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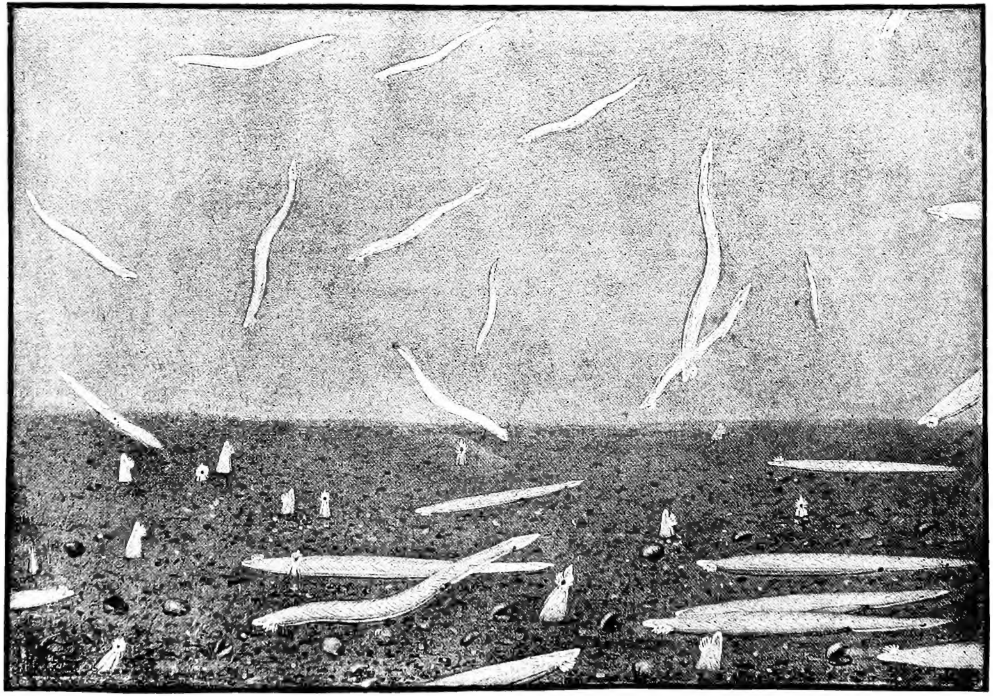

AMPHIOXUS IN THE PANTANO AT FARO (MESSINA).

Frontispiece

COLUMBIA UNIVERSITY BIOLOGICAL SERIES. II.

AMPHIOXUS AND THE ANCESTRY OF THE VERTEBRATES

BY

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WITH A PREFACE

BY

HENRY FAIRFIELD OSBORN

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IN GRATITUDE AND ESTEEM

TO

PROFESSOR E. RAY LANKESTER, F.R.S.

BY

HIS FORMER PUPIL

THE AUTHOR

PREFACE.

THIS volume originated in a course of University lectures prepared at my suggestion by the author. It seemed important that he should bring within the reach of students and of specialists among other groups, his own extensive observations upon Amphioxus and other remote ancestors of the Vertebrates, as well as the general literature upon this group. While our detailed knowledge of the structure and habits of these animals has been rapidly increasing in recent years, it is still in the main very widely scattered in monographs and special papers.

Probably no single group illustrates more beautifully the principles of transformism; for the Protochordates in their embryonic development exhibit remarkable reminiscences of past adaptations, and, in their adult development, the most varied present adaptations to pelagic, deep-sea, littoral, free-swimming, and sessile life. As Lankester has shown, the Ascidians alone give us a whole chapter in Darwinism. But degeneration and change of function constitute only one side of their history. In progressive development some of these types have come to so closely resemble, superficially, certain of the larger groups of Invertebrates, such as the Molluscs and Worms, that it is only at a comparatively recent date they have found their way out of these groups into the Protochordata. Many of these misleading resemblances are now interpreted as parallels of structure springing from parallels in life habit, seen not only in the general body form, but in special organs, such as the breathing apparatus of the Ascidians and Molluscs.

By the side of parallelisms are real invertebrate and vertebrate affinities; so that the problem of resolving these various cases of original and acquired likeness in their bearing upon descent has become one of the most fascinating which modern Zoölogy affords. For example, among the real invertebrate ties of the Protochordates are the ciliated embryos of Balanoglossus and Amphioxus, the Tornaria larva and ciliated ectoderm of Balanoglossus. The nervous system of Balanoglossus presents both vertebrate and invertebrate characters; the respiratory system is identical with that of Amphioxus, while in the embryonic development there are many resemblances *inter se.* In short, in Balanoglossus and the Ascidians the invertebrate type of structure, whether original or acquired, predominates. But in Amphioxus the balance is far on the other or vertebrate side of the scale, and this, with its resemblances to lower forms, gives us the connecting link between Protochordate and Chordate organisation. Before entering into any of these discussions, the author has given a thorough systematic and structural treatment, especially of Amphioxus.

This exquisite form, Amphioxus, is of almost world-wide distribution and has enjoyed the attention of every great zoölogist for over half a century, yet the most recent studies upon it have been among the most productive of discovery. Its interest and value as an object of biological education has steadily increased with the knowledge that in contrast with all the related forms, it stands as a persistent specialised but not degenerate type, perhaps not far from the true ancestral line of the Vertebrates.

H. F. O.

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INTRODUCTION.

THE first zoölogist to put forward, in a definite manner, the view of the existence of a direct relationship between Vertebrates and Invertebrates was the celebrated ÉTIENNE GEOFFROY SAINT-HILAIRE.

It would appear that without any previous zoölogical training, having been brought up as a botanist and mineralogist, he was appointed Professor of Vertebrate Zoölogy at the Museum of the Jardin des Plantes in the year 1793, being then twenty-one years old. His colleague as Professor of Invertebrate Zoölogy was the no less distinguished Lamarck.

Saint-Hilaire's study of the comparative anatomy and osteology of the different groups of Vertebrates — Fishes, Amphibians, Reptiles, Birds, and Mammals — impressed him strongly with the conviction that, in spite of the many obvious contrasts existing between these animals, they are nevertheless essentially constructed upon the same plan, the same parts recurring in all the groups under a more or less altered form. Moreover, such observations as, for example, that the bones of a fish's skull can be more readily compared with the bones of an embryonic mammalian skull than with those of the adult, and that the bones of a bird's skull are separated in the young by sutures just as they are in the skull of a mammal, led him to frame his three great principles in terms of which the phenomena of animal organisation were to be, to a certain extent, explained.

The three principles of Saint-Hilaire, each of which contains a large element of truth, were the following:—

1. The *Theory of Analogues*, according to which the same parts occur, in various grades of form and development, in all animals.

2. The *Principle of Connexions* (Le principe des connexions), according to which the same parts always tend to occur in similar topographical relations.

3. The *Principle of the Correlation of Organs* (Le principe du balancement des organes), according to which, *cæteris paribus*, the bulk of the animal body remains in a measure the same, and any given organ can only become enlarged or reduced according as another organ becomes reduced or enlarged.

Having established these principles in his own mind from the exclusive study of the Vertebrates, the thought next occurred to him that probably they were capable of equal application to the rest of the animal kingdom, and he therefore undertook the task of identifying in the Insects the typical structural peculiarities of the Vertebrates.

According to his theory he would expect to find in the Insects, in some form or other, the same organs that occur in the Vertebrates. At the outset he was, as his successors have since been, confronted by the palpable fact that, while the longitudinal nerve-cord of the Insects lies next to the ventral surface of the body, the spinal cord of the Vertebrates lies below the dorsal surface. Accordingly he came to the conclusion which has since been strongly advocated by the upholders of the so-called "Annelid-theory," that the "back" and "belly" of an animal were gross conceptions of the ignorant and had no morphological meaning. These expressions merely indicated the position which an animal assumed in locomotion relative to the earth, and were in this sense convertible terms, since many invertebrate animals prefer to swim on their "backs," while some fishes also do the same, others again (flat-fishes, Pleuronectidæ) swimming on their sides.

The surfaces of the body in the respective groups having been thus reconciled, Saint-Hilaire proceeded to a detailed comparison between an insect and a vertebrate. The chitinous rings of an insect represent the vertebræ of the higher animals. The viscera of an insect are thus enclosed within its vertebral column, and this condition is compared with what is found in turtles and tortoises where the carapace is fused with the vertebral column. It was necessary to conclude, and Saint-Hilaire did not hesitate to do so, that the legs of insects were equivalent to the ribs of Vertebrates.

It was not the intention of Saint-Hilaire to speculate concerning the ancestry of the Vertebrates, for this would have been impossible at the period in which he did his work, but he merely wished to demonstrate the truth of his principle of the unity of the plan of composition of the animal body. He had therefore no reason to be satisfied with having shown, as he believed, how the Insects could be regarded as possessing a structure essentially similar to that of the Vertebrates, but he had next to show how his principle could be applied to other groups, above all to the group of the Cephalopod Molluscs (squids, cuttle-fish, etc.). This happened in the year 1830, and it precipitated the celebrated and somewhat bitter dispute between the great Cuvier and Saint-Hilaire with regard to the question of "types." While Saint-Hilaire only recognised one universal type, Cuvier arranged the different groups of animals under four entirely distinct types; namely, Vertebrata, Mollusca, Articulata, and Radiata. Cuvier's system of classification remained in use for many years; in fact, until the progress of knowledge necessitated the adoption of a better one.

For the first time, in 1864, the attempt was made by Leydig to grapple with the problem of the origin of the Vertebrates in the light of Darwin's Theory of Evolution (1858). Singular to say, although Leydig approached the subject from an entirely different point of view from that of Saint-Hilaire, yet he also attempted to find points of affinity between the highest Insects and the Vertebrates, and to identify the various subdivisions of the Vertebrate brain in the brain of the bee.

Leydig and all those later authors who would derive the Vertebrates from an articulate ancestor, have started out with the *a priori* conviction that the segmentation of the body (metamerism) which is such a prominent feature (at least with regard to the musculature and skeleton) in fishes, and can be traced throughout the vertebrate series, especially in the embryonic stages, is morphologically identical with the familiar annulation or segmentation of the Articulates (Annelids, Arthropods).

This is obviously a very natural assumption to make, but there is a large mass of facts which run counter to it, some of which will be referred to in the following pages.

An unexpected light was thrown upon the problem of Vertebrate descent in 1866, when the Russian naturalist Kowalevsky published an account of his researches on the embryology of Amphioxus and the Ascidians.

The Ascidians or Tunicates form a curious and in some respects well-defined group of animals, which used to be generally regarded as a subdivision of the Mollusca and as being closely related to the section of the bivalves or Lamellibranchiata. Kowalevsky, however, discovered that their embryonic development takes place on a plan so similar to that of Amphioxus as almost to amount to an identity. The development of the nervous and respiratory systems, and of the axial skeleton or notochord in the Ascidian embryo, as determined by Kowalevsky, showed in the clearest manner that the relationship of the Ascidians to Amphioxus, and through the latter to the Vertebrates, was an extraordinarily close one.

Kowalevsky's discovery of the chordate or sub-vertebrate character of the Ascidian larva, was considered by HAECKEL as affording a direct solution of the problem of the connecting link between Vertebrates and Invertebrates. This was a somewhat extreme view to take of the matter, since Kowalevsky showed that the Ascidians could no longer be regarded as true Invertebrates.

In 1875 the foundation of the Annelid theory of Vertebrate descent was laid independently by SEMPER and DOHRN; and Kowalevsky's observations were explained away in favour of the new line of speculation. It was the discovery of the segmental origin of the excretory tubules of the Selachian (shark) kidney, made independently and simultaneously by SEMPER and BALFOUR, which may be said to have led to the definite framing of the Annelid theory.

Dohrn approached the subject from a different point of view. According to him, not only were the Vertebrates *not* descended from forms allied to the Ascidians and Amphioxus, but the latter were, by a process of almost infinite *degeneration*, derived or degenerated from the former.

That the Ascidians are degenerate animals, to the extent that they have become adapted to a fixed habit of life, is of course obvious; but that they have phylogenetically undergone the immeasurable degeneration which was postulated by Dohrn, is a view which is entirely unjustified by facts. We shall now proceed to a presentation of some of these facts, devoting the first two chapters to the anatomy of Amphioxus, the third to the development of Amphioxus, the fourth to a brief sketch of the structure and development of the typical Ascidians, and the fifth to a consideration of the more abstruse relationships of the lower Vertebrates or Protochordates.

The following classification of the forms more particularly dealt with may be of service: —

Group. — PROTOCHORDATA.

Division 1. HEMICHORDA (Balanoglossus, Cephalodiscus, and Rhabdopleura. See Chap. V.).
Division 2. UROCHORDA (Ascidians).
Division 3. CEPHALOCHORDA (Amphioxus).

I.

ANATOMY OF AMPHIOXUS.

HISTORICAL.

THE historical progress of our knowledge of Amphioxus has often been told, but for the sake of completeness it may be well to sketch its main outlines once more.

It is interesting as being one of the few animals that were not known to Aristotle, having been described and figured for the first time in 1778 by the German zoölogist PETER SIMON PALLAS. Pallas based his description on a specimen preserved in spirit, which had been sent to him from the coast of Cornwall; and as he confined himself to the examination of the external form, he made what may appear to us the somewhat gross error of regarding it as a Mollusc, a species of slug, and he accordingly named it *Limax lanceolatus*. He gives a perfectly recognisable figure of it, but was led astray by its flattened and pleated ventral surface, which might be construed into bearing a faint resemblance to a Molluscan "foot."

This not very extensive knowledge of Amphioxus served the zoölogical world for nearly sixty years, until, in 1834, it was discovered for the second time in the Mediterranean, by the Italian naturalist, GABRIEL COSTA. Costa found it on the shores of Posilippo, in the Gulf of Naples, and was the first to make observations on the living animal and to recognise its true nature. He thought at first that he had absolutely discovered it, but subsequently came across Pallas's description. He showed that it was a *fish* allied to the Cyclostomata, a group which includes the lampreys and hag-fishes.

In his account of its habits he pointed out how sensitive it was to light, and although without apparent eyes, yet the light stimulated it to such an extent that it could by no means tolerate it. Costa mistook the curious tentacle-like processes or cirri, which form a circlet round the mouth (see Fig. 1, p. 12), for respiratory filaments or branchiæ, which suggested to him the name of *Branchiostoma* for the genus, the specific name given by him being *lubricum*, referring to the way in which it slips through the fingers with the rapidity of an electric spark when touched.

WILLIAM YARRELL, in his History of British Fishes (1836), was the next to describe the remarkable creature and to give it the name Amphioxus, by which it has become so well known and which refers to the fact that it is pointed at both ends. Yarrell was also the first to describe the *notochord* or *chorda dorsalis* of Amphioxus as a cartilaginous vertebral column.

Subsequently other observers had taken specimens of Amphioxus from various points, notably from the coast of Sweden, so that the attention of morphologists was at last definitely directed to the interesting form, and in 1841 there were produced three independent memoirs on the anatomy of Amphioxus, which laid the foundation of our present knowledge. The authors of these memoirs were JOHN GOODSIR of Edinburgh, HEINRICH RATHKE of Königsberg, and JOHANNES MÜLLER of Berlin. The work of the last-named author is a masterpiece. With regard to the systematic position of Amphioxus, the outcome of all these researches was, that it was allied to the Cyclostomata, but, as Johannes Müller put it, differed from them to a greater extent than a fish differs from an Amphibian.

HABITS AND DISTRIBUTION.

In consequence of the extension of the firm, and at the same time elastic, notochord to the tip of the snout, Amphioxus possesses an extraordinary capacity for burrowing in the sand of the sea-shore or sea-bottom. If an individual be dropped from the hand on to a mound of wet sand which has just been dredged out of the water, it will burrow its way to the lowest depths of the sand-hillock in the twinkling of an eye.

The frontispiece is designed to illustrate the chief positions in which Amphioxus may be observed. It is represented swimming, lying on the sand, and buried in the sand.

Its usual *modus vivendi* is to bury the whole of its body in the sand, leaving only the mouth with the expanded buccal cirri protruding. When obtained in this position in a glass jar a constant inflowing current of water in which food-particles are involved can be observed in the neighbourhood of the upstanding mouths.

The food consists almost entirely of microscopic plants (Diatoms, Desmids, etc.) and vegetable *débris.*

While passing through the pharynx the food becomes involved in the slimy secretion of a gland at the base of the pharynx known as the *endostyle* or *hypobranchial groove* (cf. Figs. 2 and 3), and is thus held in the pharynx while the water with which it entered flows out through the gill-slits into the atrial chamber. The food is then carried through the intestine enveloped in a continuous cord of slime or mucus, which is kept in perpetual motion and rotation by the action of the cilia with which the epithelium of the alimentary canal is richly provided. After the digestible elements in the food have been dissolved in the secretions of the intestinal wall the cord of slime with the attached fæces is duly ejected.[2] *

The extreme shyness to a bright or sudden light which, as Costa observed, is manifested by Amphioxus, is probably correlated with the presence of black pigment spots in the nerve-cord. If a lighted candle is carried into a dark room in which Amphioxus are being kept in glass jars, the excitement produced among the small fish is indescribable.

Occasionally it emerges from its favourite position in the sand, and after swimming about for some time it will sink to the bottom, and there recline for a longer or shorter period upon its side on the surface of the sand. When resting on the sand, it is unable to maintain its equilibrium in the same position as an ordinary fish would do, but invariably topples over on its side, indifferently on the right or left side.[3] In the higher fishes, including the lampreys, there is a special apparatus for controlling the equilibrium; namely, the semicircular canals of the ear. There is nothing of the kind in Amphioxus, but in the Ascidian larva and in the Appendicilariæ there is, as we shall see, a structure situated in the floor of the brain known as the *otolith*, which possibly exercises an equilibrating influence.

From what has been said above it follows that Amphioxus is an entirely passive feeder; it does nothing in the way of biting, or even sucking, and has not to search far for its food, but merely takes what is brought in with the

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* This number and others which are scattered through the text refer to the Notes at the ends of the chapters.

water which is drawn into the mouth by the powerful ciliary action of the cells lining the roof of the mouth and the wall of the pharynx.

Speaking generally, Amphioxus is an inhabitant of shallow water; it is essentially a littoral form, and is apt to occur in the neighbourhood of any sandy shore. Its occurrence, however, is often curiously local, as shown by its behaviour at Messina. In the vicinity of Messina there are a couple of rather extensive salt-water pools, at some points of considerable depth, which, in the course of ages, have apparently been shut off from the adjacent sea by the formation of sandbanks. In the more northerly of these small lakes, lying almost at the extreme north-eastern point of Sicily, Amphioxus occurs in astonishing abundance; while in the more southerly lake, which is connected with the former by a narrow artificial canal, it is entirely absent. Both of these lakes communicate by narrow outlets with the Straits of Messina, where, however, Amphioxus is somewhat rarely met with. In the Gulf of Naples it is extremely abundant; while in Plymouth Sound, in the English Channel, it is comparatively rare. On the coast of France it is said to grow to an unusually large size. It has been taken in greater or less numbers from many other localities in Europe, on the Atlantic and Pacific shores of North and South America, and from the shores of Australia, Japan, and Ceylon. Its geographical distribution may therefore be said to be pre-eminently world-wide, and, in fact, it is liable to turn up on any shore in the temperate and tropical regions. And yet with all this world-wide distribution there is only a single genus, with some eight species,[4] the different species being remarkably alike, differing slightly in the height of the dorsal fin and in the number of muscle-segments, the latter forming one of the chief diagnostic characters for a given species.

The extensive geographical distribution of Amphioxus, combined with the fact that it is a shore-dweller and not a roving pelagic animal, and also with its remarkably constant features and, as a rule, trifling specific differences, shows that we have to do with an extremely archaic form.

