, yolk-sac.

the träger in all directions. Concurrently with the increase of the allantoidean placenta, the maternal tissue above it has disintegrated, and its place has been taken by tropho-

blastic tissue into which the allantoic villi do not penetrate. The omphaloidean placenta has disintegrated and disappeared altogether, and with it the distal wall of the yolk-sac, so that now the epithelium of the proximal wall of the yolk-sac is

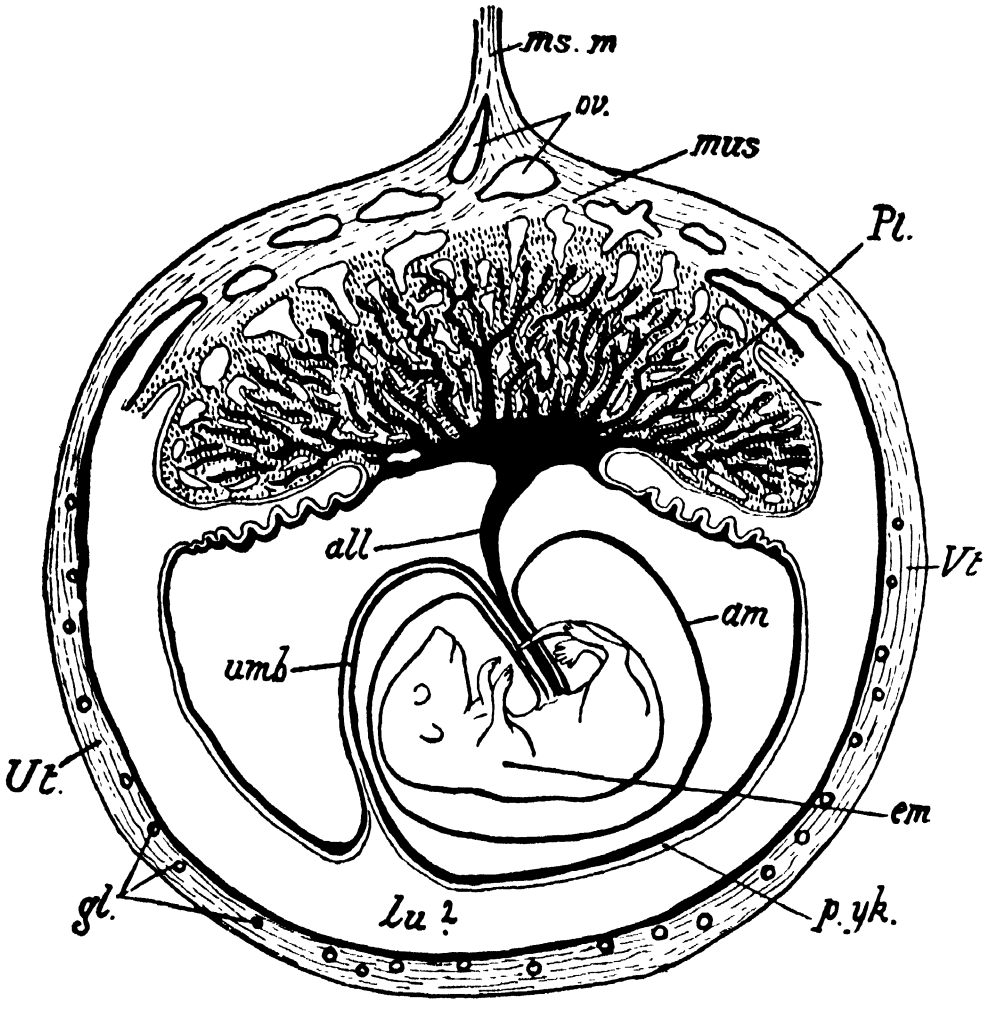


Fig. 77

Diagrammatic transverse section of a pregnant uterus, illustrating the later phase of placentation. *all*, allantois; *am*, amnion; *bv*, uterine blood-vessels; *em*, embryo; *gl*, uterine glands; *lu*^{2}, secondary lumen of uterus; *ms.m*, mesometrium; *mus*, muscular wall of uterus; *Pl*, allantoidean placenta; *p.yk*, proximal wall of yolk-sac; *umb*, stalk of yolk-sac; *Ut*, uterus.