EXTERNAL FORM.

A good idea of the external appearance an proportions of *Amphioxus lanceolatus* can be obtained from the accompanying figure (Fig. 1). Its actual length varies from about four to as much as eight centimetres. In the fresh condition it is semi-transparent, so that some of the internal organs can be seen through the skin, which is often iridescent.

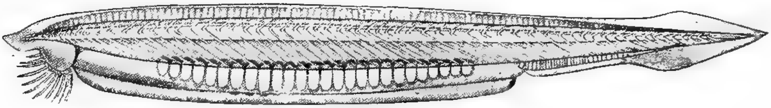

Fig. 1. — *Amphioxus Lanceolatus* from the left side, about twice natural size. (After LANKESTER.) The gonadic pouches are seen by transparency through the body-wall; the atrium is expanded so that its floor projects below the metapleural fold; the fin-chambers of the ventral fin are indicated between atriopore and anus. The dark spot at the base of the fifty-second myotome represents the anus.

The figure shows the pointed extremities of the body and the circlet of tentacles or *buccal cirri* round the margin of the mouth, or more accurately, the *oral hood*, because the mouth proper is covered over by a hood-like fold of the integument, from the margin of which these processes grow out. Extending from near the anterior extremity of the body to the posterior end are seen some sixty-two oblique parallel lines, each bent upon itself in such a way as to form two sides of a triangle, the apex of which is directed forwards. These are the partitions or *septa* which divide the longitudinal muscles of the body into a series of separate muscle-chambers or *myotomes*. In virtue of the longitudinal muscles being broken up, so to speak, into a great number of segments, the animal is enabled to swim rapidly with a serpentine motion. In the remarkable pelagic animal, *Sagitta*, where the muscles are not segmented, this motion is impossible, and instead, it darts forward by sudden and spasmodic jerkings of its tail.

In Amphioxus, the tail or post-anal region of the body is very much reduced, and the muscle-segments of the trunk therefore constitute its only means of locomotion, there being no muscular fins. Beyond the muscle-plates, both in front and behind, the *notochord*, which forms the *axial skeleton* of the body, is seen to extend to the anterior and posterior extremities. The extension of the notochord beyond the anterior limit of the dorsal nerve-tube is a very exceptional condition, and has led to the creation of a special order for the reception of Amphioxus; namely, the *Cephalochorda*.

The oval structures seen lying below the muscle-plates in Fig. 1 are the reproductive organs, male or female as the case may be. Instead of being represented by a single genital gland on each side of the body as they are in the higher fishes and Vertebrates generally, they consist here of some twenty-six pairs of perfectly distinct chambers, occurring in correspondence with the muscle-segments or myotomes of the region to which they belong, and extending from the tenth to the thirty-fifth myotome inclusive. These chambers are known as the *gonadic pouches*. (See Fig. 2.)

About two-thirds of the way from the front end of the body there is a comparatively large aperture in the mid-ventral line. It is the excurrent orifice of a spacious cavity which surrounds to a large extent the internal organs, including above all the pharynx, and is known as the *atrial chamber*, or simply *atrium*, while its opening to the exterior is the *atriopore.*

The *anus* or outlet of the digestive tract occurs near the posterior end of the body; it does not lie in the mid-ventral line, but high up on the left side. At its first appearance in the young embryo, the anus does lie approximately in the mid-ventral line (cf. Fig. 64, p. 117), but as soon as the caudal fin begins to develop, it is pushed on to one side, always the left, and so attains its final position. A similar displacement of the cloacal aperture occurs in the Dipnoan fish *Protopterus*, where, however, the direction of displacement is not constant, the aperture lying now to the right, now to the left, of the middle line. Again, in the tadpoles of certain Batrachians the cloacal aperture is displaced to the right of the middle line.* (Cf. Fig. 8.) The fact of the displacement of openings by the

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* The asymmetrical position of the cloacal aperture of certain Batrachian tadpoles has been systematically worked out by BOULENGER. In tadpoles of the genera *Rana* and *Hyla*, the cloacal aperture is dextral, while in the Toads and Pelobatoids it is median. (See G. A. BOULENGER, *A Synopsis of the Tadpoles of the European Batrachians.* Proc. Zool. Soc. London, 1891. pp. 593–627. Plates 45–47.)

In Rana the cloacal aperture may occasionally occur in a median position as a variation. (WILLEY, *Note on the position of the cloacal aperture in certain Batrachian tadpoles.* Transactions New York Acad. of Sciences, Vol. XII. 1893. pp. 242–245.) My attention to the previous literature on this subject was kindly drawn by Mr. G. A. Boulenger.

Since writing the above my attention has been called to the following paper by Professor BURT G. WILDER, *Lateral Position of the Vent in Amphioxus* [Branchiostoma] *and in the Larvæ of Rana Pipiens* [Catesbiana]. Proc. Amer. Assoc. Adv. Sc. XXII. 1873. pp. 275–300.

differential growth of neighbouring structures is a very curious one, and should be borne in mind. It will have a special significance when we come to consider the development.

There are no paired muscular fins in Amphioxus, but running along the whole length of the back is a median ridge which is called the *dorsal fin*. It extends round the front end of the body, where it becomes continuous with the right half of the oral hood. (Cf. Fig. 9.) Posteriorly it becomes enlarged to form the tail expansion or *caudal fin*, and is continued round the hinder extremity of the body past the anus as far as the atriopore. Along the back, this continuous fin is supported by a series of gelatinous *fin-rays*, each of which lies in a chamber of its own. The fin-rays, whose number may exceed 250, do not extend to the extreme anterior and posterior ends of the body. The ventral portion of the fin in the region between atriopore and anus is supported by a similar series of fin-rays, but there are two of them placed side by side in each compartment. In other words, the fin-rays of the ventral fin are paired.

Amphioxus, like most fishes, is laterally compressed so that a transverse section through the body in front of the atriopore is found to have the form of an equal-sided spherical triangle, the base of which consists of the floor of the atrial chamber. At each of the basal angles of the triangle there is a fold of the integument containing a cavity (Fig. 2). This is the *metapleural fold*[1] which stretches on each side of the body from the region of the mouth to slightly beyond the atriopore. (Cf. Fig. 1.) The cavity in the folds is the *metapleural lymph-space*. The apex of the triangular cross-section is formed by one of the dorsal fin-chambers enclosing a lymph-space into which a fin-ray is projecting.

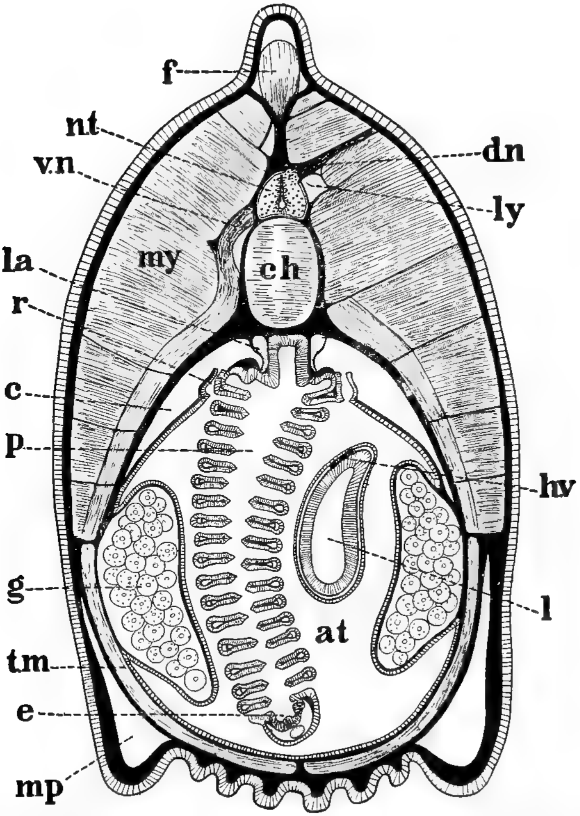

Fig. 2. — Diagrammatic transverse section through pharyngeal region of female Amphioxus. (After LANKESTER and BOVERI, from R. Hertwig's *Lehrbuch d. Zoologie.*)

at. Atrial cavity. *c.* Dorsal cœlom, separated from atrial cavity by the double-layered membrane known as the ligamentum denticulatum. *ch.* Notochord. *d.n.* Dorsal spinal nerve. *e.* Endostyle, below which is the endostylar cœlom containing the branchial artery. *f.* Fin-ray of dorsal fin. *g.* Gonadic pouch containing ova. *h.v.* Hepatic vein lying in the narrow cœlomic space which surrounds *l*, the liver or hepatic cœcum. *l.a.* Left aorta separated from the right aorta by the hyperpharyngeal (epibranchial) groove. *ly.* Lymph-space. *mp.* Metapleur. *my.* Longitudinal muscles of myotomes; over against the dorsal cœlom these muscles are arranged vertically, and form the rectus abdominis of Schneider. *n.t.* Spinal cord. *p.* Pharynx. *r.* Excretory tubule. *t.m.* Transverse or subatrial muscles. *v.n.* Ventral (motor) spinal nerve, the fibres of which have the appearance of passing directly into the muscle-fibres.

N.B. The connective tissue (cutis, notochordal sheath, cœlomic epithelium, etc.) is indicated by the black lines

In young transparent individuals, such as that of which the anterior portion is represented in Fig. 3, the pharynx, or first division of the digestive tract, into which the mouth leads directly, can be seen through the body-wall, and it is found to be perforated on each side by a great number of elongated vertical slits, whose number varies with the age of the individual, but may eventually attain the astonishing figure of 180 pairs. They are the *gill-clefts* opening from the pharynx into the atrial chamber. In the living Amphioxus an almost continuous stream of water is being drawn through the mouth into the pharynx for purposes of respiration and nourishment, then passing out of the pharynx, by way of the gill-clefts, into the atrial chamber and thence to the exterior through the atriopore.

Cranium and Sense-organs.

Besides lacking differentiated lateral fins, Amphioxus differs fundamentally from the higher Vertebrates in the absence of a *cranium*, of *paired eyes*, and paired or unpaired *auditory organs.*

On account of the absence of a cartilaginous cranium it has been placed by itself in a separate division, the *Acrania*, in contrast to all the other Vertebrates proper, from the Cyclostomata upwards, which all possess a cranium of one sort or another and are hence known as the craniate Vertebrates or *Craniota.* In Amphioxus the only cartilage in the head-region consists of a ring lying round the margin of the oral hood at the base of the buccal cirri. It is formed of separate pieces corresponding to the number of the cirri, and each piece sends up a process into its adjacent cirrus, so that the latter is provided with a stiff skeletal axis (Figs. 3 and 4). These are the *buccal cartilages.* As pointed out by Johannes Müller, they are not to be compared with the jaw-apparatus, nor to the hyoid or tongue-bone of the jaw-bearing Vertebrates, but they belong to the same category as the mouth-cartilages of the Cyclostome fishes (which possess a hyoid cartilage in addition) and the *labial cartilages* of Selachians (sharks).

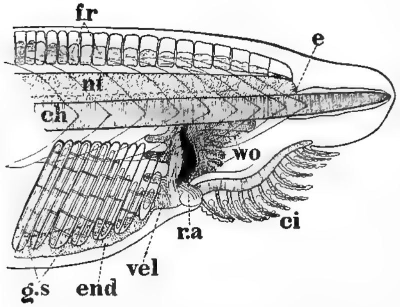

Fig. 3. — Anterior portion of body of young transparent individual. (After J. MÜLLER, slightly altered.)

ch. Notochord. *ci.* Buccal cirri. *e.* Eye-spot. *end.* Endostyle. *f.r.* Fin-rays lying in the fin-chambers. *g.s.* Gill-slits; the skeletal rods of the gill-bars are indicated by black lines. *nt.* Spinal cord, with pigment granules near its base. *r.a.* Downgrowth from right aorta lying to the right of *vel.* the velum; with velar tentacles projecting back into pharynx. *w.o.* Räderorgan; ciliated epithelial tracts on inner surface of oral hood.

The absence of paired eyes and of any kind of auditory organ has been mentioned above. There is, however, a median eye, which consists of a comparatively large unpaired pigment spot lying at the anterior extremity of the dorsal nerve-tube.* A row of similar, but much smaller, masses of pigment lie along the floor of the spinal canal, commencing some distance behind the eye (Fig. 3).

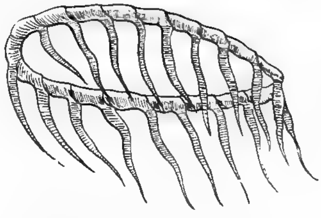

Fig. 4. — Buccal cartilages of Amphioxus. (After J. MÜLLER.) The basal pieces lie end to end in the margin of oral hood, and each basal piece sends up an axial process into the corresponding buccal cirrus.

Immediately above and behind the eye-spot is a small pit in the body-wall reaching from the outer surface of the

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* The eye-spot has been observed to be sometimes broken up into two pigment masses. (See AYERS, No. 105 bibliog.)

body to the anterior wall of the brain. This is known as *Kölliker's olfactory pit,* after its discoverer. The cells which line its walls carry long vibratile cilia, and it possibly subserves in some degree an olfactory function. In the larva the cavity of the brain opens into the base of the olfactory pit by a pore known as the *neuropore,* which we shall consider later. In the adult this pore becomes closed, but the base of the olfactory pit appears to remain connected with the roof of the brain by a solid stalk. The olfactory pit, like the anal opening, lies asymmetrically on the left side of the body (Fig. 5). It is forced to one side in the course of the development consequent on the formation of the fin-like expansion of the integument in this region, which, as we have seen, is nothing more than the cephalic continuation of the dorsal fin.

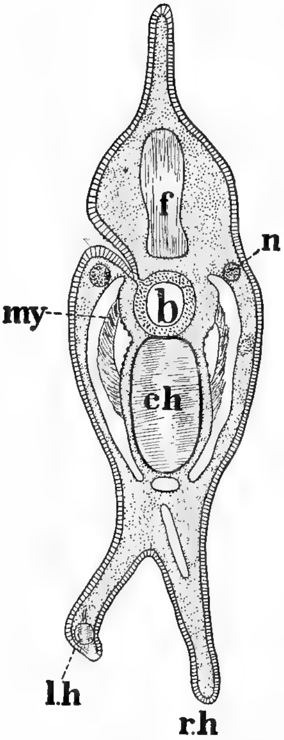

Fig. 5. — Transverse section through region of olfactory pit. (After LANKESTER.)

The olfactory pit is seen as an ectodermic involution on the left side in contact with the wall of *b*, the cerebral vesicle. *ch.* Notochord. *f.* Lymph-space of cephalic portion of dorsal fin. *r.h.* and *l.h* Right and left portions of oral hood. *my.* Muscles of first myotome; outside of the muscles is the myocœlic lymph-space of first myotome; inside of the muscles is the apex of the myocœlic lymph-space of the second myotome. *n.* Cranial nerve (second pair).

N.B. — The dotted shading represents the thickened gelatinous connective tissue of the head-region in which irregular lymph-spaces occur.

The mouth of Amphioxus would seem to be well guarded against the intrusion of noxious substances. Everything entering the mouth has to pass through a vestibule richly provided with sensitive epithelial cells. This vestibule consists of the oral hood with its marginal cirri, at the back of which lies the definite oral opening or *velum*, as it was called by HUXLEY on account of its resemblance to a similar structure in the young lamprey (Ammocœtes). (Cf. Fig. 3.) In the adult the velum carries twelve tentacles of its own, the *velar tentacles*, which are not to be confused with the *buccal cirri* of the oral hood. The velar tentacles project in a backward direction freely into the pharynx.

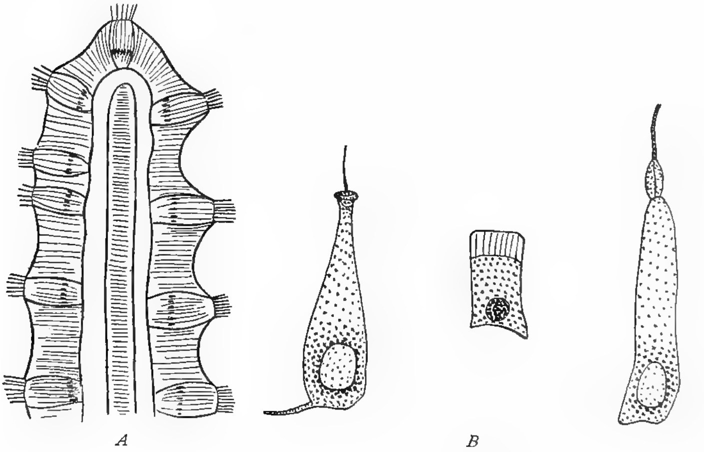

Fig. 6. — *A*. Portion of a buccal cirrus to show groups of sense-cells.
B. Isolated cells of the skin; two columnar sense-cells carrying a sensory hair, and one cylindrical epidermic cell with striated cuticular border. (After LANGERHANS.)

Groups of sense-cells occur on the side of the buccal cirri at intervals (Fig. 6). Some of these cells bear a vibratile cilium at their free ends, and others bear stiff hairs. Both kinds of cells are mingled in the same group.

Similar groups of sensory cells occur on the margin of the velum and its tentacles (Fig. 7). It may be noted, in anticipation, that the velum is derived directly from the mouth of the larva, which becomes secondarily hidden from superficial view by the overgrowth of the oral hood.

According to LANGERHANS, similar cells to those mentioned above, carrying stiff sensory hairs, are scattered diffusely all over the external surface of the body. (Cf. Fig. 6 *B.*) But a concentration of sense-organs comparable to the *lateral line* of the higher fishes is apparently absent.[7]

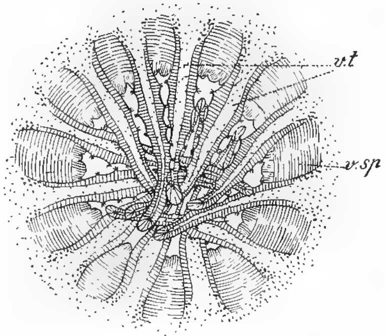

Fig. 7.—Velum of Amphioxus seen from the inside of the pharynx. (After LANKESTER.)

v.sp. Sphincter muscle of velum. *v.t.* Velar tentacles lying across the oral opening.

A remarkable structure which seems to combine the properties of gland and sense-organ occurs on the under surface of the oral hood. It consists of a patch of modified epithelium drawn out into finger-shaped epithelial tracts, the cells of which carry long cilia. (See Fig. 3.) It was discovered and accurately described by Johannes Müller, who called it the "Räderorgan" on account of the resemblance of its ciliary movements to those of the wheel-apparatus of a Rotifer. The result of the combined action of the cilia is to cause a flow of water into the pharynx. In connection with the Räderorgan must be mentioned a special depression forming a peculiar sense-organ (Geschmacksorgan) lying against the right side of the notochord, known as the *groove of Hatschek.*

INTERNAL ANATOMY.

Atrial Cavity.

In making a dissection of a frog or a fish, as soon as the body-wall is cut through, we find ourselves groping about in a large cavity in which the viscera lie. This is the *body-cavity* or *peritoneal cavity*, or, again, the *cœlom.*

If we slit open the ventral body-wall of Amphioxus, we discover what appears to be an exactly similar cavity. It is, however, not the cœlomic cavity, but the *peribranchial* or *atrial cavity*, into which the pharyngeal gill-slits open. The older anatomists, including Johannes Müller, regarded it as the true body-cavity, and the latter author was forced to the conclusion that Amphioxus differed fundamentally from all the other Vertebrates in that the gill-slits opened into the peritoneal cavity. Although that condition of things was hard to imagine, yet it seemed to be obviously the case, since the reproductive organs appeared to lie in the same cavity, and it went without saying that a cavity containing the gonads could only be the peritoneal cavity. In reality, the gonads do not lie in this cavity; they only project into it and lie in a space of their own which is separated from the atrial cavity by a double-layered membrane. (Cf. Fig. 2.)

Huxley threw some light on the matter in 1874, when he compared the atrial or peripharyngeal cavity of Amphioxus to the *opercular cavity* which surrounds the gills of the tadpoles of the frog and tailless Amphibia generally. In the case of the tadpole, as is well known, there are some four pairs of gill-slits which open at first directly to the exterior. Subsequently an opercular fold grows backwards over them as in fishes, but with this difference, that in the frog-tadpole the fold of one side becomes continuous ventrally with that of the other, so that in effect we have one large semicircular fold covering over the gill-slits. Eventually the hinder free margin of the fold undergoes concrescence with the body-wall, so that a single peribranchial cavity is formed about the gills. This cavity is closed all round except at one point, usually on the left side, but sometimes in the mid-ventral line, where it remains open as the *porus branchialis*, or so-called *spiraculum*.

This comparison of Huxley's was extremely well taken, and although the two cavities, namely, the peribranchial cavity of the frog-larva and the atrial chamber of Amphioxus, are probably by no means homologous, or genetically related to each other, still the close analogy that exists between them is most instructive, and yet, singular to say, it did not lead Huxley to a correct interpretation of the atrial chamber.[5]

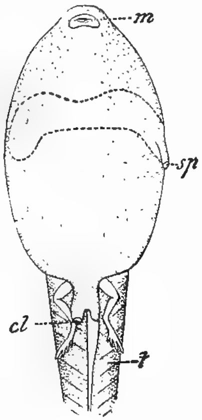

Fig. 8.—Tadpole of Frog (*Rana clamata*) from ventral side. (Original.)
cl. Dextrally placed cloacal aperture. *m.* Mouth. *sp.* spiraculum; the dotted line indicates the extent of the opercular chamber. *t.* Tail.

Its true nature was at length established by Rolph in 1876. By comparing his own observations on the adult with those of Kowalevsky on the larva, Rolph came to the conclusion that the atrial cavity of Amphioxus originated by the growth of two folds of the body-wall over the gill-slits on each side, and by their subsequent fusion in the mid-ventral line except at one point, which remained open as the atriopore. Although the details in the formation of the atrium are not exactly such as they were supposed to be by Rolph (see below), yet the end-result is virtually the same, and his work marks a distinct advance in our knowledge of the structure of Amphioxus, by showing that the epithelium lining the walls of the atrial chamber is not peritoneal, but is derived by a process of in-folding, from the ectodermic covering of the surface of the body. In other words, the atrial cavity, like the opercular cavity of the Amphibian tadpole, is lined by *ectoderm.*

Viscera.

A bird's-eye view of the internal organs, as exposed by cutting the animal open ventrally by incisions extending forwards and backwards from the atriopore, is shown in Fig. 9. First and foremost, our attention is arrested by the relatively enormous pharynx occupying more than half the length of the body, with its right and left perforated walls and parallel gill-bars abutting at the mid-ventral line on the *endostyle.*

The alimentary canal is seen in the dissection to have a perfectly straight course between mouth and anus, with no windings whatever. Growing out ventrally from what may be termed the pyloric region of the intestine, a short distance behind the pharynx and in front of the atriopore, there is a large diverticulum ending blindly in front, which in the adult lies for the greater part of its extent applied against the right wall of the pharynx (Fig. 9). This is the so-called *hepatic cæcum*, corresponding to the liver of higher forms. The permanent condition of the liver in Amphioxus is comparable to its embryonic condition in the Vertebrates, where it attains a much more complicated structure in the older stages by subsequent branching and anastomosing of the branches, etc. It is essentially a median ventral outgrowth from the intestine, and its lying on one side of the pharynx in Amphioxus is only a secondary topographical necessity.*

Attached to the lateral muscular body-wall on each side are the gonadic pouches, which project into the cavity of the atrium. (Cf. Fig. 2.) Their number, which is usually twenty-six pairs, varies slightly, and sometimes there are more on one side than on the other, as in Fig. 9.

The atrial cavity does not end at the atriopore, but is continued beyond it as a blind sac lying to the right of the intestine, and reaching back nearly as far as the anus. In Fig. 9 the position of this *post-atrioporal extension* of the atrium is indicated by means of a dotted line.

Finally, in Fig. 9, the anus is seen lying to the left of

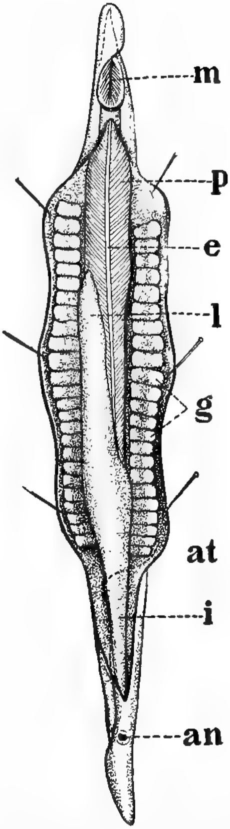

Fig. 9.—Amphioxus dissected from the ventral side. (After RATHKE, slightly altered.)

m. Entrance to mouth with the buccal cirri lying over it. *p.* Pharynx. *e.* Endostyle. *l.* Hepatic cœcum. *g.* Gonadic pouches. *at.* Position of atriopore; the post-atrioporal extension of the atrium is indicated by the dotted line passing over to the right side of *i*, the intestine. *an.* Anus.

N.B.—Note absence of differentiated stomach.

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* The cœcum is held in position by cord-like attachments to the ligamentum denticulatum.

the caudal fin, and the right margin of the oral hood is shown to be continued round the front end of the body into the cephalic expansion of the dorsal fin.

Cœlom.

The question now arises: if the atrial cavity is not the true body-cavity, what has become of the latter? In order to determine this point, it is necessary to have recourse to transverse sections through the body, such as the one represented in Fig. 2, which is taken through the middle of the pharyngeal region. In a section like this, the work of tracing the limits of the atrial cavity is often greatly facilitated by the presence of a rich brown pigment in the epithelium lining its walls. We find, accordingly, that the atrial cavity has extended itself at the expense of the cœlom, and has reduced the latter, in the main, to a small space on either side of the dorsal aorta, the aorta being double in this region (Fig. 2). This portion of the cœlom is sometimes spoken of as the *supra-pharyngeal cœlom*, and sometimes as the *subchordal cœlom*, since it lies dorsal to the pharynx on the one hand, and below the notochord on the other. Other fragments, so to speak, of the cœlom are found accompanying some of the branchial bars, namely, every alternate one; and another portion occurs below the endostyle. (See Fig. 13.) The hepatic cœcum is also surrounded by a division of the cœlom, but its cavity is reduced to a minimum, and the same applies to the cœlom surrounding the intestine immediately behind the pharynx. Behind the atriopore, as we have seen, the atrial cavity is confined to the right side, so that on the left side of the intestine in this region the cœlom presents its original proportions.

Structure of Pharynx.

We have already had occasion to mention the fact that the wall of the pharynx on each side is perforated by a great number of vertically elongated slit-like apertures — the gill-clefts. In the middle region of the pharynx the gill-slits stretch almost from the roof to the base of the pharynx, but in front and behind they gradually become much lower in vertical height (Fig. 10). In the fully expanded condition the gill-slits are nearly vertical, as in Fig. 10, but by the contraction of the transverse muscles, which lie in the floor of the atrium, they are often found to be directed very obliquely backwards, and this is the condition in which they almost invariably occur in preserved specimens. That is the reason why so many of the bars are involved in a single transverse section. (Cf. Fig. 2.) On account of the prodigious extent to which

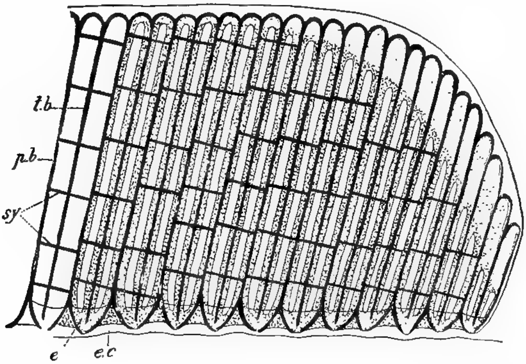

Fig. 10. — Anterior portion of right wall of pharynx, to show arrangement of skeletal rods. (After J. MÜLLER.)

e. Endostyle. *e.c.* Endostylar cœlom. *p.b.* Skeletal rod of primary gill-bar. *t.b.* Skeletal rod of tongue-bar. *sy.* Cross-bars or synapticula.

N.B. — A simple gill-slit undivided by a tongue-bar should have been inserted in the figure in front of the first double slit. J. Müller failed to observe this.

the pharynx is perforated by the gill-clefts, it is necessary for it to have some sort of skeletal support to prevent it from collapsing. This is effected by a series of stiff gelatinous rods which lie in the walls bounding the gill-clefts. These rods have the consistency of chitin, — the material that forms the exoskeleton of insects, — and are insoluble in caustic potash. The portion of the pharyngeal wall which lies between any two gill-slits is called a *gill-bar.*

It will be seen at once in Fig. 10 that there are two kinds of *skeletal rods* differing in the behaviour of their lower extremities. Dorsally the rods arch over into one another, but ventrally they are independent, and every alternate rod is bifurcated, while the somewhat shorter intermediate rods end plainly. The forked rods form the skeletal support of the *primary gill-bars*, while the intermediate simple rods support the *secondary gill-bars*, or *tongue-bars*, as they are usually called. The primary bars constitute the walls of the primary gill-clefts. The latter, at their first origin, appear as simple oval openings in the wall of the pharynx. Later on the simple opening becomes divided into two by the gradual dipping downwards of its dorsal margin until it meets and fuses with the ventral margin. In this way is the tongue-bar formed and the gill-slit doubled. (Cf. Fig. 11.) The statement which was made above, therefore, that there could be as many as 180 openings on each side of the pharynx, signified that there might be some ninety pairs of primary gill-clefts.

Eventually the gill-slits become still further subdivided, though not so obviously, by the formation of small *cross-bars* which pass over from one primary bar to another, skipping over the tongue-bar, although eventually fusing with the skeletal axis of the latter on their inner faces (Fig. 10).

Evolution of the Thymus Gland.

Tongue-bars, like those occurring in the gill-slits of Amphioxus, are only known otherwise to occur in the remarkable worm-like creature, *Balanoglossus.* In the higher Vertebrates they appear to be entirely absent, but in the course of the development of the higher forms there is a structure which arises from the dorsal wall of the gill-slits which may very well be the homologue of the tongue-bars of Amphioxus. This structure is the *thymus gland.* The thymus is one of those enigmatical ductless glands which are so eminently characteristic of the Vertebrate organisation, and are of the utmost physiological and pathological importance to the individual. In their structure and development they give clear indications of having undergone an extensive change of function in the course of their evolution.

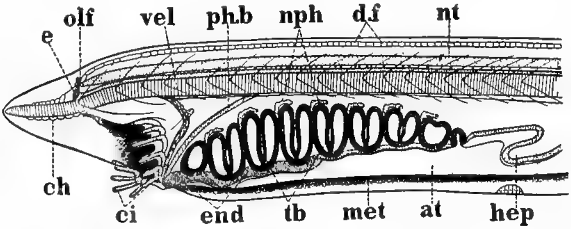

Fig. 11.—Anterior region of young Amphioxus from left side. (After WILLEY; the renal tubules inserted after BOVERI.)

at. Atrium. *ci.* Buccal cirri. *ch.* Notochord. *d.f.* Dorsal fin-chambers. *e.* Eye-spot. *end.* Endostyle. *hep.* Outgrowing cœcum; the index line passes through one of J. Müller's renal papillæ. *met.* Metapleural fold. *nph.* Nephridia or renal tubules. *nt.* Spinal cord. *olf.* Olfactory pit. *ph.b.* Peripharyngeal ciliated band. *tb.* Tongue-bars. *vel.* Velum.

The thymus, therefore, is presumably the derivative of an ancestral organ, which formerly possessed an active function as opposed to the apparently passive function which this gland, and others like it, exercise in the existing Craniota. Amphioxus has hitherto been regarded as forming a marked exception among the Vertebrates in having no thymus, whereas one might reasonably have expected to find here the representative of the thymus in full activity. Although contrary to the prevailing impression, I would suggest that the thymus is represented in Amphioxus by the very actively functional tongue-bars.

Dohrn has shown that in the Selachian (shark) embryo the thymus arises by a series of distinct cell-proliferations from the epithelium of the dorsal wall of the successive gill-slits with the exception of the first, which is the spiracle (Fig. 12). Sometimes these proliferations cause a small projection downwards into the gill-slit, comparable to an incipient tongue-bar. Eventually these separate thymus rudiments pass inwards and come together so as to form the definite thymus gland. Dohrn concluded from its mode of origin that the thymus resulted from the metamorphosis and introversion of gill-filaments; and in point of fact, this view of its morphological nature is probably correct. But the tongue-bars of Amphioxus, which correspond closely in position to the thymus rudiments in the Selachian embryo, and are, like the latter,

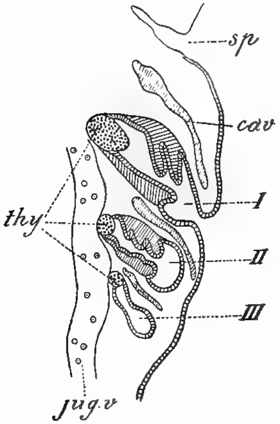

Fig. 12. — Horizontal section through the branchial region of an embryo of *Scyllium canicula* to show the rudiments of the thymus. (After Dohrn.)

sp. Spiracle. *cav.* Cavity (cœlom) of branchial bar. I, II, III. First, second, and third gill-pouches. *jug.v.* Jugular vein. *thy.* Thymus rudiments.

essentially epithelial structures, are nothing else than gill-filaments or gill-lamellæ. It appears, therefore, that we are justified in supposing that the tongue-bars of Amphioxus are the functionally active organs, of which the thymus of the higher forms is a metamorphosed derivative.

Endostyle.

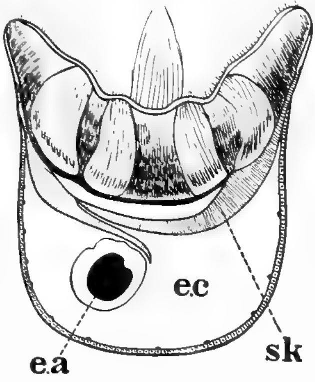

Fig. 13. — Transverse section through endostyle of Amphioxus. (After LANKESTER, slightly altered.)
e.a. Branchial artery with blood-clot. *e.c.* Endostylar cœlom. *sk.* Skeletal plate.

Returning, then, to the consideration of the more intimate structure of the pharynx, — the endostyle has been already mentioned as a ventral groove of the pharynx accompanying the latter throughout its whole length. A transverse section of it alone is shown in Fig. 13. It is composed of very high columnar cells arranged throughout in one layer, although the tenuity of the cells, whose nuclei are often placed at different levels, gives rise to the impression of cells occurring in several layers. The four groups of gland-cells, placed symmetrically two on either side of the median line, are the distinguishing feature of the endostyle. The cells are all ciliated, but those in the middle line bear a bunch of specially long cilia, which are of great importance in putting in motion the cord of mucus secreted by the glandular cells of the endostyle. Below the endostyle, there is a well-defined portion of the true body-cavity in which the branchial artery lies. This is the *endostylar cœlom.*

Besides the rods in the gill-bars, there is a series of paired skeletal plates lying immediately below the endostylar epithelium (Fig. 13). These plates correspond in number to the primary gill-slits. Their shape and arrangement are shown in Fig. 14. They slightly overlap each other, and alternate with one another just as the primary gill-slits alternate. This alternation of paired structures is of very general occurrence in Amphioxus, and affects almost every system of organs, — such as muscular, nervous, reproductive, and branchial systems. It may be stated as a general rule, to which there are some exceptions, that with regard to the paired organs of Amphioxus, the organs of one side (*e.g.* myotomes, primary gill-slits, gonads, spinal nerves) do not lie opposite to their *antimeres* on the other side, but alternate with them.

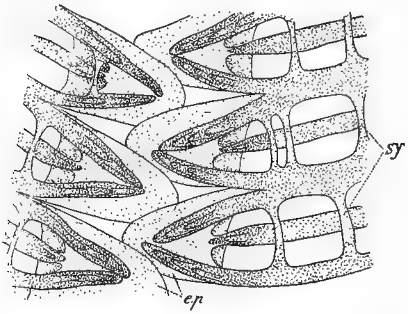

Fig. 14. — Lower portions of skeletal rods of pharynx with three pairs of endostylar plates, seen from above. (After SPENGEL.)

The substance of the skeletal rods passes into that of the endostylar plates (*e.p*), thus producing an arcade like the cover of a shoe (Spengel). *sy*. Cross-bars (synapticula).

Branchial Bars.

The structure of the branchial bars is shown in section in Fig. 15. Both kinds of bars, primary and secondary, have the same general appearance, being compressed and band-like, but the secondary bar is the smaller of the two.

The chief point of difference between them is, that in the primary bar a portion of the cœlom is involved, which is absent in the secondary bar. In the case of the primary bar (Fig. 15 B), commencing from the outside, that is to say, from the edge turned towards the atrial cavity, we have first a patch of columnar atrial epithelium, at the corners of which some of the cells contain a quantity of the rich brown pigment which has been referred to above as being characteristic of the atrial epithelium generally.

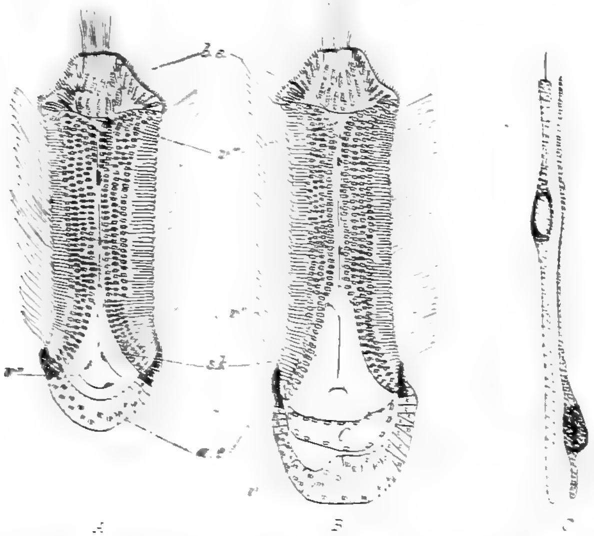

Fig. 15. A and B.—Transverse sections through primary (B) and secondary (A) gill-bars. (After BENHAM, slightly altered.)

a.e. Atrial epithelium. b.e. Branchial epithelium. c. Cœlomic space of primary bar. sk. Skeletal rods. v. Cœlomic vessel of primary bar. v'. External vessel of both bars. v''. Internal vessel of both bars.

N.B.—Benham takes the space at the inner edge of the skeletal rod of tongue-bar for a blood-vessel.

C. Isolated ciliated cells of the branchial epithelium. (After LANGERHANS.)

Next comes a cavity which is a portion of the cœlom, and is lined by the flat cœlomic epithelium. In fact, the dorsal, or subchordal cœlom on each side (cf. Fig. 2) is put in connection with the endostylar cœlom by a canalicular detachment of the cœlom which accompanies each primary bar of the pharynx. Wedged in between the cœlomic and atrial epithelia of the primary bar is a small blood-vessel, *v*. Internal to the cœlomic space lies the skeletal rod, which in section has the shape of a triangle, at whose apex there is another blood-vessel, v''. The sides and inner edge of the bar are composed of the ciliated pharyngeal epithelium. The cells of the latter are always arranged in a single layer, but at the sides of the gill-bars they are very long and thin, and the nuclei are crowded together at different layers so as to give the idea of a many-layered epithelium (Fig. 15 *C*). The cells of one side of the bar are in juxtaposition with those of the opposite side, except at a point near the internal edge of the bar, where a space occurs. In this space there is a third blood-vessel, v'''.[6]

In the secondary bar, there is no vessel corresponding to the one marked *v* in the primary bar, and the vessel that corresponds with v'' is entirely enclosed within the skeletal rod.