exposed in the new lumen of the uterus, from which it absorbs nutriment in the form of fat globules secreted by the uterine glands. At an earlier stage certain cells in the uterine wall in the region of the allantoidean placenta were full of glycogen granules, and now somewhat similar

cells of the trophoblastic tissue of the placenta are found to contain glycogen. The maternal glycogen was converted into sugar, passed into the maternal blood circulating in the placental lacunæ, was there taken up by the trophoblastic cells, reconverted into glycogen, and once more converted into sugar and passed into the embryonic circulation by way of the allantoic blood-vessels. This complicated series of changes from glycogen to sugar, and back again, emphasises the fact that, although there is free exchange of material between, there is no actual intermingling of, maternal and embryonic tissue except in the case of the blood. Consequently when the fœtus is born—*i.e.* expelled by the contractions of the uterus through the vagina to the exterior—the placenta, consisting of trophoblastic and allantoic (*i.e.* embryonic) tissue, is pulled off from the uterine wall and carried away with the fœtus, forming the so-called **decidua**. But no part of the maternal tissue, excepting the blood circulating in the trophoblastic lacunæ, is carried away at birth, previous statements to the contrary notwithstanding.

There is a good deal of variety in the mode of placentation in the different orders of mammalia. The foregoing account is chiefly applicable to the mouse, and it may be taken as fairly typical of the orders Rodentia, Carnivora, Insectivora, Cheiroptera, Monkeys, and Man. In the remainder of the Eutheria the placenta is simpler.

It will be noticed that in describing the placentation, continual reference has been made to a yolk-sac, and yet no food-yolk is present in the ovum, and the sac in question is only a vesicle with fluid contents. The fact is that the "yolk sac" of the mammalian embryo corresponds to the similarly named organ in the embryos of reptiles and birds, which is filled with food-yolk, and gradually absorbed during the growth of the embryo. There is no doubt that many of the peculiar features of the early stages of the development of mammals are to be explained by their derivation from an ancestor which laid large-yolked eggs, and it should not be forgotten that the lowest mammals, *Echidna* and *Ornithorhyncus*, do, in fact, lay such eggs.

CONCLUSION

THE animals described in this book as examples of the different grades of organisation, belong to one or the other of the two great divisions of the animal kingdom, the **Protozoa** or the **Metazoa.** The Protozoa may be roughly described as unicellular animals, but it has been pointed out sufficiently clearly in the first volume that such a description is inexact, and that it is impossible to make a sharp distinction between the two divisions. There are Protozoa which can only be described as multicellular, and although consistency forbids the idea of a unicellular Metazoon, it must not be forgotten that all Metazoa begin their existences in the unicellular condition. But all adult Metazoa are multicellular, and the cells of which their bodies are composed, show a tendency to arrange themselves in definite layers about a central cavity or system of cavities. In one of the great sub-divisions of the Metazoa, the **Cœlenterata**, there is only one such cavity, the gastrovascular cavity, serving for digestion and circulation alike. This cavity is bounded by two cellular layers, known as the ectoderm and endoderm, with a gelatinoid, structureless layer between. The structural plan of a cœlenterate animal is, therefore, of the simplest kind, and, however complicated the variations of the plan may seem in the different jelly-fishes, corals, sea-anemones, and other polyps belonging to the group, it is always easy to reduce the complexity to the fundamental plan of a simple two-walled sac, with an opening at one end, and the organs disposed radially with regard to that opening.

The other great division of the Metazoa, the **Cœlomata**, comprises a vast and very varied assemblage of animals, which have this one character in common, that the muscular, circulatory, and reproductive organs are dissociated from the external and internal epithelial layers—*i.e.* from the ectoderm and endoderm, and form an intermediate layer or layers, collectively described as the mesoderm or mesoblast.

In most of the cœlomata, the mesoblast contains a definite cavity, the **cœlom**, separate from the alimentary cavity.

The various examples of Cœlomata described in the present volume fall into five main groups or **phyla**, according to their several plans of organisation. Thus, *Distomum* is an example of the phylum **Platyhelmia**; *Lumbricus* is an example of the phylum **Chætopoda**; *Anodonta* and *Helix* are examples of the phylum **Mollusca**; *Apus* and *Astacus* belong to the class **Crustacea**, *Periplaneta* to the class **Insecta**, both classes being included in the phylum **Arthropoda**. Lastly, *Amphioxus*, *Scyllium*, *Rana*, and the Mammalia are examples of the phylum **Chordata**. There are other phyla included in the division Cœlomata, but as no examples of them have been described in this book, they need not be discussed here.

When we speak of a "phylum," we mean an assemblage of animals whose structure and organisation may be referred to a particular plan. Thus in the phylum Chordata, the rabbit, the frog, the dogfish, and Amphioxus, much as they differ from one another in detail, resemble one another in certain essential points, such as the dorsal position and tubular nature of the central nervous system, the possession of an axial skeleton lying between the nervous tube and the gut, the ventral position of the main contractile blood-vessel or heart, the existence of myotomes, etc. This much can be learnt from a study of their adult anatomy, but their embryonic anatomy teaches us something more—namely, that certain structures which are absent in the adults of the higher members of the phylum are nevertheless present in the embryos of all the members of the phylum, though they persist in the adults of the lower forms only. The gill-slits are an excellent example of this phenomenon. They are important functional organs in Amphioxus and Scyllium, conspicuous and functional in the tadpole, but aborted in the adult frog, and present, but in a functionless condition, in the embryo of the mammal. Further than this, we learn from embryology that other important structures, such as the arteries and some of the cranial nerves, are moulded, so to speak, on the gill apparatus, and that the original pattern is carried over into those adults in which all traces of gill-slits, as such, are lost. Clearly, then, the possession of gill-slits must form a part of the structural plan which we conceive of as

common to all the Chordata. The same may be said of other organs, such as the excretory tubules.

A plan may be constructed on similar principles for the Arthropoda, another for the Mollusca, and so forth, and the greater the number of animals that one studies the more one is impressed with the fact that each is built upon a particular plan characteristic of the phylum to which it belongs.

It is the first business of the comparative anatomist to convince himself that the various animals included in a single phylum are really constructed upon a common plan, and to form as clear a conception as possible of that plan. Having done this he may ask himself the question, Why are all these animals constructed after the same pattern? And further, Why do the embryos of higher vertebrates develop organs resembling those which are permanent in lower vertebrates, only to lose them again before their development is completed?

There is only one satisfactory answer to these questions—viz. that the similarity of plan, the likeness, is due to blood-relationship, and the embryonic characters of the higher forms are the relics, the reminiscence, if one may use the term, of the structure of some remote ancestor whose organisation had not advanced beyond the stage of complexity now exhibited by the lower members of the phylum in question.

It has been the object of these volumes to show that there are good grounds for the belief that this explanation of the phenomena of anatomy and embryology is a true one; that the animals comprised in a phlyum are what they are because they have diverged in various directions and to various amounts from the structure of a common ancestor, while retaining the main features of that structure.

But it must be understood that this explanation cannot be *proved* to be true; it can only be shown that the evidence in its favour is so cogent that no other explanation is possible. Naturally, one cannot bring forward a sufficiently overwhelming mass of evidence from the study of a few selected examples. But the student who has mastered the contents of these volumes should have no difficulty in extending his studies to other animals, until he has accumulated an amount of evidence that is practically irrefutable.

Lastly, there is the question of the relationship between different phyla of the animal kingdom. Enough has been said, in the proper places, to show that there is some evidence of relationship between the Mollusca and the Chætopoda, or the Chætopoda and the Arthropoda, not to mention other examples. But, in the opinion of the author, these questions do not properly fall within the scope of an elementary work, and should rather form the subject of advanced studies.

INDEX

[The names of species, genera, families, orders, etc., are printed in Italics.]

Abbreviation in development, 262
Abdomen, of crayfish, 113
—— of cockroach, 155, 157
Abdominal pores, 204
Acanthias vulgaris, 203
Acicula, 49
Acmæa, 84
Acromion, 292
Actinotrichia, 217
Afferent branchial arteries, 225, 272
Alæ cordis, 101, 129
Albumen gland, 81
Alimentary canal, of Distomum, 3, 7
—— of Earthworm, 21
—— of Anodonta, 58
—— of Helix, 76
—— of cockroach, 157
—— of Amphioxus, 179
—— of dogfish, 218
—— of mammals, 288
Allantoidean placenta, 304
Allantois, 304
Alternation of generations, 14
Ametabola, 170
Amnion, 166, 301
Amniotic cavity, 301
Amphicœlous vertebræ, 210
Amphioxus, 172
Annelida, 45
Annuli, 91, 94
Anodonta cygnea, 53-68
Antennæ, 95, 100, 107, 110, 117, 123, 142, 152, 168
Apus cancriformis, 92-117
—— *glacialis*, 105-106
—— *spitzbergensis*, 105
Appendages of Apus, 95
Appendicular skeleton, 209, 216
Aqueductus vestibuli, 211
Archenteron, 190
Archiannelida, 45
Archigetes, 2
Arterial arches, of frog, 272
—— of mammals, 294
Arteries, of crayfish, 129
—— of dogfish, 225
Arthrobranchiæ, 131, 132
Arthropoda, 91, 150
Ascidia, 202
Asymmetry in Amphioxus, 196
Atrial folds, 197
Atriopore, 175, 197
Atrium, 175, 181
Auditory capsules, 211
—— nerve, 238
—— organs, 124, 136, 245, 279, 286
—— ossicles, 291
Auricle, 224
Axial skeleton, 209
Azygos nerve, 136
—— vein, 296