The dorsal wall of the pharynx is closely appressed against the sheath of the notochord, and separates the two dorsal aortæ from one another. It has here the form of a groove running parallel with and opposite to the endostyle. It is known as the *hyperbranchial groove*. (Cf. Fig. 2.) Two special tracts of ciliated epithelium form the sides of it, and pass downwards in front to join the anterior extremity of the endostyle on each side. In front, where these tracts bend downwards with a crescentic curve, they are known as the *peripharyngeal bands*. (See Fig. 11, *ph.b.*)

Musculature.

The musculature of Amphioxus is composed almost entirely of striated muscle-fibres. Involuntary or smooth muscle-fibres are remarkable for their extreme tenuity, and in correlation with this condition is to be noted the absence of a distinct *sympathetic nervous system.*

The striated muscles can be arranged in two groups: (i.) the *parietal* muscles constituting the myotomes or muscular segments of the body, and (ii.) the *visceral* muscles which arise independently of the myotomes and are not segmentally arranged. The smooth muscle-fibres, which occur on the walls of the alimentary canal and blood-vessels, may be grouped together as the *splanchnic* muscles.

The parietal muscles are the great longitudinal muscles which make up the thick lateral walls of the body. In Amphioxus they form collectively the essential organ of locomotion. The portion of them lying next to the atrium on each side, and stretching from the notochord to the base of the myotome, is placed at an angle to the rest, and has a more vertical direction. (Cf. Fig. 2.) This has been described by SCHNEIDER as the *rectus abdominis.* It probably co-operates with the muscles of the floor of the atrium to cause the contraction of the latter cavity for the purpose either of expelling water or reproductive elements through the atriopore.

The visceral muscles consist of (*α*) the transverse muscles stretching across the floor of the atrium (cf. Fig. 2), (*β*) muscles of the oral hood and cirri, (*γ*) sphincter muscle of the velum (cf. Fig. 7), (*δ*) anal sphincter.

All the striated muscles of Amphioxus are composed of highly characteristic flat lamelliform plates, which can often be resolved into a great number of finer fibrils. In the longitudinal muscles of the adult, nuclei are very rarely met with, but in other places they are to be found; as, for instance, in the fibres composing the velar sphincter (Fig. 16).

This peculiar plate-like muscular tissue is found in connection with the lateral muscles only of the Cyclostome fishes. The muscle-fibres of the mouth and velum, as LANGERHANS pointed out, closely resemble those found in the walls of the heart of the higher Vertebrates. In transverse section the cut edges of the longitudinal muscle-plates are to be seen stretching across the myotome. (Cf. Figs. 2, 26.)

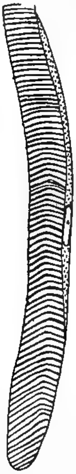

Fig. 16.— Isolated muscle-fibre of the velar sphincter. (After LANGERHANS.)

The transverse or *sub-atrial* muscles are divided by a median longitudinal septum of connected tissue into right and left halves. They are further subdivided into a series of compartments by thin transverse septa. These compartments, however, are not arranged segmentally, since they are more numerous than the myotomes. The muscle-plates of these muscles are placed edge on, so that they do not lie one over the other as the plates of the myotomes do, but one behind the other. They are attached to the septum at the base of the myotomes on the one hand, and to the median septum or *raphe* on the other, and also they are attached at numerous points to the connective-tissue sheath or *fascia* which covers them above and below. When they contract, therefore, the floor of the atrium is thrown into a number of characteristic pleats. (Cf. Fig. 2.) The individual muscle-plates of Amphioxus appear universally to be devoid of a protecting sheath or *sarcolemma*. The sub-atrial muscles end at the atriopore, round which they form a sphincter muscle.

The muscles of the oral hood, which serve for the erection and supination of the buccal cirri, consist of two portions, an *inner* and an *outer* (Fig. 17). The outer one, by whose contraction the cirri are retracted in such a way that they come to lie across the entrance to the mouth, those of one side interlacing with those of the other so as to form a perfect barrier to the mouth, is a powerful muscle lying outside the bases of the cirri. The inner muscle, which apparently serves to erect the cirri, consists of distinct muscular tracts lying between every two consecutive cirri.

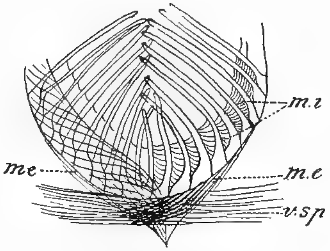

Fig. 17.—Muscles of the oral hood. (After LANGERHANS.)

m.e. Outer muscle (m. externus) whose fibres interlace with those of the velar sphincter (*v.sp*). *m.i.* Inner muscle (m. internus).

The sphincter muscle of the velum has been already referred to. (Cf. Fig. 7.) A sphincter muscle of a similar character also surrounds the anus.

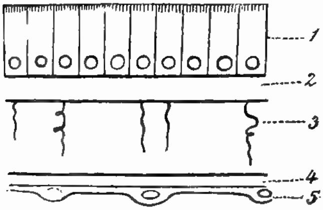

Fig. 18.—Diagram illustrating the different layers of the integument. (After HATSCHEK.)

1. Epidermis. *2.* Outer layer of cutis (basement membrane of Hatschek and Spengel). *3.* Middle layer of cutis with radial fibres. *4.* Inner layer of cutis. *5.* Epithelial layer of cutis (limiting membrane).

The septa which separate the myotomes from one another are composed of fibrous connective tissue. The fibres are imbedded in a gelatinous matrix. The salient feature in connexion with the entire connective tissue-system of Amphioxus is the great preponderance of the gelatinous element. It forms the bulk of the dorsal and ventral fin-rays, and of the cephalic and caudal integumentary expansions.

The middle layer of the cutis below the epidermis (cf. Fig. 18) is composed mainly of this tissue with radial fibres superadded. In the metapleural folds it attains a greater development than in the rest of the integument. (Cf. Fig. 2.) It also constitutes the middle layer of the sheath of the notochord, but the fibres in this case run concentrically, and not radially.* The outermost layer of the cutis (Fig. 18) and the innermost layer of the sheath of the notochord are composed of a peculiar and very highly refringent and homogeneous tissue of the same order as that which forms the skeletal rods of the pharynx.[6] The layer of connective tissue which separates the myotomes from the body-cavity, and which springs out from the base of the notochordal sheath (Fig. 2), occupies the same position as the ribs of the higher Vertebrates.

NOTES.

1. (p. 15.) *Metapleural Folds.*—In the development of the paired fins of Selachians it was discovered, in 1876, by **Balfour**, that at a certain stage there appears along each side of the body "a thickened line of epiblast (*i.e.* ectoderm), which from the first exhibits two special developments." "These two special thickenings are the rudiments of the paired fins, which thus arise as special developments of a continuous ridge on each side, precisely like the ridges of epiblast which form the rudiments of the unpaired fins." After giving more details, Balfour says, "The facts can only bear one interpretation, viz. *that the limbs are the remnants of continuous lateral fins.*"

Shortly afterwards (1877), but quite independently, **James K. Thacher** was led by a comparative study of the adult skeleton of

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* In that portion of the sheath of the notochord which lies above the dorsal groove of the pharynx there is a special tract of connective-tissue fibres which run longitudinally. A similar tract can sometimes be observed in the dorsal portion of the sheath below the nerve-cord. (Schneider, Lankester, Spengel.)

Selachians and other fishes, to a belief in the homodynamy of median and paired fins, and he therefore concluded that the latter arose as differentiations from primitively continuous lateral fins just as the median fins are obviously differentiated from a continuous dorsal and ventral fin-fold. Thacher further suggested that the original continuous lateral fins were represented in Amphioxus by the metapleural folds. He said, "As the dorsal and anal fins were specialisations of the median folds of Amphioxus, so the paired fins were specialisations of the two lateral folds (metapleural folds), which are supplementary to the median in completing the circuit of the body."

It has recently been observed by Professor E. A. Andrews, that in a new species of Amphioxus from the Bahamas, the right metapleural fold is continued behind into the median ventral fin. Subsequently I found the same condition to obtain in a species of Amphioxus from the Torres Straits.

From these observations, and from the fact that the right half of the oral hood (which apparently arises in continuity with the right metapleur—*vide infra*) is continued in front into the cephalic expansion of the dorsal fin, it would appear that there is a great measure of truth in Thacher's suggestion, notwithstanding the fact that in the condition in which we find them in the existing Amphioxus, the metapleural folds do not function as fins. Thacher's hypothesis has also been supported by Van Wijhe.

2. (p. 10.) The accompanying diagram (Fig. 19) will serve to illustrate the actual course of the food through the pharynx of Amphioxus, as recently determined by Andrews, from observations on transparent specimens from the Bahamas. The food, enveloped in the mucous secretion of the endostyle, passes along the dorsal groove of the pharynx (hyperpharyngeal groove) into the intestine.

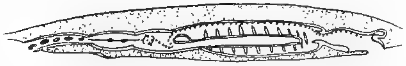


Fig. 19.—Diagram illustrating (by a dotted line) the course of the food as it passes through the pharynx and intestine of Amphioxus. (After Andrews.)

The small diverticulum on the dorsal side of the oral hood represents the *groove of Hatschek* somewhat exaggerated. The arrows behind the cœcum indicate the rotation to which the food is here subjected by the action of the cilia of the intestinal epithelium.

3. (p. 10.) On those occasions on which Amphioxus is not buried in the sand, but lies on the surface of the sand, occasions which frequently occur when it is kept in captivity, and especially after having been confined for a considerable length of time, it lies on one side, as mentioned in the text. The percentage of instances in which it lies on the right or left side has not been taken, and consequently it is not possible to say that it prefers lying on one side rather than on the other. Since the olfactory pit and the anus occur on the left side, it is conceivable that it prefers to lie on the right side. If this had been a definite habit, it would probably not have escaped the observation of Johannes Müller. It is a fact which is too frequently overlooked, that the lying on one side is entirely incidental, and is emphatically *not* the result of adaptation to a peculiar mode of life, as it is in the case of the Pleuronectidæ.

4. (p. 11.) *Species and Distribution of Amphioxus.* — A useful synopsis of the genus Branchiostoma has recently been prepared by Andrews, as an appendix to his paper on the remarkable species which occurs at the Bahamas. In this species there is a long caudal process into which the notochord extends. It is an active swimmer. Gonadic pouches are only present on the right side, those on the left being suppressed. The latter is also true of *Branchiostoma cultellum.* The peculiarities of the species from the Bahamas were such that Andrews deemed it necessary to form a new genus, *Asymmetron.*

In the table of species on page 41 it will be noticed that the lengths of the different species are not in any proportion to the number of myotomes.

Insufficiently described species occur off the coasts of *Japan, Ceylon,* and *Fiji Islands.* It is interesting to note that while in Europe, Amphioxus occurs as far north as Scandinavia, on the Atlantic coast of North America, *Chesapeake Bay* appears to be its northern limit, and it is therefore wholly unknown at the Marine Biological Station at Woods Holl. Attention may further be called to the simultaneous occurrence of two distinct species, *B. cultellum* and *B. belcheri,* in the Torres Straits. *B. cultellum* is easily recognisable on account of the unusual height of its dorsal fin.

Name of Species.	Number of Myotomes.	Length in Millimetres.	Geographical Distribution.
1. B. lanceolatum . .	59–61	35–80	Scandinavia, Heligoland, England, France, Mediterranean, and Chesapeake Bay.
2. B. caribæum . .	58	43	Brazil, Mouth of La Plata, Jamaica, Tampa Bay, Gulf of Mexico, Beaufort, N.C.
3. B. cultellum . .	52–55	25–35	Thursday Island (Torres Straits), Moreton Bay (E. Australia).
4. B. bassanum . .	75	—	Bass Straits, Australia.
5. B. belcheri . . .	65	65	Borneo and Torres Straits (Prince of Wales Island).
6. B. elongatum . .	79	60	Peru.
7. B. californiense .	69	70	San Diego, California.
8. B. lucayanum . . =Asymmetron lucayanum, Andrews	66	13–16	Bimini and Nassau Harbour (Bahamas).

5. (p. 22.) Huxley had recognised in 1874, in the light of Kowalevsky's work, that the atrial cavity of Amphioxus was lined by an epithelial layer derived from the ectoderm, but came to the conclusion that it was, by the very fact of its inversion within the body, converted into peritoneal epithelium. He applied the same interpretation to the opercular chamber of the Amphibian tadpole, and gave to a body-cavity of this character the general name of *epicœle*. Rolph's merit consisted in distinguishing clearly between atrial epithelium and peritoneal epithelium, and hence between atrial cavity and true body-cavity.

6. (p. 38.) There is a great deal of difference of opinion as to the exact nature of that dense refringent tissue which forms the outer layer of the cutis and the skeletal rods of the gill-bars. Lankester regarded them both as the products of connective tissue-cells, hence belonging to the mesoderm, while Hatschek and Spengel looked upon the outer layer of the cutis as the product of the ectoderm, of the nature of a *basement membrane*. Spengel again has advocated the view that the skeletal rods of the

pharynx are special developments of the basement membrane, which separates the two opposed epithelial layers of each gill-bar from one another. (Cf. Fig. 15.) More recently, BENHAM has described nuclei in the latter membrane, thus showing it to be a sheet of connective tissue. In this case the substance of the skeletal rods should be regarded as a variety of connective tissue.

A further difference of opinion prevails as to the nature of the space which traverses the skeletal rod of the tongue-bar. LANKESTER supposed it to be a diverticulum of the cœlom. SPENGEL and BOVERI interpreted it as a blood-vessel; and, finally, BENHAM thinks that it is both, inasmuch as he conceives there to be a blood-vessel contained in a cœlomic space. It should be added that these finer details are extremely difficult to determine.

7. (p. 21.) *Lateral Line.* — Since the lateral line constitutes one of the most characteristic and constant features in the organisation of fishes, its absence in Amphioxus has always been one of the most serious difficulties in the way of a conception of this animal as, in any sense, an ancestral form. It need hardly be pointed out that from whatever point of view we regard Amphioxus, it must necessarily have become specialised and modified along its own particular line of evolution, and cannot, as it stands, be taken as a direct ancestral form, but rather as a more or less close relative of, or an exceedingly ancient offshoot from, the actual ancestor of the Vertebrates. The modifications which it has undergone will, as in every other case, have resulted in more or less extensive changes both in the function and structure of different parts. Thus, while the metapleural folds are very probably the homologues of the primitive continuous lateral fin-folds, yet in their actual form and function they may or may not represent the primordial condition of these folds. Certain peculiar features in connexion with the origin and innervation of the metapleural folds of Amphioxus have led me to form a conception as to the origin of the lateral line sense-organs which may perhaps have some value as a working hypothesis.

In those primitive fishes which possessed the continuous lateral fin-folds, it is very clear that the latter could not have performed a locomotor function, but they must have served primarily as *balancers.* Without going into the difficult question as to how such structures could have arisen *de novo*, we may at least attempt to appreciate the necessity for their existence.

There is one difference between the general form of the body in Invertebrates and Vertebrates respectively which seems to be of fundamental importance, but which has not been sufficiently emphasised. As a general rule, in the Invertebrates, the body is not bilaterally compressed, but, on the contrary, is either cylindrical, sub-cylindrical, or flattened dorso-ventrally. Obvious exceptions to this rule are presented by the Lamellibranchiate Molluscs and by many Arthropods; but these exceptions are readily intelligible as secondary modifications.

On the other hand, in the more primitive Vertebrates (*i.e.* fishes), the bilateral compression of the body is one of the cardinal features of the external form. To this fundamental rule there are of course exceptions afforded, for example, by the skates; but it is a self-evident fact that these again have arisen by secondary modification from originally bilaterally compressed forms. With the evolution of the pentadactyle appendages and the assumption of a terrestrial existence, the shape of the body in the higher Vertebrates has undergone such changes that the primitive bilateral compression of the body is, as a rule, only present at some period of the embryonic development.

Amphioxus exhibits the characteristic vertebrate bilateral compression of the body in a very typical manner; while Balanoglossus shows invertebrate affinities in regard to the shape of the body, which is sub-cylindrical.

The bilateral compression of the primitive vertebrate body did not arise in itself as a special adaptation to a particular mode of life; but rather in correlation with other characters of the organisation. The development of the dorsal medullary tube and the notochord above the digestive tube and the concentration of the myotomes would necessarily lead to a bilaterally compressed form of body. We see this not only in fishes, but in the course of the development of all Vertebrates.

It is obvious that such a shape of the body is highly unfavourable for the maintenance of the equilibrium except with the assistance of some special mechanical and sensory apparatus.

Now in Amphioxus, the metapleural folds, whatever their exact function may be, do not serve in any way as balancers; and, as mentioned in the text, Amphioxus has no means of maintaining its equilibrium when not actually swimming.

We will therefore keep in mind more especially those Palæozoic fishes which presumably possessed continuous lateral fin-folds serving as balancers. The nearest known fossil relatives of these fishes appear to be the *Cladoselachidæ* (see BASHFORD DEAN. *Contributions to the Morphology of Cladoselache* (*Cladodus*). Jour. Morph. IX. 1894. pp. 87–112. Also A. SMITH WOODWARD. *The Evolution of Fins*. Natural Science, I. 1892. pp. 28–35).

The lateral fin-folds may be spoken of as *mechanical* balancers, and to render them efficient organs, there must be a *sensory* apparatus in connexion with them. The suggestion lies near that *the ectoderm which took part in the formation of the lateral fin-folds also produced the sense-organs of the lateral line*.

The lateral line, through its capacity for receiving impressions of wave-movements, etc., would thus serve as the agent in the co-ordination of such muscular activities as are necessary to the maintenance of the equilibrium.

Having been once established, no special difficulty is presented by the fact that the lateral line has spread over the head-region. Moreover, it may be taken as a well-established morphological fact that the auditory organ (internal ear) became evolved as a specialisation of part of the lateral line in the cephalic region, and that it therefore belongs to the same category as the less elaborate sense-organs of the remainder of the lateral line.

As is well known, the internal ear has two functions, *audition* and *equilibration*. It must be supposed that, at its first origin, the whole lateral line served in a general way the function of equilibration, and that this function eventually became chiefly localised in the semicircular canals of the ear, the remainder of the lateral line perhaps undergoing a slight change or limitation of function.

It seems certain that at first the sense-organs of the lateral line must have been innervated by spinal nerves. This follows both from *a priori* considerations and also from the condition in Amphioxus, where the ectoderm of the metapleural folds is innervated by the *Rami cutanei ventrales* of the dorsal spinal nerves. Under these circumstances it is necessary to suppose with Eisig that the lateral line nerve (*Ramus lateralis vagi*) arose as a *collector.*

The removal of the lateral line from the immediate neighbourhood of the paired fins in existing fishes is easily intelligible on the ground that the fins have become discontinuous and elaborated into effective locomotor organs.

It is not impossible that the lateral line nerve (*R. lateralis vagi*) is homodynamous with the remarkable *Ramus cutaneus quinti* (*R. recurrens trigemini et facialis* or *Nervus lateralis trigemini*, Stannius) of Teleosteans, which runs to the base of all the fins, paired as well as unpaired; just as the paired fins themselves are known to be homodynamous with the median fins. In this case the *R. cutaneus quinti* would be of primitive significance, notwithstanding the fact that it is absent in Selachians; and it would be another of those features of organisation in the possession of which Teleosteans exhibit more primitive relations than do the existing Selachians. (Compare the functional pronephros of Teleosteans and the entirely rudimentary pronephros of Selachians.)