Basibranchial cartilage, 215
Basihyal cartilage, 215
Basi-occipital bone, 290
Basipodite, 117
Basipterygium, 216
Basisphenoid bone, 290
Bilateral symmetry, 1
Bile duct, 219
Blastocœle, 48, 190, 250, 254, 256
Blastocyst, 300
Blastoderm, 165
Blastopore, 38, 141, 166, 192, 247, 250, 254
Blastula, 36, 190, 247
Blood-vascular system, of earthworm, 27
—— of crayfish, 129, 132
—— of Amphioxus, 184
Botryoidal tissue, 49

Brachial plexus, 243
Bract, 96
Brain, 135, 258
Branchiæ, 49, 91, 114
Branchial aorta, 184
—— arches, 215, 266, 296
Branchio-cardiac canals, 131
—— grooves, 114
Brown funnels, 188
Buccal cirrhi, 175
—— folds, 175
Bulbils, 184
Byssus, 65

Cæcum, 289
Calciferous glands, 21
Canine teeth, 287
Capsulogenous glands, 35
Caput epididymis, 298
Carcinuric acid, 134
Cardiac aorta, 224
Cardiac ossicle, 126
Cardinal sinuses, 228
Cardo, 152
Carotid arch, 274
—— arteries, 225
—— gland, 274
Carpopodite, 120
Caryophyllæus, 2
Caudal styles, 92
—— vertebræ, 289
Cement, 208
Centrum, 209
Cephalic lobe, 168
—— shield, 92
—— tentacles, 70, 72
Cephalochorda, 179, 202
Cephalothorax, 113
Ceratobranchial cartilages, 215
Ceratohyal cartilages, 215
Cercaria, 14
Cerci, 156
Cerebellum, 236, 278
Cerebral hemispheres, 235, 278
Cervical groove, 114
Cestoda, 2
Chætæ, 19, 31
Chætopoda, 19, 45, 170
Chelæ, 117, 119, 120
Chiastoneurous, *see* Streptoneurous
Chlamydoselache, 207
Chloragogen cells, 23, 32
Chorda dorsalis, *see* Notochord
Chordata, 202
Chorion, 165
Choroid, 279
Chrysalis, 170
Ciliated rosettes, 34
Cirrhi, of polychætes, 49
Cirrhus, 5
Claspers, 205, 216
Clitellum, 19
Cloacal bladder, 264
Club-shaped gland, 197
Clypeus, 151
Cochlea, 298
Cockroach, 149
Cocoon, 35
Cœlom, 1, 16, 21, 40, 45, 51, 74, 86, 90, 146, 169, 171, 181, 217, 262, 303
Cœlomic fluid, 23
Collar, 71
Colleterial gland, 164
Colon, 158
Columella, 70
Commissure, 64
Conchiolin, 54
Conglobate gland, 164
Connective, 64
Conus arteriosus, 224
Copepoda, 107
Coracobranchialis muscle, 243
Coracohyoideus muscle, 243
Coracoid, 216, 292
Coracomandibularis muscle, 243
Cornea, 137, 280
Corpora bigemina, 236, 278
—— quadrigemina, 297
Corpus callosum, 297
Corpuscles, 297
Coxa, 154
Coxopodite, 117
Cranial nerves, 189, 236, 241, 279
Craniata, 202
Cranium, 209, 211, 268, 281, 290
Crayfish, 112
Cribriform plate, 290
Crop, 158
Crura cerebri, 278
Crustacea, 91
Crystalline cone, 137, 139

Ctenidium, 61, 69
Cystogenous cells, 13
Cytophore, 35

Dactylopodite, 120
Dart-sac, 81
Darwin, 17, 20
Decidua, 307
Demibranch, 220
Dendrocœlum lacteum, 2
Dental formula, 288
Denticles, 208
Dentine, 208
Deuto-cerebrum, 168
Development of Amphioxus, 190
—— of frog, 245
Dextral shell, 72
Diastema, 288
Diaphragm, 293
Digenetic parasite, 8
Digestive gland, 128
Distomum hepaticum, 2-16
—— *volvens*, 4
Dogfish, 203
Dorsal cœlom, 182
—— pores, 20
—— root of spinal nerve, 108, 279
Drain-pipe cells, 26
Dreissensia polymorpha, 67
Ductus arteriosus, 296
—— Botalli, 275
—— Cuvieri, 224, 228, 272
—— ejaculatorius, 5, 164
—— endolymphaticus, 211, 245