The above suggestion that the lateral line arose in the first instance as a sensory equilibrating apparatus in conjunction with the mechanical equilibrating apparatus effected by the continuous lateral fin-folds, will of course meet with numberless difficulties when it is attempted to carry it out in detail. As in some other respects, so here, a great difficulty is presented by the Cyclostomes. It may, however, be pointed out that if the various conclusions which have been drawn with regard to the morphology of Amphioxus are correct, it must be assumed that the Cyclostomes have entirely lost the lateral fin-folds and that the sense-organs of the lateral line have secondarily become diffused in their distribution over the body. The latter conclusion is also indicated, firstly, by the fact that there is a fairly well developed internal ear in the Cyclostomes which, as noted above, must have been differentiated from a primitive lateral line; and secondly, by the fact that although the sense-organs are scattered, there is nevertheless (at least in Petromyzon) a definite lateral line nerve.

II.

ANATOMY OF AMPHIOXUS.

INTERNAL ANATOMY (*continued*).

In the preceding chapter we have seen how Amphioxus, while possessing the general facies of a fish, and the primary essential attributes of a Vertebrate, is nevertheless destitute of many of the most obvious structural features which we usually associate with our conception of a fish. Thus it has no skull, or, in other words, it is *Acraniate* (Haeckel). It has no jaws, and is therefore a *Cyclostome*, as opposed to a *Gnathostome.* Finally, it has no paired sense-organs and no paired muscular fins. Its eye-spot is median, like that of a Cyclopean monster. There is no trace of an auditory organ of any kind, while the single so-called olfactory pit, abutting on the anterior end of the nerve-tube, has been regarded as an indication of a monorhinic condition preceding the amphirhinic, *i.e.* with paired nostrils.

Vascular System.

Now, in turning our attention to the vascular system, we shall find that Amphioxus has no heart. In any animal with a comparatively well-developed vascular system, the presence of a heart might be regarded as a *sine quâ non.* This, however, is by no means always the case; and although, among the Invertebrates, the extensive groups of the Arthropoda (Insects and Crustacea) and the Mollusca are characterised by the possession of a definite muscular heart, yet in the various groups of worms there are many which possess a very elaborate vascular system, while not one of them possesses a heart. In fact, in the last-mentioned forms, the place of a heart is taken, functionally, by *contractile blood-vessels.* And this is the case with Amphioxus. Among the Vertebrates, including the Ascidians, it forms the unique instance in which such an acardiac condition of the vascular system is met with.

Lying below the pharynx in the endostylar cœlom, there is a blood-vessel known as the *branchial artery*, which contracts more or less rhythmically, and corresponds in its position and relations to the heart and truncus arteriosus of the higher forms.

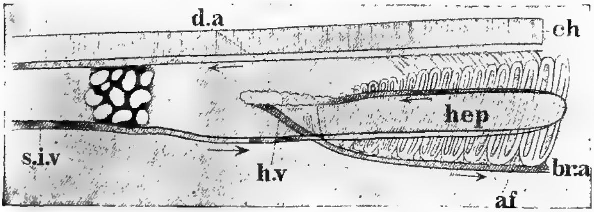


Fig. 20.—Diagram illustrating the chief parts of the vascular system of Amphioxus. (Constructed after J. MÜLLER and SCHNEIDER.)

The arrows indicate the direction of flow of the blood. *ch.* Notochord. *hep.* Hepatic cœcum. *af.* Afferent branchial vessels (vascular bulbils of J. Müller) entering the primary bars from *br.a*, the branchial artery; the efferent branchial vessels are seen emerging from the tops of both primary and secondary bars and running into *d.a*, the dorsal aorta. From the dorsal aorta, the blood enters the capillaries over the wall of the intestine (indicated by the dark reticular shading), and finally reaches *s.i.v*, the sub-intestinal vein. The latter carries the blood to the base of the hepatic cœcum, over which it passes into another system of capillaries (not indicated), and is then collected into *h.v*, the hepatic vein, which passes backwards and curves round into the branchial artery.

From this branchial artery, lateral branches running up into the primary bars of the pharynx are given off on both sides alternately. (Cf. Fig. 20.) There appears to be no direct communication between the vessels of the tongue-bars and the branchial artery.

At the base of the primary bars the lateral offshoots of the branchial artery are found to be enlarged to form vascular bulbils, which are also contractile. Furthermore, at this point they divide into three branches of smaller calibre, which constitute the vessels of the primary bar. (Cf. Fig. 15.) One of these branches, as we have seen, runs up between the cœlomic and atrial epithelium, and may be called after Boveri the *cœlomic vessel*, of the primary bar (Figs. 15 and 21). Another lies at the inner edge of the skeletal rod, and is the so-called *external vessel*, while a third lies immediately below the inner pharyngeal epithelium of the bar, and forms the *internal vessel*.

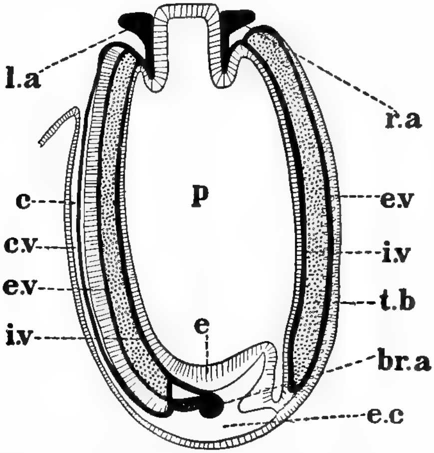


Fig. 21.—Diagram of a section through the pharynx involving a primary bar (to the left), and a tongue-bar (to the right), to illustrate the circulation in the branchial bars. (After Spengel.)

br.a. Branchial artery. *c.* Cœlom; outside of which is the atrial epithelium. *c.v.* Cœlomic vessel of primary bar. *e.* Endostyle. *e.c.* Endostylar cœlom. *e.v.* External vessel. *i.v.* Internal vessel. *l.a.* Left aorta. *r.a.* Right aorta. *p.* Cavity of pharynx. *t.b.* Tongue-bar.

The two last-named vessels only are represented in the tongue-bars, and differ in their arrangement in the latter in so far as the *external vessel* is enclosed within the skeletal rod.

The blood which circulates in the tongue-bars flows into them, not from the branchial artery, but from the primary bars through the cross-bars of the pharynx. The vessels of each gill-bar unite above into a single *efferent vessel*, which conducts the blood into the dorsal aorta of either side. So that while efferent vessels issue alike from both primary and tongue-bars, the *afferent vessels*, which lead the blood directly from the branchial artery into the gill-bars, are confined to the primary bars (Fig. 20). The blood, having been oxygenated during its passage through the gill-bars, past which a constantly renewed stream of water is kept flowing, enters the dorsal aorta, and is then carried backwards to the region of the intestine. The two halves of the dorsal aorta, which we have already noted on either side of the hyperpharyngeal groove, become united into a common trunk behind the pharynx, so that in the region of the intestine there is a single dorsal aorta (cf. Fig. 28), from which lateral branches are given off to the wall of the intestine. These then break up into capillaries, which anastomose freely together, and so form a perfect vascular network round the intestine. Finally, the blood emerges from this capillary system into a large vein lying below the digestive canal, the *sub-intestinal vein*. Here it flows in a forward direction until it reaches the base of the hepatic cœcum. At this point the vein appears to stop short, but in reality breaks up into another system of capillaries surrounding the liver.[1] From these again the blood is collected into the large multiple hepatic vein lying above the cœcum. Here it flows backwards as far as the angle formed by the cœcum with the alimentary canal, where the vein bends sharply round into the branchial artery, and so the cycle is completed (Fig. 20). According to JOHANNES MÜLLER, the time required for one complete circulation of the blood in Amphioxus is one minute, and in this time any given droplet of blood will have traversed the whole body. Contrary to what takes place in the higher Vertebrates, a single contraction of the heart (*i.e.* branchial artery) in Amphioxus suffices for a complete circulatory cycle.[2]

The right and left dorsal aortæ differ from one another in respect to the behaviour of their anterior cephalic terminations. At the front end of the pharynx, the right aorta opens out into a wide vascular expansion which flanks the velum on the right side (Figs. 3 and 22, *r.a.*). Johannes Müller, who first figured this structure, took it for the anteriormost aortic arch connecting the branchial artery directly with the dorsal aorta.

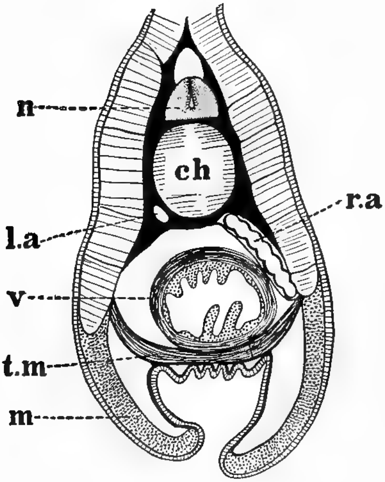


Fig. 22.—Transverse section through region of velum to show difference in behaviour of right and left aortæ. (Altered from LANGERHANS.)

ch. Notochord. *l.a.* Left aorta. *m.* Metapleur. *n.* Spinal cord. *r.a.* Right aorta. *t.m.* Transverse muscles; the septum (raphe) which divides these muscles into two halves is no longer median, but shifted towards the right side in consequence of the fact, discovered by VAN WIJHE, that the right transverse muscles dwindle out and end in this region, while the left transverse muscles are continued into the outer muscle of the oral hood. *v.* Velum.

However, according to the recent researches of Professor

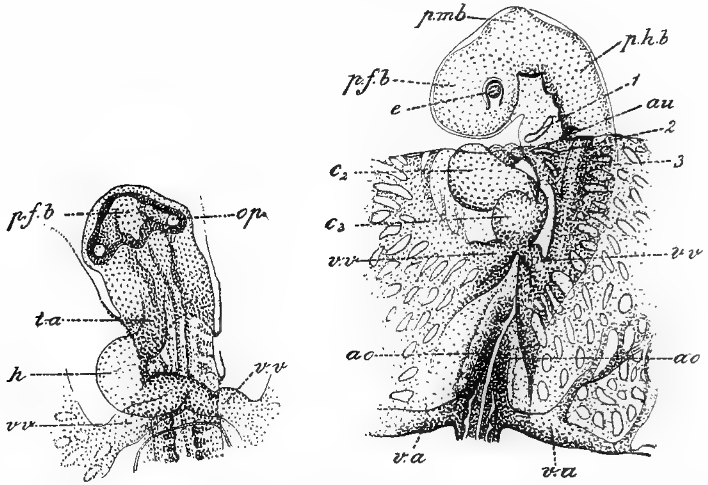
J. W. VAN WIJHE, it would appear that this so-called aortic arch does not communicate with the branchial artery, but ends blindly below in the neighbourhood of the right metapleur. Dorsally, the aorta from which this lateral arch-like outgrowth occurs, is continued forwards (not as a simple vessel, but as a complex of vessels) as far as a peculiar sense-organ known as the *groove of Hatschek*, after its discoverer. This groove lies in the roof of the oral hood to the right of the notochord, and is derived from the *præoral pit* of the larva (see below). (Cf. Fig. 76.)

In front of the sense-organ this dilated continuation of the right aorta communicates beneath the notochord by means of a transverse vascular commissure with the left aorta, which retains its small calibre and simple character throughout. From the vascular complex of the right aorta arise the vessels which supply the buccal cirri.

Hitherto we have only spoken of those blood-vessels which are related to some part or other of the alimentary canal. In point of fact the parietal or somatic vessels of Amphioxus, if present at all, must have a very subordinate physiological significance. Their place is taken by *lymph-spaces*, of which there are a great number in various parts of the body. Such are the dorsal and ventral fin-chambers, the spaces in the metapleural folds, spaces at the apices of the myotomes and in connexion with the dorsal nerve-roots, etc. (Cf. Fig. 2.)[3]

The vascular system of Amphioxus presents several features of great interest from a phylogenetic or evolutionary point of view.

We have seen that the heart is in no way differentiated from the branchial artery and is therefore a simple tubular vessel. This is the primary condition of the heart in the embryos of all the craniate Vertebrates. In the latter, as the embryonic development proceeds, this simple tubular heart widens out, acquires a series of constrictions, and undergoes a remarkable flexure known as the *sigmoid flexure.* Two stages in the formation of the sigmoid flexure of the heart of the chick-embryo are shown in Figs. 23 and 24. At a somewhat earlier stage than that represented in Fig. 23 the heart was perfectly straight. In this figure it is still a simple dilated tube, but no longer straight. It has become bent outwards into a U-shape. At the stage of Fig. 24 well-marked constrictions (the indications of the later division into auricle and ventricle, etc.) have appeared in the heart, and the simple U-shaped flexure of the latter has become



Figs. 23 and 24.—Anterior portions of chick-embryos of the 38th and 48th hour of incubation, seen from below, to illustrate formation of heart. (After DUVAL.)

ao. Right and left aortæ. *au.* Auditory involution. c_2. Ventricular portion of heart. c_3. Auricular portion of heart. *e.* Eye. *h.* Heart. *op.* Primary optic vesicle. *p.f.b.* Primary fore-brain. *p.m.b.* Primary mid-brain. *p.h.b.* Primary hind-brain. *t.a.* Truncus arteriosus. *v.a.* Vitelline arteries. *v.v.* Vitelline veins. *1, 2, 3,* Transitory gill-slits.

complicated by the occurrence of a further flexure in a different direction, in consequence of which the hinder limb of the U has been raised, so to speak, to nearly the same plane as the anterior limb. The shape of the heart at this stage bears a characteristic resemblance to the Greek letter sigma. The permanent condition of the heart in Amphioxus therefore corresponds to an early stage of its development in the higher Vertebrates.

Again, in the craniate embryo the dorsal aorta arises as a pair of vessels on either side of the notochord, which later fuse together into one median dorsal vessel. (Cf. Fig. 24.) In Amphioxus, throughout a great portion of its extent, — namely, in the region of the pharynx, — the two halves of the dorsal aorta remain permanently separated from one another by the dorsal groove of the pharynx. (Cf. Figs. 2 and 28.)

One of the most striking peculiarities of the vascular system of Amphioxus is the presence of the *sub-intestinal vein*, in its capacity as the main venous trunk of the body. It collects the blood from the capillaries of the intestinal wall, and conducts it to the base of the liver, where it again breaks up into capillaries.* It acts, therefore, physiologically, as a *portal vein*, while morphologically it is the *sub-intestinal vein.* Curiously enough, it is much larger in its posterior than in its anterior moiety, and in transverse sections through the hinder region of the intestine there appear to be several separate vessels lying side by side, sometimes as many as six. These, however, if traced backwards or forwards, are found to anastomose with one

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* In the larva of Amphioxus the sub-intestinal vein and branchial artery form one continuous blood-vessel. Later, when the hepatic cœcum (liver) grows out from the ventral wall of the alimentary canal, an interruption occurs in the continuity of the vessel, through the insertion of a capillary portal system in its course.

another, as shown in Fig. 25, and so there is produced a fenestrated structure in the vein. The hepatic vein has a similar fenestrated character, and this was what was meant by speaking of it above as being "multiple."

The sub-intestinal vein reappears in the embryos of all the higher fishes and Amphibia, where it breaks up into capillaries in the liver. In these forms, however, it does not persist long as the main venous trunk, but becomes replaced almost entirely by the development of two large veins, which arise on either side of the dorsal aorta. These are the so-called *cardinal veins.* The sub-intestinal vein mostly disappears after the formation of the cardinal veins, but persists as a second-class vessel in the lampreys and in some sharks, lying, in the latter, in the spiral valve of the intestine.* Moreover, its posterior portion, which lies in the tail, persists as the *caudal vein.*

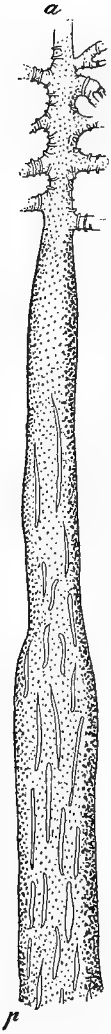

Fig. 25.—View of portion of sub-intestinal vein of Amphioxus, to show its fenestrated character in the posterior region. (After SCHNEIDER.)
a. Anterior. *p.* Posterior.

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* The sub-intestinal vein is also persistent in the following Urodele Amphibia—*Salamandra*, *Triton*, and *Pleurodeles.* (See F. HOCHSTETTER. *Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte des Venensystems der Amphibien und Fische.* Morph. Jahrb. XIII. 1888. pp. 119–172.)

The same vessel, therefore, which constitutes the main venous trunk of the *adult* Amphioxus performs the same function in the *embryos* of the higher fishes. We can thus deduce a good deal of evidence from a consideration of the vascular system alone, pointing to the primitive and ancestral character of Amphioxus.

If we compare broadly the vascular system of Amphioxus with that of a segmented worm like the common earthworm, we are at once confronted with certain obvious superficial resemblances. Here, as in Amphioxus, the vascular system comprises two main longitudinal trunks, one lying above the intestine and the other below it, and furthermore, they are connected together at intervals by circular vessels which form complete rings round the alimentary canal in the same way as do the vessels which pass through the pharyngeal bars of Amphioxus.

It is only when we come to enquire into the direction of flow of the blood in the two cases that we meet with a striking contrast between them. Whereas in Amphioxus the blood flows in the dorsal aorta from before backwards (see Fig. 20), and in the sub-intestinal vein together with the branchial artery, from behind forwards, in the worm, on the contrary, these directions are reversed, and the blood flows from behind forwards in the dorsal vessel, and from before backwards in the ventral vessel.

The Excretory System.

The excretory function is so intimately bound up with the circulation that a description of the organs which serve this function follows naturally after the consideration of the vascular system. The apparent absence of definite excretory organs in Amphioxus was for a long time one of the greatest difficulties in the way of a correct appreciation of the peculiarities of its organisation. Thanks, however, to recent researches, it is now known to possess such organs in luxuriant abundance.

From first to last several entirely different structures have been credited with a renal function. JOHANNES MÜLLER first discovered certain glandular epithelial tracts in the floor of the atrial chamber in its hinder portion. These cellular thickenings are distinguished by their high cylindrical cells from the flattened atrial epithelium which surrounds them. (Cf. Figs. 11 and 26.) Johannes Müller suggested that these groups of cells might be renal organs. His observation, however, failed to find general acceptance among morphologists for about thirty-five years, when, in 1876, W. ROLPH and PAUL LANGERHANS, working independently, fully confirmed his account and accepted his interpretation of the bodies as renal organs, at the same time adding a careful histological description of them (Fig. 27).

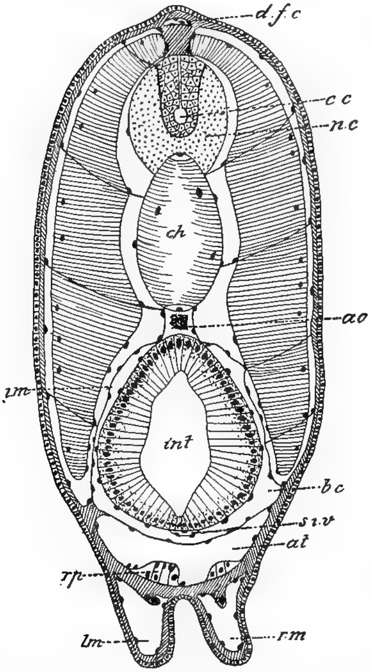


Fig. 26. — Transverse section through post-pharyngeal region of young individual, to show groups of renal cells in floor of atrium. (After LANKESTER and WILLEY.)

ao. Aorta. *at.* Atrium. *b.c.* Body-cavity (cœlom). *c.c.* Central canal of nerve-cord (*n.c*). *d.f.c.* Fin-cavity. *i.m.* Intercœlic membrane. *l.m.* and *r.m.* Left and right metapleural folds. *r.p.* One of J. Müller's renal papillæ. *s.i.v.* Sub-intestinal vein.

The individual groups of cells have an elongated and more or less ovoid shape with the long axis parallel to the long axis of the body. According to Langerhans their surface is ciliated. Two kinds of cells enter into their composition; namely, large clear dilated cells, which are separated from one another by fine fibre-like cells of extreme tenuity (Fig. 27). In the latter the nucleus of each cell is placed near the free end of the cell, while in the former it lies nearer the base of the cell. Langerhans found highly refringent concretions in the dilated cells which he took for excretory products. That these cells have a capacity for excreting waste matters has more recently been shown experimentally by F. E. Weiss. The atrial epithelium on the pharyngeal bars has a similar character to that forming these curious renal papillæ on the floor of the atrium. The distribution of these papillæ in the vicinity of the atriopore is very irregular and variable and without any regard to a symmetrical disposition. Although they are undoubtedly to be regarded as a species of renal organ, yet they could not be compared to any portion of the excretory system of the higher Vertebrates.

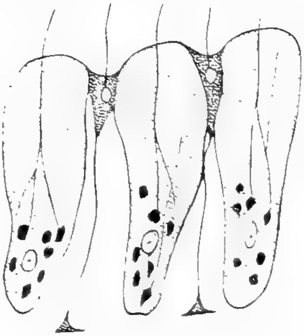


Fig. 27. — Isolated cells from renal papilla; the large cells contain concretions indicated by the black bodies. (After Langerhans.)

Another structure, or pair of structures, which has been considered to belong to the category of renal organs must next be referred to.

This consists of two funnel-shaped diverticula of the atrial cavity lying in the dorsal (subchordal) cœlom in the region of the twenty-seventh myotome, where the pharynx ends and the intestine begins. They were discovered in 1875 by LANKESTER, who called them the *atrio-cœlomic* or *brown funnels*, on account of the rich accumulation of brown pigment in their walls. We have already referred to this brown pigment as occurring very generally in the atrial epithelium. The brown funnels have the shape of an elongated cone, the apex of which is directed forwards. At the wide end each funnel opens into the atrial cavity, while at the narrow end it is possible, but not certain, that an opening exists into the dorsal cœlom (Fig. 28). The funnels are adherent throughout their entire length to the roof of the dorsal cœlom.[4]

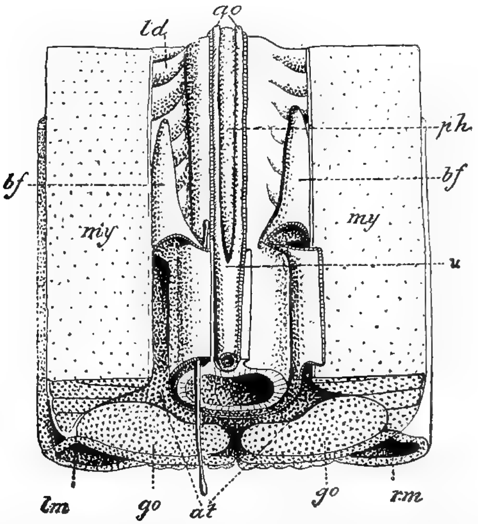


Fig. 28.—Plastic diagram illustrating the positions and relations of the atrio-cœlomic funnels. A rod is passed through the peri-enteric cœlom into the sub-chordal (suprapharyngeal) cœlom. (After LANKESTER.)

ao. Dorsal aortæ. *at.* Atrial cavity. *b.f.* Atrio-cœlomic funnels. *go.* Gonads. *l.d.* Ligamentum denticulatum (pharyngo-pleural folds, Lankester). *l.m.* and *r.m.* Left and right metapleural folds. *my.* Muscles. *ph.* Roof of pharynx. *u.* Point of union of the right and left aortæ into the median aorta.

In 1889 WEISS undertook the task of determining experimentally whether Johannes Müller's *renal papillæ* and Lankester's *brown funnels* really served an excretory function. The method of research consisted in feeding full-grown individuals with various colouring matters held in solution or in suspension in sea-water. For instance, carmine suspended in sea-water would be carried into the digestive canal and then absorbed through the intestinal epithelium into the capillaries surrounding the intestine. It would thus get into the vascular system, and also by some means into some of the lymph spaces, and finally would be excreted by the cells of the renal papillæ or by whatever other structure, or set of structures, might possess the renal function. In fact, Weiss found that the so-called renal papillæ did actually excrete a quantity of the carmine with which the animals had been fed, and, further, that a similar excretion of carmine occurred at other points of the atrial epithelium. The atrial epithelium, as a whole, probably has more or less the power of excreting waste products which have found their way into the vascular and lymphatic systems.

But above all, Weiss discovered a very active excretion of carmine in certain small *tubules* which he found lying in the dorsal cœlom applied against the most dorsal portion of the double-layered membrane (ligamentum denticulatum) which separates the cœlom from the atrial cavity (Fig. 29). There is one of these tubules to each primary gill-cleft of the pharynx. At the top of each tongue-bar Weiss made out an opening of the tubule into the atrial cavity, but he did not succeed in finding any openings into the dorsal cœlom. After the operation of feeding with carmine was completed, at the close of a week or fortnight, and time had been allowed for its absorption and subsequent excretion, the epithelium lining the walls of these tubules was found to be full of carmine granules.

At about the same time at which Weiss was pursuing his studies on Amphioxus THEODOR BOVERI, having been led by independent *a priori* considerations, largely induced by the work of RÜCKERT on the development of the excretory system of Selachians, to suspect the occurrence of excretory tubules in Amphioxus comparable to those found in the embryos of the higher Vertebrates, instituted a search for them and discovered them independently in the most brilliant manner.

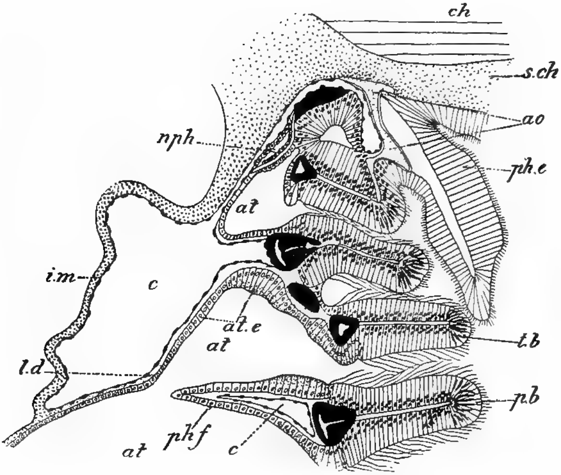


Fig. 29.—Portion of transverse section through the pharynx of Amphioxus, to show position of excretory tubule. (After WEISS.)

ao. Left aorta. *at.* Atrial cavity. *at.e.* Atrial epithelium. *c.* Cœlom. *ch.* Notochord. *i.m.* Intercœlic membrane. *l.d.* Ligamentum denticulatum. *nph.* Excretory tubule. *p.b.* Primary bar. *ph.e.* Epithelium of hyperpharyngeal groove. *ph.f.* Pharyngo-pleural fold. *s.ch.* Sheath of notochord. *t.b.* Tongue-bar.

Boveri carried his investigation to a high pitch of perfection, and has published an account of these tubules, which in point of clearness and completeness leaves nothing to be desired. The accompanying figures, taken from Boveri's finely illustrated memoir, show the appearance and topographical relations of the excretory tubules.

A tubule as seen in the living condition is shown in Fig. 30. It is a curved tube consisting mainly of two

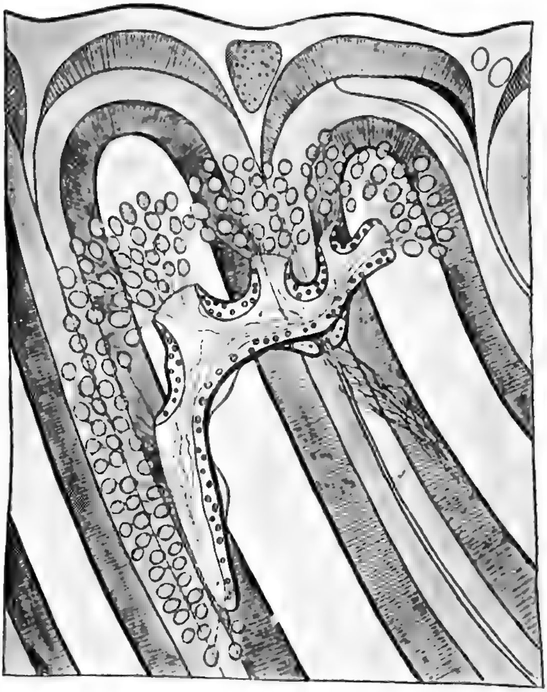


Fig. 30.—An excretory tubule of the left side, with the neighbouring portion of the pharyngeal wall, as seen in the living condition. The round bodies in the wall of the tubule represent carmine granules. Highly magnified. (After BOVERI.)

limbs, bent approximately at right angles to one another, and lying over against the dorso-lateral wall of the pharynx. (Cf. Fig. 29.) The anterior limb is directed vertically, and the posterior longitudinally. The former opens by a relatively wide and forwardly directed opening into the dorsal cœlom. The posterior end of the tube also opens into the cœlom, and between these two terminal openings there is a variable number of other *cœlomic openings*, or *funnels*, as they are called, situated on the dorsal side of the tubule, and opposite to that side which carries the opening into the atrial chamber. The cœlomic funnels are placed at the ends of short upstanding projections from the main body of the tubule. On the ventral side of the tubule, opposite in each case to a tongue-bar of the pharynx, occurs the single opening into the atrial cavity. The epithelium lining the tubule consists of cubical ciliated cells. There is a thick bunch of cilia in connection with the atrial opening of the tubule. The curious thread-like structures, carrying a round knob at their distal extremities, which radiate out from the cœlomic openings, are specially modified cells belonging to the cœlomic epithelium, which are probably concerned in promoting the excretory activity of the tubule, and are called by Boveri, *thread-cells* (Fadenzellen).

The vascular supply and exact location of the nephridial tubules (each tubule representing a *nephridium*, according to Lankester's nomenclature) are shown in Fig. 31. The figure represents a piece of the upper wall of the pharynx, cut out in such a way as to expose the inner wall of the dorsal cœlom. The cross is placed at the cut edge of the double-layered membrane which separates the dorsal cœlom from the atrial cavity. This cut edge can be traced from side to side of the figure. The membrane is seen to be continued down each primary gill-bar, in company with the extension of the cœlom, which runs down the primary bars into the endostylar cœlom as described above. On the other hand, the membrane skips over the tongue-bars, so that the atrial cavity is prolonged dorsalwards into a deep bay, corresponding to each tongue-bar. (Cf. Fig. 29.) This is what produces the sinuous, or notched, appearance to the membrane in question, and led Johannes Müller to speak of it as the *ligamentum denticulatum.* (Cf. Fig. 28.) The external or *atrial opening* of the tubule lies against the tongue-bar at the head of this bay-like extension of the atrial cavity (Fig. 31 on the right).

The vascular supply of the tubules is effected in each case by the co-operation of two blood-vessels; namely, the

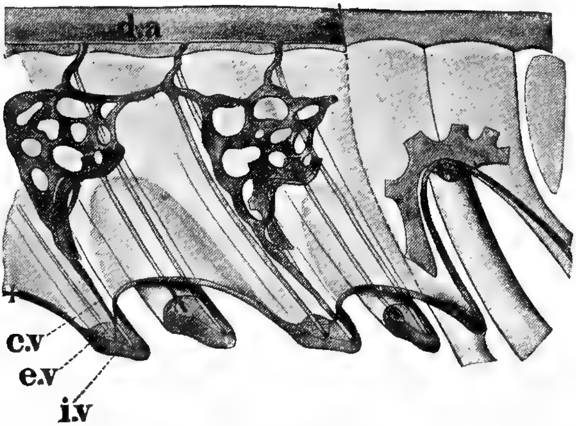


Fig. 31.—Plastic figure illustrating the blood-supply (glomeruli) of the excretory tubules. On the right, the drawing is taken at a deeper level, to show the atrial opening of the tubule over against a tongue-bar. (After Boveri.)

✠. Cut edge of ligamentum denticulatum. *c.v.* Cœlomic vessel of primary bar. *e.v.* External vessel. *i.v.* Internal vessel. *d.a.* Left dorsal aorta.

cœlomic vessel of the primary bar (cf. Figs. 15 and 21) and the *external vessel* of the secondary, or tongue-bar. As soon as the cœlomic vessel of a primary bar arrives at the level of a tubule, it gives off a number of branches, which not only anastomose among themselves, but become united with a similar series of anastomosing vessels which originate from the external vessel of the next-following tongue-bar. In this way, a complicated plexus of blood-vessels is formed around and about the tubule. This vascular plexus is known as a *glomerulus.*

The blood charged with whatever waste matters it may have gathered up in its course through the body arrives eventually at the glomeruli, where it is considerably delayed on account of the vascular plexus through which it has to pass before reaching the dorsal aorta. During this delay, it is exposed to the glandular excretory action of the tubules, by which the waste products are extracted from the blood by osmotic action. From the glomerulus the blood is conducted by two efferent vessels, corresponding respectively to the primary and tongue-bars, into the dorsal aorta. The communication between two neighbouring glomeruli, as shown in Fig. 31, is, according to Boveri, the exception and not the rule.

The distribution of these remarkable excretory tubules or nephridia is coextensive with that of the pharyngeal gill-clefts. They extend from the anterior to the posterior extremity of the pharynx, but not beyond this. They never have more than one opening into the atrial cavity, but those occurring in the mid-region of the pharynx have several, sometimes as many as nine, openings into the dorsal cœlom. The number of cœlomic openings decreases anteriorly and posteriorly, until, at the two extremities of the pharynx, there is only a single cœlomic opening to the tubules.

In a full-grown individual, Boveri has counted ninety-one tubules on one side of the pharynx, the total number therefore being double this.

The serial distribution of the excretory tubules, one after the other, is known broadly as a *metameric* arrangement. But since they correspond in number and situation to the primary gill-clefts, which are much more numerous than the myotomes in the region of the body in which they occur, their arrangement is more strictly defined as *branchiomeric.* In the larva, however, the primary gill-slits correspond numerically with the myotomes or muscle-segments of the pharyngeal region, only secondarily becoming more numerous. The branchiomeric arrangement of the excretory tubules of Amphioxus need not, therefore, prejudice their claim to be regarded as *segmental* structures.

If, now, we attempt to compare the nephridial system of Amphioxus with the kidney of the higher types, we shall find that here also, as in so many other instances, the permanent state of things in the former becomes a characteristic feature of the embryo in the latter.

As is well known, the kidney of the higher Vertebrates comprises a mass of convoluted tubules, the *uriniferous tubules,* imbedded in a matrix of fibrous connective tissue, and enclosed within a common sheath, and so producing collectively a compact organ which we call the kidney.

If, neglecting the highly elaborate structure presented by the kidney of Birds and Mammals, we take, as a typical example of a primitive Vertebrate renal organ, that of a tailed Amphibian, we find after a superficial examination the following characteristic features. In the newt, for instance, the surface of the elongated kidney is studded with numerous small apertures. These are surrounded by vibratile cilia, and lead directly from the body-cavity into the convoluted renal tubules. They are, therefore, the cœlomic openings or funnels of the latter, and are known as *nephrostomes.* Close to the nephrostome a short diverticulum of the tubule leads to a capsule which encloses a *glomerulus.* After a winding course in the substance of the kidney, the tubules emerge from the latter as a series of efferent ducts placed one behind the other, and these again open into a common longitudinal duct on each side of the body, known as the *ureter*, which leads the products of excretion backwards to the cloaca.

The permanently functional kidney of Fishes and Amphibia is known as the *mesonephros*. In Reptiles, Birds, and Mammals, this is only functional during the embryonic period, and later is replaced in a way not yet fully elucidated by the permanent kidney of these forms which is known as the *metanephros*.

The ureter, or duct, of the mesonephros, is spoken of as the *mesonephric duct*, while the renal tubules constitute, collectively, the glandular portion of the kidney.

The permanent kidney of the craniate Vertebrates is absolutely unique among all the other glands of the body, in the fact that the glandular portion of the organ arises independently of the duct, and only communicates *secondarily* with it. Moreover, the duct develops in point of time before the gland. This is a very extraordinary fact, and taken alone would be quite inexplicable. It has been found, however, that the mesonephric duct has *primary* relations with a totally distinct set of excretory tubules, which differ from those mentioned above, both in their position in the body and in their mode of development. These primitive tubules, which mark the first appearance of a renal organ in the Vertebrate embryo, constitute the *pronephros*.

The degree of development attained by the pronephros, or primitive kidney, in the life-history of the various types of Vertebrates, is very different in the different classes.

Frequently, as with the Selachians (sharks), Birds, most Reptiles, and with the Mammals, the pronephros is an entirely rudimentary structure, which puts in a fleeting appearance during the embryonic development, but never functions as a kidney.

In other cases, as with the Teleostomes, or bony fishes, Amphibians, Crocodiles, and Turtles, the pronephric system attains a higher grade of development, and actually functions for a time as the sole kidney of the animal. In some of the bony fishes (e.g. *Zoarces* and *Merlucius*), it functions as the kidney for an extraordinarily long time, apparently throughout the period of adolescence. In one curious instance of a fish, *Fierasfer*, which has acquired a semi-parasitic habit, it appears that the development has been arrested to such an extent that the pronephros functions as the principal organ of excretion throughout life, the mesonephros remaining rudimentary (EMERY).

The most extensive pronephric system which has as yet been described for any craniate Vertebrate, is that represented diagrammatically in Fig. 32. This is the *larval* excretory system of a remarkable worm-like legless Amphibian, *Ichthyophis glutinosus*, belonging to a very primitive subdivision of the Amphibia known as the *Cæciliani*, which occur in the hot regions of South America, Africa, Seychelles, East Indies, and Ceylon.

We owe our knowledge of this elaborate pronephric system to RICHARD SEMON of Jena.

It consists of some twelve pairs of irregularly contorted tubules placed dorsal to the general body-cavity in a position which is described as retro-peritoneal, and arranged segmentally, one behind the other, on either side of the dorsal aorta. Broadly speaking, the canals run outwards in a transverse direction. Near their inner extremities they usually divide into two short branches, which terminate each in a funnel-shaped opening into the body-cavity.