Ear, *see* auditory organ
Earthworm, 17-44
Ecdysis, 108
Echidna, 292, 307
Echiuroidea, 45, 49
Ectoparasite, 8
Efferent branchial arteries, 225, 273
Egg cases, 234
Elytra, 49
Embryonic knob, 300
Enamel, 208
Endite, 96, 108, 122
Endoderm plate, 140
Endogastric shell, 88
Endolymph, 245
Endoparasite, 8
Endopodite, 107, 117
Endoskeleton, 200
Endostyle, 179
End-sac, 133
Enterocœle, 195
Enteron, 141
Entomostraca, 92
Epiblast, 38, 145, 165, 166, 247, 278, 301
Epibranchial cartilages, 215
Epicranial plates, 151
Epididymis, 297
Epimeron, 114
Epiphyses, 289
Epipleur, 176
Epipleural fold, 197
Epipodite, 120, 122
Ethmoturbinal bone, 290
Eustachian passages, 266, 279
Euethria, 300
Euthyneurous, 79
Evolution, 283
Excretory organs, 3, 64, 73, 103, 132, 186, 230, 275
Exhalant aperture, 56
Exite, 96, 109, 122
Exogastric shell, 88
Exopodite, 107, 117
External auditory meatus, 268
External gills, 266
Extrabranchial cartilages, 222
Eye, of snail, 79
—— of crayfish, 115
—— of Arthropoda, 137
—— of Amphioxus, 175
—— of frog, 279

Fallopian tubes, 298
Fat-body, 161
Femur, 154
Fenestræ, 152
Fin-rays, 173, 216
Fins, 173, 205, 207, 216
Flabellum, 96
Flagellum, 81
Flame-cell, 3
Foot, of Anodon, 53, 56
—— of gastropod, 84
Foot-jaws, 95
Foramen magnum, 211
Foramina of skull, 213

Fore-brain, 235
Fresh-water mussel, *see* Anodonta

Gærtner's canal, 298
Galea, 152
Galeus canis, 203
Gall-bladder, 219
Gastric mill, 126
Gastrolith, 128
Gastropoda, 69
Gastrula, 83, 192, 255
Gastrulation, 38
Genital ridge, 268
Giant fibres, 27, 189
Gill-arches, 266
Gill-bars, 178
Gill-plate, 258
Gill-rays, 215, 216
Gill-slits, 177, 182, 197, 201, 207, 220, 248, 264, 282
Gills, 57, 59, 60, 91, 114, 120, 131, 222
Gizzard, 23
Glochidium larva, 65, 67
Glomerulus, 275
Glycogen, 307
Gnathobase, 96
Gnathopoda, 91
Gonads, 65, 146, 176, 189, 200
Gonapophyses, 157
Green gland, 132, 146
Gyri, 297

Hæmal arches, 210
Hæmocœle, 102
Hair, 284
Hair follicle, 284
Hard palate, 287, 290
Hatschek's organ, 177
Head-cavities, 196, 218
Head-kidney, 48
Heart, of earthworm, 27
—— of Anodonta, 63
—— of Helix, 74
—— of Apus, 101
—— of crayfish, 129
—— of cockroach, 160
—— of dogfish, 222, 224
—— of frog, 270, 272
—— of mammals, 294
Helix aspersa, 70
—— *pomatia*, 70
Hemiazygos vein, 296
Hemichorda, 202
Hepatic cæca, 158, 177
Hepatic portal system, 184, 229
Heptanchus, 207
Hermaphrodite, *see* Monœcious
Hermaphrodite duct, 81
Heterodont, 287
Heteromorpha, 170
Heteronomous, 46
Hexanchus, 207
Hirudinea, 45, 49
Hind-brain, 235
Histology of earthworm, 29
Homodont, 287
Homomorpha, 170
Homonomous, 46
Hyoid arch, 266
Hyomandibular cartilage, 214
—— cleft, 266
Hyperbranchial groove, 178
Hypoblast, 38, 145, 165, 166, 247, 301
Hypobranchial cartilages, 215
Hypodermis, 137