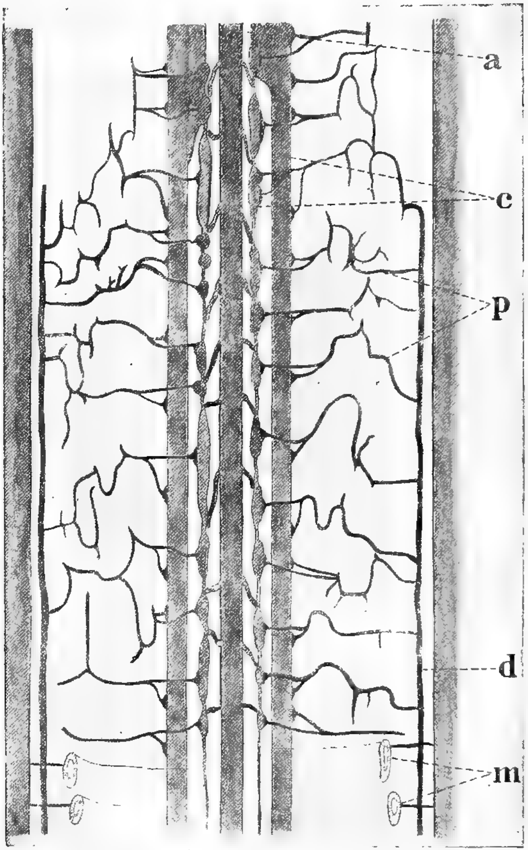


Fig. 32. — Pronephric system of embryo of Ichthyophis, reconstructed from sections, and represented as having been spread out in one plane. (After SEMON.)

a. Dorsal aorta. *c.* Portions of the cœlom into which the nephrostomes of the pronephric tubules open. The inner portion of cœlom (next to aorta) is shut off from the rest of the cœlom, and becomes associated with the vascular outgrowths from the dorsal aorta (which produce the glomeruli) to form the Malpighian capsules of the pronephros. The Malpighian tractus is continued backwards as a metamorphosed and rudimentary cord of cells, nearly to the cloaca, and constitutes the so-called Nebenniere or Interrenal body. This backward extension of the Malpighian body of the pronephros probably indicates the former existence of a much more extensive pronephric system. *p.* Convoluted pronephric tubules lying above the peritoneum (shaded light), each provided with two nephrostomes, inner and outer, and opening peripherally into *d*, the longitudinal pronephric duct (Wolffian duct), which becomes the mesonephric duct after the degeneration of the pronephric tubules and the formation of the mesonephric tubules have taken place. *m.* Rudiments of the mesonephric tubules.

N.B. — The pronephric tubules are here characterised by the possession of cœcal outgrowths.

These are the cœlomic openings, or nephrostomes, of the tubules. At their outer ends most of them open directly into a longitudinal duct, the *pronephric duct*, which extends backwards to the cloaca. The most anterior tubules, however, tend to fuse together at their outer extremities, before reaching the common duct. Corresponding to each tubule there is a short artery growing out from the dorsal aorta, and abutting with its blind end against the portion of the body-cavity into which the innermost nephrostomes open.

Later on these cœcal outgrowths from the dorsal aorta develop a vascular network at their free ends, and so produce a series of *glomeruli*.

If, now, we inquire into the mode of development of such a pronephric system as the one above described, we find that its component tubules arise as a series of knob-like segmental outgrowths from the outer or somatic layer of the peritoneum at the base of the segmented portion of the primitive body-cavity.

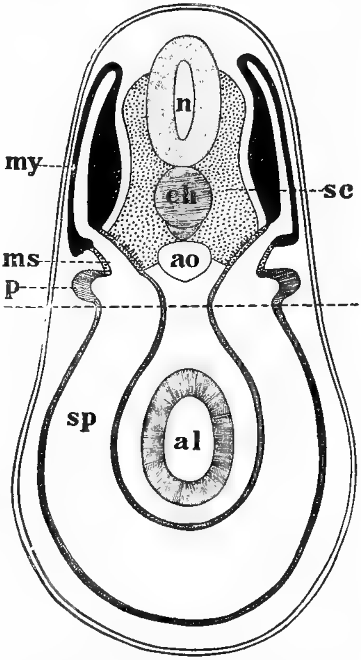


Fig. 33.—Schematic transverse section through a Selachian embryo in the region of the pronephros. (After VAN WIJHE.)

The dotted line drawn across the section indicates the plane of division between the upper segmented and the lower unsegmented portions of the primitive body-cavity (procœlom). *my.* Myotome or myomere. *ms.* Mesomere or nephrotome. *p.* Pronephric outgrowth. *sp.* Unsegmented body-cavity or splanchnocœl. *sc.* Sclerotome. *n.* Nerve-tube. *ch.* Notochord. *ao.* Dorsal aorta. *al.* Digestive tube.

These outgrowths are at first solid cell-proliferations of the peritoneal epithelium, in the midst of which a lumen is subsequently formed between the cells. As soon as this occurs, the peritoneal thickenings represent hollow diverticula of the cœlom, each communicating with the latter by a single nephrostome (Fig. 33).

The incipient tubules then grow outwards until they reach the ectoderm with which, in the Selachians, they become fused. This has been taken by Rückert to indicate that the tubules originally discharged the products of excretion directly to the exterior by a series of independent apertures at the points of fusion. (Cf. Fig. 34 *A*.)[5] The pronephric tubules next commence gradually to relinquish their coalescence with the ectoderm from before backwards, retaining, however, for the present the connection behind (Fig. 34 *B*).

Meanwhile the distal ends of the successive tubules undergo confluence (Fig. 34 B), and in this way the beginning of a longitudinal duct is produced. This duct now gradually splits itself off from the ectoderm, so that the posterior connection with the latter is carried farther and farther back until it reaches the region of the cloaca, when it leaves the ectoderm and acquires an opening into the cloaca (Fig. 34 *C*). Meanwhile, however, in the Selachians, the pronephric tubules begin to undergo a retrogressive development and atrophy, as a consequence of which the pronephros as a gland becomes aborted.

In the same way, but at a much later stage, the remarkable pronephric system of Ichthyophis becomes entirely aborted. But the duct remains, and a new set of tubules appear at the bases of the somites, which secondarily open into it (Fig. 34 *C*).

These new tubules are the *mesonephric* tubules, and, although they occur mostly behind the region of the pronephros, yet rudiments of them appear in the same segments occupied by the latter. Unlike the pronephric tubules, they arise, not as evaginations from the base of the somites, but in such a way that an adjacent portion of the somite, lying dorsal to the pronephric tract, loses its primary connection with the rest of the somite, which consists of the myotome proper, and becomes bodily converted into a mesonephric tubule whose blind end curves round the pronephric duct and eventually opens into it; while its point of communication with the unsegmented

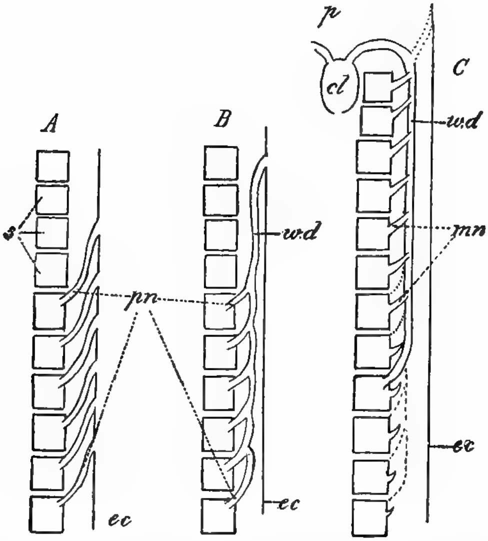


Fig. 34.—Three diagrams illustrating the hypothetical phylogenetic development of the excretory organs in Selachians. (After RÜCKERT.)

s. Somites. *pn.* Pronephric tubules fused with *ec*, the ectoderm in *A*; collected into a common duct *w.d*, the Wolffian or pronephric duct in *B*; and finally aborted in *C*, with the exception of one, which persists as the ostium abdominale. *mn.* Mesonephric tubules. *w.d.* Pronephric duct in *B*; mesonephric duct in *C*. *cl.* Cloaca. *p.* Posterior region.

body-cavity persists as the nephrostome. (Cf. Figs. 33 and 35 *B*.)

The pronephric duct, therefore, becomes secondarily employed in the surface of the mesonephros. So that, while the mesonephros and its future duct form two distinct morphological structures, the pronephros and the same duct form one inseparable whole.

From the above considerations we may conclude that the pronephros represents the primitive and ancestral excretory organ of the craniate Vertebrates. Just as the notochord has been largely replaced first by cartilage and then by bone, so the pronephros has been replaced first by the mesonephros and then by the metanephros.

Returning now to Amphioxus, we have to note in the first place the absence of a common matrix surrounding the excretory tubules, and, secondly, the absence of a common duct. Since in the higher Vertebrates the interstitial growth of connective tissue among the tubules, binding them together into a compact organ, is a secondary phenomenon, the absence of such a matrix in Amphioxus need not detain us.

Judging from the analogy of the other systems of organs in Amphioxus, it will be at once concluded that the excretory tubules of the latter represent the pronephric system of the embryos of the craniate Vertebrates. And this, in fact, is Boveri's contention.

As we have seen, the excretory tubules of Amphioxus open separately into the atrial cavity. While they do not, therefore, open directly to the exterior at the ectodermic surface of the body, they do actually open at an ectodermic surface, since the atrial cavity is a space enclosed from the outside, and so is lined by ectoderm. The primary fusion of the pronephric tubules with the ectoderm, which has been observed in some craniate Vertebrates as described above, is therefore probably of the same nature as the ectodermic openings of the tubules in Amphioxus.

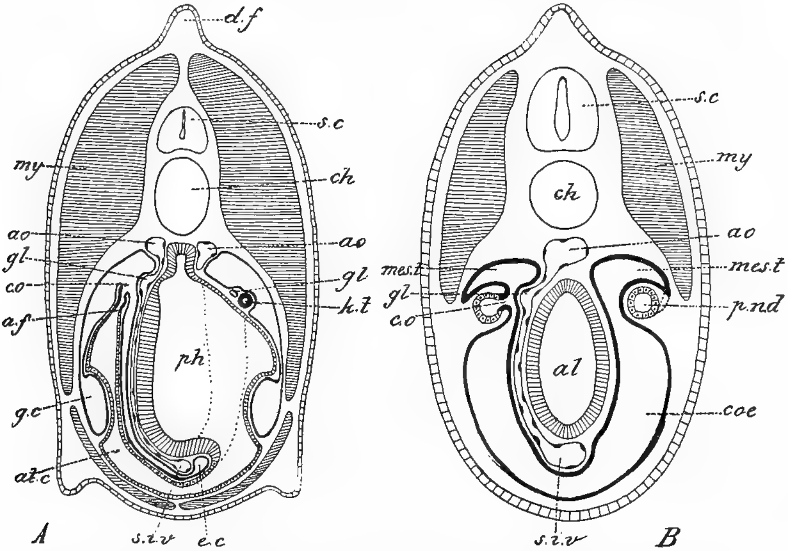


Fig. 35.—*A.* Schematic transverse section through pharyngeal region of Amphioxus. On the left is a branchial bar, cut lengthwise, and on the right a gill-slit.

B. Schematic transverse section through Selachian embryo. (After BOVERI.)

at.c. Atrial chamber. *p.n.d.* Pronephric duct. *c.o.* Nephrostome of pronephric tubule. *k.t.* Cross-section of excretory tubule in Amphioxus. *a.f.* Opening of excretory tubule into atrium in Amphioxus. *g.c.* Gonadic cavity (perigonadial cœlom) in *A*; compared by Boveri with the mesonephric tubule, *mes.t.* in *B.* *gl.* Glomerulus. *cœ.* Cœlom. *e.c.* Endostylar cœlom. *s.i.v.* Branchial artery in *A*; sub-intestinal vein in *B.*

Other letters as in previous figures.

N.B.—In *B* the future opening of the mesonephric tubule into the pronephric duct is indicated by dotted lines on the right. The vessel connecting the sub-intestinal vein with the aorta is placed on the left of the alimentary canal for comparison with Fig. *A.* It is really only present on the right side, although a rudiment occurs on the left. (See Note 6.)

The glomeruli of the tubules in Amphioxus are supplied by blood-vessels which connect the dorsal aorta with the branchial artery. It should be remembered that the branchial artery represents the anterior portion of the sub-intestinal vein, and in the young larva the two vessels are continuous. The direct continuity is subsequently interrupted by the development of the hepatic cœcum, and the consequent insertion of a capillary portal system into the circulation. In the Selachian embryo, a series of similar vessels, six in number, connecting the dorsal aorta with the sub-intestinal vein, have been shown to be in close correspondence with the pronephric tubules, and to form at the level of the tubules a series of rudimentary glomeruli (Figs. 35 *A* and *B*).[6]

Such resemblances as the above are demonstrative, and are sufficient to prove that the excretory tubules of Amphioxus belong to the pronephric system, and that in this respect, also, the adult Amphioxus presents features which are characteristic of the embryos, or larvæ, of the higher forms.

Although convinced as to the essential identity of the excretory tubules of Amphioxus with the pronephros of the craniate Vertebrates, it must be remembered that there is one apparently great difference between them. Whereas in Amphioxus the pronephros (applying this term to the tubules considered collectively) occurs in the region of the perforated pharynx, in all the higher Vertebrates it occurs behind the pharynx, and is quite absent from the region of the gill-slits. This difference, however, which might at first sight appear serious, is, in reality, most instructive. As Boveri points out, it shows almost conclusively that the pharynx of Amphioxus does not correspond to the pharynx alone of the higher forms, but to the pharynx together with the anterior portion of the alimentary canal.

In the Craniota the gill-clefts, which are present in a limited number, have become involved in the complicated process of cephalisation, by which the Vertebrate head has been evolved. They are innervated exclusively by the cranial nerves, and in fact are considered as forming part of the head. In Amphioxus there is, broadly speaking, no head, and the region of the gill-slits forms part of the trunk. In the evolution of the Craniota, therefore, what has happened is that the gill-clefts have been relegated to the head, while the excretory tubules have become confined to the trunk, and have ceased to occur in the neighbourhood of the gill-clefts. Only the anterior region of the pharynx of Amphioxus is represented by the pharynx of the higher forms. The greater part of it corresponds to the unperforated portion of the alimentary canal, which follows immediately behind the pharynx in these forms, extending to the liver.

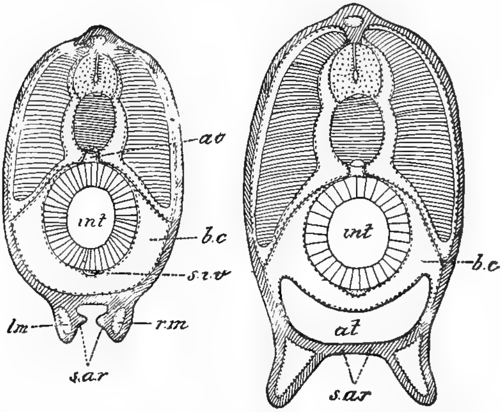
We have referred above to the absence of a pronephric duct in Amphioxus. Although this is true in the strict sense of the term, yet Boveri gives reasons for supposing that the right and left pronephric ducts are in a measure represented by the right and left halves of the atrial chamber. (Cf. Fig. 35, *A* and *B*). We will first glance briefly at the mode of

Development of the Atrial Cavity.

For the sake of avoiding complications, it will be well to confine the description at present to the mode of origin of the atrial cavity in its posterior region. It arises of course on the same principle throughout its whole extent (except the post-atrioporal continuation, which grows back later), but anteriorly it is involved in the asymmetry which is such a marked feature of the larva, and will be considered in the chapter on the general development.

The first indication of the future atrial cavity appears in a young larva with some six or seven gill-slits in the form of two longitudinal thickenings of the integument on the ventral surface of the body. These are at first solid, but eventually become hollowed out so as to enclose a longitudinal canal on each side. This is the so-called metapleural canal or lymph-space. The thickenings enlarge to the extent of forming two well-marked folds of the body-wall; namely, the *metapleural folds.*

The next stage is marked by the formation of two small solid longitudinal ridges on the inner opposed faces of the metapleural folds (Fig. 36). It is by the subsequent meeting and coalescence of these *subatrial ridges* that the atrial cavity becomes enclosed as a small median tube lined by ectoderm.



Figs. 36 and 37. — Schematic transverse sections through post-pharyngeal region, illustrating mode of origin of atrial chamber. (After LANKESTER and WILLEY.)

ao. Aorta. *b.c.* Cœlom. *r.m and l.m.* Right and left metapleural folds. *s.a.r.* Subatrial ridges, which fuse together to form the floor of *at*, the atrium. *int.* Alimentary canal. *s.i.v.* Sub-intestinal vein.

As soon as it has become closed off from the exterior, the atrial tube commences to grow in size, and it gradually expands laterally and also in an upward direction, proportionately reducing the extent of the cœlom as it does so (Fig. 37; cf. also Fig. 26). At its posterior extremity the atrial tube does not become closed in, but remains permanently open as the atriopore. It is a curious fact that the fusion of the subatrial ridges to enclose the atrial tube takes place gradually from behind forwards, so that for a long time the latter has the form of a canal open to the exterior at both ends. The chief features in the formation of the atrium are shown diagrammatically in Fig. 38, *A*, *B*, and *C*.

In Fig. 38 *A* the atrial tube has not begun to be closed in, but the two metapleural folds are seen running side by side for some distance. Anteriorly the development of the right metapleur is in advance of that of the left, and it is seen to bend round to the right side of the body in correspondence with the asymmetry of the gill-slits (*vide infra*). Having arrived at the front end of the pharynx, the right metapleur bends sharply inwards to the mid-ventral line and then gradually dies out in front. In Fig. 38 *B* the subatrial ridges have met and fused for a short distance behind the

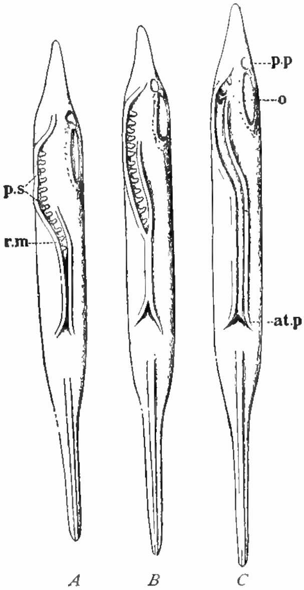


Fig. 38. — Three plastic diagrams of larvæ of Amphioxus from the ventral aspect, illustrating the mode of enclosure of the atrial tube from behind forwards. The atrium is still entirely unclosed in *A*; partially closed in *B*; and almost completely closed in *C*. (After LANKESTER and WILLEY.)

p.s. Primary gill-slits. *r.m.* Right metapleur. *p.p.* Præoral pit. *o.* Mouth. *at.p.* Atriopore.

pharynx, so as to enclose a tube which corresponds to that portion of the future atrial cavity which lies between the atriopore and the hinder end of the pharynx. Finally, in Fig. 38 *C*, the closure of the atrial tube has advanced forwards over the gill-slits almost to the anterior extremity of the pharynx, still leaving, however, one or two gill-slits open directly to the exterior in front. Meanwhile, the floor of the atrium has increased in width, and the metapleural folds are separated by a wider interval than before (Fig. 38 *C*). Eventually the atrium closes up completely in front, so that the gill-slits no longer open directly to the exterior.

Remembering that the atrium of Amphioxus arises as an unpaired median tube (see below, IV.), while the pronephric duct is always paired, the following are some of the reasons for supposing a partial homology between the two structures :—

(*a*) They are both derived, either wholly (atrium), or in a large measure (pronephric duct), from the ectoderm.[5] (β) They both receive and carry away the excretory products from the pronephric tubules ; and (γ), they are both, to a greater or less extent, lined by an epithelium, which is itself glandular and excretory.[7]

Comparison between the Excretory System of Amphioxus and that of the Annelids.

Having considered the relation existing between the pronephric system of Amphioxus and the corresponding system in the embryonic and larval stages of the higher Vertebrates, we will now pass on to a brief comparison with the excretory system of the Invertebrates.

The excretory system of a typical Annelid presents certain resemblances to that of Amphioxus, in that it occurs in the form of distinct segmental tubules, or *nephridia*, each possessing a funnel-shaped opening into the body-cavity, and an opening to the exterior at the surface of the body.

It was, in fact, the recognition, some twenty years ago, by Semper and Balfour, of the resemblance between the arrangement of the nephridia of the Annelids and the primary segmental origin of the kidney of the Craniota that was chiefly instrumental in placing the Annelid-theory of Vertebrate descent on a temporarily firm basis.