Ileum, 158
Imago, 170
Incisor teeth, 287
Incus, 291
Infundibulum, 235, 278
Inhalant aperture, 56
Intercalary segment, 168
Interlamellar junctions, 62
Intervertebral discs, 290
Iris, 280
Ischiopodite, 120
Intestine, *see* Alimentary canal
Intestino-tegumentary vessels, 28

Jaws, 214, 266, 270
Joints, 94

Labial palp, 57
Labium, 152
Labrum, 145, 151
Lacinia, 152
Lagena, 245
Larva of Amphioxus, 196
Laurer-Stieda canal, 3, 6
Lens, 279

Lentigen cells, 138
Lepidurus productus, 100, 106
Leptodora hyalina, 134
Leydig's organs, 124, 136
Ligamentum denticulatum 187
Ligula, 152
Limbs, of crayfish, 119
—— of mammals, 293
Limnæa stagnalis, 70, 77
—— *truncatula*, 10, 15
Limpet, 84
Lingua, 158
Lips, 286
Liver, 264
Liver-fluke, 2
Lobi inferiores, 235
Lobster, 113
Lower jaw of mammals, 291
Lubbock, Sir J., 106
Lumbricus herculeus, 17-44
Lungs, 266
Lymph spaces, 183

Macromeres, 36, 83
Malleus, 291
Malpighian body, 276
—— tubules, 159
Mammalia, 284
Mammary glands, 285
Mandibles of Apus, 99, 107
—— of crayfish, 117, 123, 142
—— of cockroach, 152
Mandibular arch, 266
Mantle, 55, 72
Mantle cavity, 55, 72
Marsupials, 299, 300
Maxillæ of Apus, 99, 108
—— of crayfish, 117, 123
—— of cockroach, 152
Maxillipeds, 117, 119, 120
Maxillo-turbinal bone, 290
Meckel's cartilage, 214, 270, 292
Medulla oblongata, 236
Membranous labyrinth, 245, 279
Mentum, 152
Meropodite, 120
Mesenchyme, 262
Mesentery, 181
Mesethmoid, 290
Mesoblast, 1, 36, 48, 141, 145, 165, 247, 256, 260, 266, 301
Mesoblastic somites, 39, 43, 48, 146, 194, 198, 262
Mesocardium, 272
Mesogaster, 220
Mesomere, 36, 48, 51, 83
Mesometrium, 234
Mesonephros, 230, 232, 275
Mesonephric tubules, 276
Mesonotum, 154
Mesopterygium, 216
Mesorchium, 232
Mesothorax, 154
Mesovarium, 233
Metabola, 170
Metamere, 21
Metameric segmentation, 50, 52
Metanauplius, 107
Metanephros, 231, 298
Metanotum, 154
Metapleur, 175, 176
Metapterygium, 216
Metatheria, 299, 300
Metathorax, 154
Micromere, 36, 83
Mid-brain, 235
Mid-gut, 126
Milk dentition, 287
Miracidium, 9, 10, 15
Molar teeth, 287
Mollusca, 53
Monœcious, 33, 80
Monogenetic parasite, 8
Mouth of Amphioxus, 177
Mullerian duct, 232, 233, 277, 298
Muscle segments, 209
Mushroom-shaped gland, 163
Mustelus lævis, 203
Myocœle, 199
Myotomes, 173, 180, 209, 218, 267
Mytilus edulis, 61

Nacreous layer of shell, 54
Naso-oral groove, 204
Nauplius, 107, 142
Nauplius eye, 94
Neck gland, 94
Neck organ, 107
Nephridium, 9, 24, 40, 42, 49, 51, 74, 90, 160, 187, 188
Nephridiopore, 20
Nephroblast, 40

Nephrostome, 24, 42, 275, 276
Nervous system, of Distomum, 6
—— of earthworm, 26
—— of Anodonta, 64
—— of gastropods, 77
—— of Apus, 104
—— of crayfish, 134
—— of cockroach, 162
—— of Amphioxus, 188
—— of dogfish, 234
—— of mammals, 297
Nervures, 154
Neural arches, 209
Neural crest, 279
Neural flexure, 262
Neural folds, 256, 257, 301
—— groove, 258, 301
—— plate, 210, 257
—— spines, 210
—— tube, 192
Neurenteric canal, 193, 258
Neuroblast, 40
Neuropodium, 49
Neuropore, 175, 188, 193
Notochord, 173, 179, 194, 201, 209, 210, 248, 260, 262, 267, 281
Notochordal tissue, 179
Notopodium, 49
Nuchal groove, 92
Nucleus pulposus, 290
Nymph, 170

Oblique muscles of eye, 238, 242
Occipital condyles, 211
—— foramen, 153
—— nerves, 243
Odontophore 69, 76
Œsophagus, *see* Alimentary canal
Olfactory capsules, 211
—— hairs, 136
—— lobes, 235, 278
—— nerves, 236
—— organs, 245, 279
—— pit, 175
Oligochæta, 48
Omentum, 220
Ommatidium, 137
Omphaloidean placenta, 304
Ontogeny, 282
Oostegopod, 98, 106, 111
Optic capsules, 211
—— chiasma, 236
—— cup, 280
—— ganglion, 144
—— lobes, 140
Optic nerve, 236, 280
—— vesicles, 280
Oral tentacles, 177
Organs of Bojanus, 64, 73
Organ of Corti, 298
Ornithorhynchus, 292, 307
Orthoneurous, *see* Euthyneurous
Os articulare, 292
Os orbiculare, 291
Osphradium, 65
Otocyst, 65, 80, 87
Otolith, 65
Ovary, of Distomum, 5
—— of earthworm, 33
—— of Apus, 106
—— of crayfish, 139
—— of cockroach, 164
—— of Amphioxus, 189
—— of dogfish, 233
—— of mammals, 299
Oviducal pores, 20
—— funnel, 277
Oviduct, of Distomum, 5
—— of earthworm, 33
—— of Apus, 106
—— of crayfish, 140
—— of dogfish, 232
—— of frog, 277
—— of mammals, 298
Ovisac, 33
Ovotestis, 80

Palp, 123, 152
Paludina vivipara, 70, 79
Pancreas, 219, 264
Parachordal plates, 269
Paraglossæ, 152
Parapodia, 48, 49
Pareiopods, 117, 144
Parenchyma, 6
Parotarium, 298
Parthenogenesis, 14, 106
Pedal ganglia, 64
Pelvic girdle, 293
Penis, 81
Pericardial sinus, 160, 161

Pericardium, 57, 63, 272, 293
Pericardio-peritoneal canal, 218
Perilymph, 245
Perinæum, 287
Periophthalmic sac, 94
Periostracum, 54
Peripatus, 91, 134
Periplaneta americana, 149, 154
—— *orientalis*, 156, 157
Peristome, 70
Peritoneal funnels, 42, 51, 134, 187
Perivisceral sinus, 131
Pharyngeal bands, 178
Pharyngobranchial cartilages, 215
Pharynx, 21, 177
Phyllites, 96
Phyllopoda, 99
Phylogeny, 282
Pineal body, 235, 278
Pituitary body, 235, 264
—— fossa, 269
Placenta, 299
Placoid scales, 208
Platyhelmia, 1
Pleopods, 117
Pleuron, 114
Pleura, 293
Pleural ganglia, 87
Pleurobranchiæ, 131, 132
Podical plates, 156
Podobranchiæ, 131, 132
Polychæta, 48
Polygordius, 45, 46
Post-trematic nerve, 241
Premolar teeth, 287
Pre-oral cavities, 196
Prepyloric ossicle, 126
Presphenoid, 290
Prespiracular liagment, 215
Pre-trematic nerve, 241
Primary gill-bars, 178
Primitive hypoblast, 192
—— streak, 140, 301
Prismatic layer of shell, 54
Proctodæum, 101, 145, 158, 264
Proglottides, 2
Pronephridia, 48
Pronephros, 230, 275, 277
Pronotum, 154
Propodite, 120
Propterygium, 216
Prostomium, 17, 19, 43, 45, 48, 51, 108, 171
Prothorax, 154
Protopodite, 117
Prototheria, 289, 292, 298
Proventriculus, 23, 124, 147, 158
Pseudobranch, 220
Pterocardiac ossicle, 126
Pulmocutaneous artery, 275
Pulmonary chamber of snail, 72, 73
Pulmonary veins, 273
Pulp, 208
Pulp cavity, 208
Pupa, 170
Pyloric ossicle, 126

Quadrato-pterygo-palatine cartilage, 214

Radula, 76, 77
Raia batis, 204
—— *clavata*, 204
Receptaculum ovorum, 33
Rectal gland, 220
Recti muscles of eye, 238, 242
Rectum, 158
Redia, 12
Renal portal system, 229, 272
Renopericardial canal, 73
Reproductive organs, 106, 162
Restiform bodies, 236
Rete mirabile, 275
Retina, 279, 280
Retinula, 137
Rhabdom, 137, 139
Rhabdomere, 139
Rostrum, 114
Rotation, of frog's egg, 252

Sacci vasculosi, 235
Sacculus, 245
Sacral vertebræ, 289
Scales, of Distomum, 7
Scaphognathite, 122, 131
Scapula, 216
Sclerotic, 280
Sclerotome, 199
Scyllium canicula, 203
—— *catulus*, 103
Sebaceous glands, 285

Segmental plates, 261
—— duct, 275, 277
Segmentation, 43, 46, 166
Segmentation of head, 218, 246
Segments, 17
Semicircular canals, 245
Semper's cells, 138
Sense plate, 258
Septa, 21
Serosa, 166
Sharks, 203
Shell, 54, 70, 86
Shell-gland, of Distomum, 5
—— of gastropods, 84
—— of Apus, 93, 108, 110
Shoulder girdle, 292
Sinistral shell, 72
Sinus venosus, 224
Skeleton, of dogfish, 209
—— of mammals, 289
Skull, of frog, 270
Snail, 53, 69-82, 88
Soft palate, 287
Somatopleur, 40, 181, 198, 267, 301, 303
Somites, 17, 168
Spermatheca, 35, 81, 164
Spermathecal pores, 20
Spermatozoa, 35, 139
Spermiducal pores, 20
Spermophore, 81
Sperm sacs, 34, 232
Spiracle, 207, 220
Spiral valve, 219
Splanchnocœle, 199
Splanchnopleur, 40, 181, 198, 267, 301, 303
Spleen, 220
Sporocyst, 10, 12
Squame, 123
Stapes, 291
Sternebræ, 292
Sternum, 114, 115, 155, 292
Stigmata, 156, 161
Stipes, 152
Stomatogastric nerves, 104, 136, 162
Stomodæum, 39, 87, 100, 124, 145, 147, 158, 264
Streptoneurous, 79
Sub-apical lobe, 96
Sub-endostylar cœlom, 182
Submentum, 152
Suckers, 2
Sulci, 297
Supra-renal capsules, 241
Sweat glands, 285
Sylvian aqueduct, 236, 278
Sympathetic nervous system, 243
Symplectic ligament, 215
Synapticula, 178
Syncerebrum, 105, 135, 144
Systemic arch, 275

Tadpole, 248
Tarsus, 154
Teats, 286
Teeth, 208, 287
Tegmina, 154
Teloblast, 40
Telson, 113
Tergum, 114, 155
Testis of Distomum, 4
—— of earthworm, 33
—— of Apus, 106
—— of crayfish, 139
—— of cockroach, 162
—— of dogfish, 232
Tibia, 154
Thalamencephalon, 235, 278
Third ventricle, 235
Thoraco-abdominal swelling, 142, 144
Thymus gland, 293
Tongue-bars, 178
Torsion of larval gastropod, 87
Trabeculæ cranii, 269
Tracheæ, 156, 161
Trager, 300, 303, 304
Trematoda, 2
Trigeminal nerve, 238
Trito-cerebrum, 168
Trochanter, 154
Trochosphere, 46, 49, 50, 84
Trophoblast, 300
Tunicata, 202
Turbellaria, 2
Tympanic cavity, 266, 279
Typhlosole, 23, 28

Umbilicus, 70
Umbo, 54
Urocardiac ossicle, 126

Urochorda, 202
Urogenital organs of mammals, 298
—— sinus, 232, 233
Uterus, 6, 278, 298, 300
Uterus masculinus, 298
Utriculus, 245

Vagina, 298
Vagus nerve, 241
Valves of shell, 54
Vas deferens, 5
Vasa efferentia, 232
Veins, 272, 296
Veliger, 67, 84
Velum, 84, 177
Velum medullæ posterius, 236
Venous sinuses of dogfish, 228
Ventral plate, 165
— roots of spinal nerves, 188, 279
Ventricle, 224
Vertebral centra, 268
—— column, 209, 289
Vesicula seminalis, 5, 164, 232
Vestibule, 175
Visceral ganglia, 65, 87
—— hump, 57, 70, 76
—— skeleton, 209
Vitelline glands, 5
—— membrane, 164
Vitrella, 137, 139
Vitreous humour, 280

Walking legs, *see* Pareiopods
Wheel organ, 177
White, Gilbert, 149
Wings, 154
Wolffian body, 275
—— duct, 232, 277, 298

Yolk epithelium, 300, 301
—— plug, 252
—— pyramids, 140, 142
—— sac, 306

Zygocardiac ossicle, 126
Zygomatic arch, 290