A dissection of the anterior portion of the body of an earthworm, exposing the nephridial tubules, is shown in Fig. 39. A pair of such convoluted tubules occurs in each segment, or ring, of the body, commencing from the third. Physiologically, of course, they are directly comparable to the renal tubules of the Chordata, and in their general features, allowing for the absence of a common duct, the similarity in the two cases is striking enough. But when this undoubted similarity is used as an argument for deriving the Vertebrate excretory system directly from that of the Annelids, we tread on very uncertain ground.

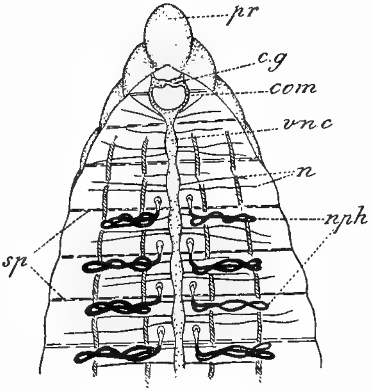


Fig. 39.—Anterior portion of earthworm dissected open from above to show the nephridia and nervous system. (From W. T. Sedgwick and E. B. Wilson's *General Biology*.)

pr. Prostomium (præoral lobe). *c.g.* Cerebral ganglion, which has receded from the prostomium from the ectoderm of which it arose. *com.* Circumœsophageal commissure surrounding the buccal tube (latter not represented). *v.n.c.* Ventral nerve-cord. *n.* Segmental nerves. *nph.* Nephridia. *sp.* Dissepiments.

If we were to consider the excretory system apart from the rest of the organisation, this would be the only course to follow. But when the whole organisation is taken into account, the only justifiable conclusion seems to be, not that the Vertebrate renal system is to be derived from that of the Annelids, but that, as Rückert suggests, both may possibly have been evolved from a common starting-point.

It is eminently probable that, in respect to this and the other systems of organs, as well as the segmentation of the body, the Annelids and Vertebrates present an instance of *parallel evolution.* This will become more evident as we proceed. Those who uphold the so-called Annelid-theory have no cause to complain of the absence of a common duct to the nephridia, since this has been found in some cases to occur.

In 1884 EDUARD MEYER discovered that in certain marine Annelids (*Lanice conchilega* and *Loimia medusa*) belonging to the family of the Terebellidæ, the nephridia of each side were joined together by longitudinal ducts, which he compared, though with great reserve, to the mesonephric ducts of the Vertebrata.* In these worms the nephridia do not occur in all the segments of the body, but are confined to the anterior so-called thoracic region, their number being very limited. In the thorax, the dissepiments which typically divide the segments from one another are absent, so that the body-cavity would here form a continuous uninterrupted space, were it not that it is divided into two chambers, an anterior and a posterior, of which the latter is the larger, by a muscular diaphragm. In the anterior thoracic chamber (Fig. 40) there are three pairs of nephridia which are united together on each side by a short duct opening to the exterior by a single aperture.

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* This discovery was also made later but independently by J. T. CUNNINGHAM for *Lanice conchilega.*

In the posterior chamber there are four pairs of much larger nephridia, which are similarly joined together by a prominent longitudinal duct from which short processes corresponding in number to the nephridia lead to the external apertures. The duct itself ends blindly at both ends, but is prolonged posteriorly far beyond the region of the nephridia (Fig. 40).

The presence of this longitudinal duct in these worms is a very remarkable circumstance, but it is undoubtedly an expression of the same phenomenon as the anastomoses between successive nephridia which have been described by EISIG for the Capitellidæ, as well as the complicated series of anastomoses which convert the entire nephridial system into a marvellous network of tubules discovered by A. G. BOURNE in the marine leech, *Pontobdella*, and by BEDDARD in the curious earthworm, *Perichæta*.

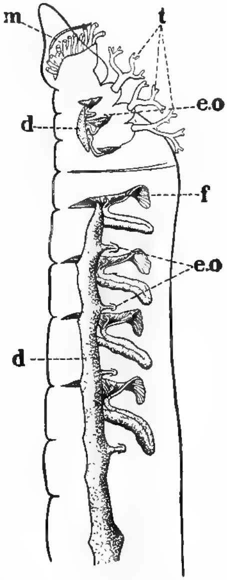

Fig. 40. — Schematic lateral view of anterior end of *Lanice conchilega* to show the nephridia. (After EDUARD MEYER from Hatschek's *Lehrbuch's der Zoologie.*)

The ventral side of the body is to the left of the figure. *d.* Longitudinal ducts of the nephridia. *e.o.* Position of external openings. *f.* Nephridial funnel (=cœlomic opening of nephridium). *m.* Position of mouth; bounded by two prominent lateral lobes, and fringed by a great number of "feelers," which are cut short in the figure. *t.* Branchial tentacles (three on each side of the body).

The present state of our knowledge does not admit of an attempt to specify the particular type of nephridial system from which that of the Annelids, on the one hand,

and that of the Vertebrates, on the other, took their origin.

In view of the apparent absence of nephridial tubules in Balanoglossus and the fact that in the Ascidians the renal organs are special structures peculiar to this group, it is extremely difficult to associate the Vertebrate type of excretory system with that of any Invertebrate.

Since the Annelid-theory precludes the possibility of Amphioxus being regarded as an ancestral form, and yet if, nevertheless, it is, as we believe, primitive and not essentially degenerate, the discovery of the excretory tubules in Amphioxus happily releases us not only from necessity, but also from the possibility of referring the Vertebrate excretory system back to that of the Annelids.

Nervous System.

The central nervous system of Amphioxus consists of a closed thick-walled tube lying along the dorsal side of the body above the notochord.

Viewed externally, it is a perfectly plain, more or less cylinder-shaped structure, without any constrictions or enlargements whatever. Its largest diameter in the adult occurs about the middle of its course, and not at its anterior end.

Posteriorly it is nearly coextensive with the notochord, and, like it, tapers down almost to a point.* Anteriorly it terminates abruptly some distance behind the front end of the notochord. (Cf. Figs. 3 and 11.)

If the dorsal nerve-cord be removed from the body and

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* The extreme posterior end of the nerve-cord is usually swollen out into a small ampulla-like dilatation. (POUCHET, ROHON, RETZIUS.) RETZIUS has observed that occasionally the nerve-cord is prolonged beyond the dilatation and actually bends round the posterior end of the notochord.

examined from above, its general appearance will be as shown in Fig. 41. In front there is a pair of nerves which proceed symmetrically from the sides of the nerve-tube. Farther back there is another pair of nerves which arise more dorsally than the anterior pair, but are likewise placed symmetrically one opposite the other. Behind this second pair of nerves the spinal nerve-roots are no longer disposed symmetrically, but alternate with one another, in correspondence with a similar alternation of the myotomes, the alternation becoming more and more pronounced as we proceed backwards. Again, behind the second pair of nerves there are two kinds of spinal nerve-roots, *dorsal* and *ventral.* The former leave the nerve-cord from its dorsal surface, and the latter from the margins of its ventral side. In the dorsal roots the nerve-fibrils are collected together to form a single compact nerve round which the sheath of the nerve-cord is continued, while in the ventral roots the nerve-fibres emerge separately in loose bundles unsurrounded by a sheath, from the spinal cord. A pair of dorsal roots and a pair of ventral root-bundles go to each

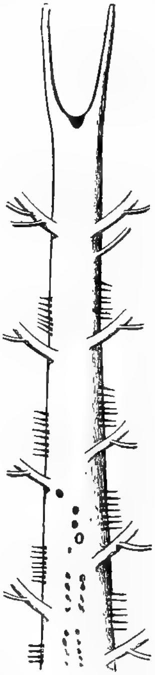

Fig. 41. — Anterior portion of spinal cord of Amphioxus; seen from above. (After SCHNEIDER.) Between the first pair of cranial nerves is seen the eye-spot; one of the branches of the second pair of cranial nerves sometimes arises directly from the spinal cord as shown on the right; farther back are seen the pigment spots of the nerve-cord.

segment of the body. Dorsal and ventral roots are entirely independent of one another, and at no point do they coalesce as they do in the Craniota. In further contrast to

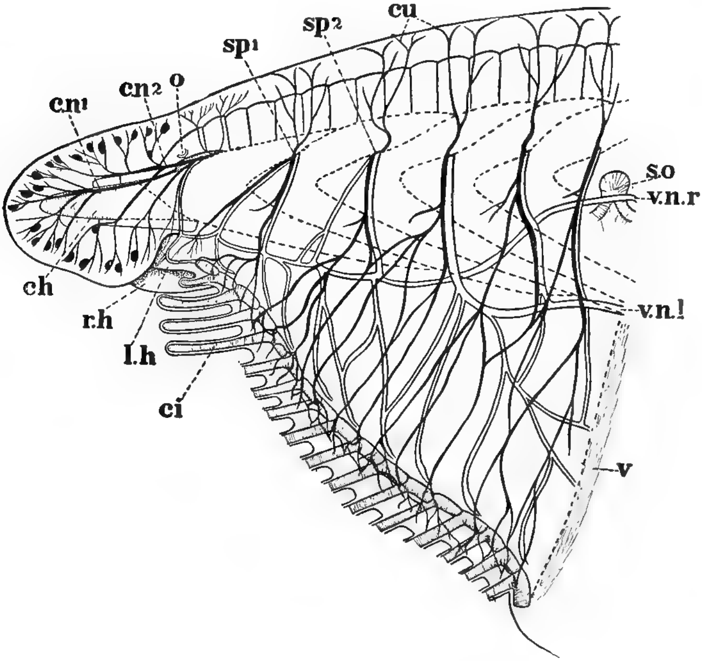

Fig. 42 *A.* — Innervation of the region of the oral hood and snout. (After HATSCHEK, slightly altered according to the statements of VAN WIJHE.)

ch. Anterior end of notochord. *ci.* Buccal cirri. *cn*^{1}, *cn*^{2}. First and second cranial nerves with their peripheral ganglia. *cu.* Rami cutanei dorsales. *l.h.* Left half of oral hood. *r.h.* Right half of oral hood. *o.* Olfactory pit. *sp*^{1}, *sp*^{2}. First and second dorsal spinal nerves. *so.* Sense-organ of oral hood (groove of Hatschek) indicated as if seen through body-well by transparency. *v.* Velum. *v.n.l.* Nerve to left side of velum. *v.n.r.* Nerve to right side of velum.

N.B. — The septa between the myotomes are indicated by dotted lines. The superficial nerves of oral hood are rendered in black; the deeper nerves, which anastomose to form the *plexus of Fusari*, are left white.

the condition met with in the latter there is no ganglionic enlargement on the dorsal root.

The first two pairs of nerves differ in many points from those which succeed them, and are known as the *cranial nerves.* Thus they have no corresponding ventral roots; they appear to be exclusively sensory, and do not innervate any muscles; their distribution is confined to the snout, and they are above all characterised by the presence of peripheral ganglionic enlargements which occur chiefly on the finer branches of the nerves near their distal extremities. Furthermore they lie in front of the first myotome. The first pair of dorsal *spinal* nerves (*i.e.* the third pair altogether) belonging to the first myotome passes from the nerve-tube to the skin through the dissepiment which separates the first myotome from the second. And so with all the succeeding dorsal roots, they lie at the back of the myotome to which they belong, between it and the next following segment. (Cf. Figs. 2 and 42 *A.*)

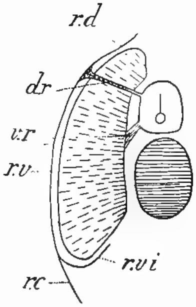

Fig. 42 *B.* — Diagram illustrating the branching of a dorsal spinal nerve of Amphioxus. (After HATSCHEK.)

d.r. Dorsal root. *r.d.* Ramus dorsalis. *r.v.* Ramus ventralis. *r.vi.* Ramus visceralis. *r.c.* Ramus cutaneus ventralis innervating ectoderm of metapleur. *v.r.* Ventral or motor root, indicated as if in the same plane as the dorsal root.

Shortly after leaving the central nervous system, the dorsal roots divide into two branches, a *ramus dorsalis* and a *ramus ventralis* (Fig. 42). These two branches run upwards and downwards respectively, in the gelatinous layer of the sub-epidermic cutis; that is to say, *external* to the muscles.

In the Craniota the corresponding branches of the spinal nerves lie for the first part of their course *internal* to the muscles, between the latter and the notochord. The *cranial* nerves of the Craniota so far resemble the dorsal spinal nerves of Amphioxus that they run external to or ectad of the somites of the head.

The ramus dorsalis of a spinal nerve breaks up into a number of finer nerves, which supply the skin of the back. The ramus ventralis similarly gives rise to a number of cutaneous nerves, but in addition it gives off a branch which passes inwards below the longitudinal muscles of the body-wall, between them and the transverse muscles which lie in the floor of the atrium. This is the *visceral branch* of the spinal nerve. The visceral nerves innervate the transverse muscles and form an elaborate plexus on the surface of them.*

Thus the dorsal spinal nerves of Amphioxus are of a mixed nature, *sensory* and *motor*, but chiefly sensory.

The ventral roots are entirely *motor*. On their emergence from the spinal cord they spread out like a fan and terminate upon the muscle-fibres of the myotomes (Fig. 43).[8]

The muscles which are not innervated by the ventral spinal nerves are the *transverse* or *subatrial muscles*, the muscles of the *mouth* (velum), and *oral hood*, and probably the anal sphincter. These are supplied by the so-called visceral branches of the dorsal nerves. The nerve-supply of the oral hood is illustrated in Fig. 42. It arises from branches of the third to the seventh dorsal nerves. These branches are distributed in two different ways: one set

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* The visceral nerves also send up branches, which pass up through the ligamentum denticulatum to the wall of the pharynx. (FUSARI; see below, p. .) Here they form the branchial plexus described by ROHON, who thought these nerves contained elements of the *Vagus* of the Craniota. The portions of the visceral nerves innervating the transverse muscles (these branches being discovered by ROLPH) were held by ROHON to contain elements of the *Sympathetic system* of Craniota.

of them runs beneath the outer surface of the oral hood and, by the occurrence of frequent anastomoses, forms a coarse network known as the *outer plexus*, while the other set lies beneath the inner surface of the oral hood and gives rise to the *inner plexus*. The latter was discovered by FUSARI in 1889. The two plexuses are distinct from one another, except in so far as their component nerves have a common origin from the dorsal roots (Fig. 42). The outer plexus is continued up into the individual cirri, while the inner plexus appears to stop short at the base of the cirri. It has recently been discovered by VAN

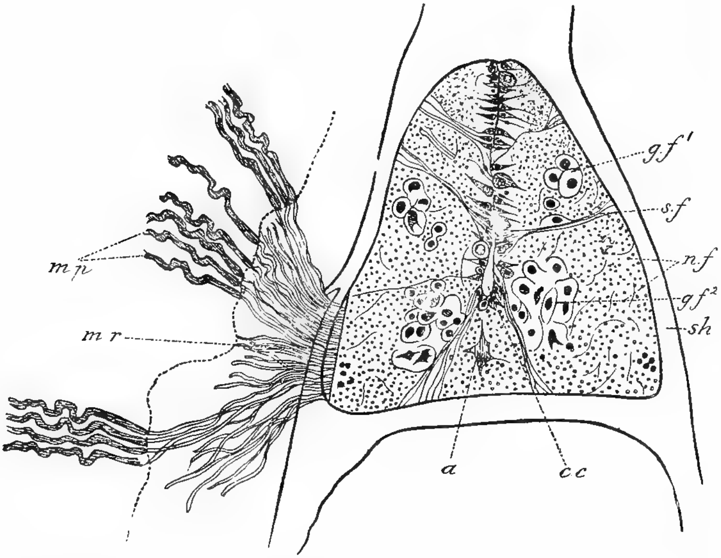

Fig. 43.—Transverse section through the spinal cord in the middle region of the body. (After ROHDE.)

a. Giant fibre proceeding from the giant ganglion-cell *A* (see below). *c.c.* Central canal. *g.f*¹. Giant nerve-fibres, which traverse the spinal cord from before backwards. *g.f*². Giant fibres, which traverse the spinal cord from behind forwards. *m.p.* Muscle-plates. *m.r.* Motor nerve-fibres. *n.f.* Longitudinal nerve-fibres cut across. *s.f.* Supporting fibres. *sh.* Sheath of nerve-cord (= *dura mater*; FUSARI).

WIJHE that the inner plexus on both right and left halves of the oral hood is exclusively formed by nerves which arise from the *left* side of the central nervous system; and, further, that the nerve-supply of the velum is furnished by branches from the fourth, fifth, and sixth dorsal nerves of the left side only. This asymmetrical innervation of the velum and inner (glandular) surface of the oral hood will be referred to again after the consideration of the larval development.

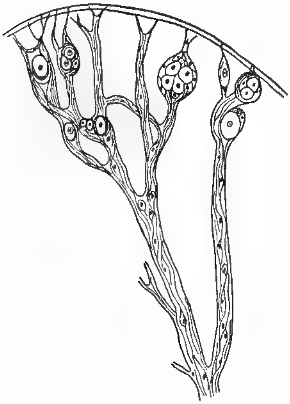

Fig. 44. — Peripheral ganglion-cells of the cranial nerves of Amphioxus. (After FUSARI.)

The peripheral ganglionic enlargements which are so characteristic of the two pairs of cranial nerves must be correlated with the sensibility of the snout. As the nerve-fibres are continued beyond them, they are not to be regarded as end-organs, but simply as peripheral ganglia. Their structure is shown in Fig. 44. They were discovered by the great French naturalist QUATREFAGES in 1845. Each of them is composed of from one to four nerve-cells, with granular protoplasm and a large nucleus. Each group is enclosed in a sheath which is a continuation of the sheath of the nerve itself. The sheath is lined internally by an endothelium. According to FUSARI the nerve-fibres enter into direct connexion with the cells, though some would appear to pass round them.

The peripheral nervous system of Amphioxus can only be compared definitely, at present, in its broadest features with that of the higher Vertebrates. The determination of the particular homologies in the two cases forms one of the most difficult problems of comparative morphology. In correlation with the low grade of cephalisation to which Amphioxus has attained, there are only two pairs of cranial nerves, the succeeding nerves retaining their primitive spinal character. The dorsal spinal nerves, furthermore, possess features which are specially characteristic of the cranial nerves of the Craniota. Such are their mixed sensory and motor functions, and the position of their dorsal and ventral branches ectad of the musculature. As already indicated above, the walls of the gill-slits of the craniate Vertebrates are innervated by cranial nerves, while in Amphioxus this is done by spinal nerves. (Cf. Fig. 92; see also below, p. 163.)

In transverse section the spinal cord of Amphioxus is seen to have somewhat of a triangular shape. The central canal has the form of a vertically elongated split, commencing from the vertex of the triangle, and extending two-thirds of the way downwards into the cord. For the greater part of its extent, however, the two sides of the canal are closely approximated together so as to obliterate the lumen, which widens out again below, and presents the appearance of a circular or oval tube. The sides of the canal are lined by an epithelium the cells of which, starting from an indifferent condition in the embryo, have become modified in several different directions. Some are *ganglion-cells*, and others send out long radial processes which traverse the substance of the nerve-cord, and serve to hold it together. These are the *supporting fibres* (Fig. 43). The cells in the nerve-cord form a much smaller proportion of the bulk of it than the nerve-fibres do. The latter run mostly in a longitudinal direction, and produce a punctate appearance in cross-section.

Anteriorly in the region of the cranial nerves the lumen of the central canal widens out into a relatively spacious vesicle, known as the cerebral vesicle (Fig. 45). In young individuals this cavity opens by an aperture called the *neuropore* into the base of an epidermal pit, which we have already described under the name of the *olfactory pit.* Later on the neuropore closes up, but its former presence is indicated by a shallow groove at the base of the otherwise solid stalk connecting the olfactory pit with the roof of the brain.

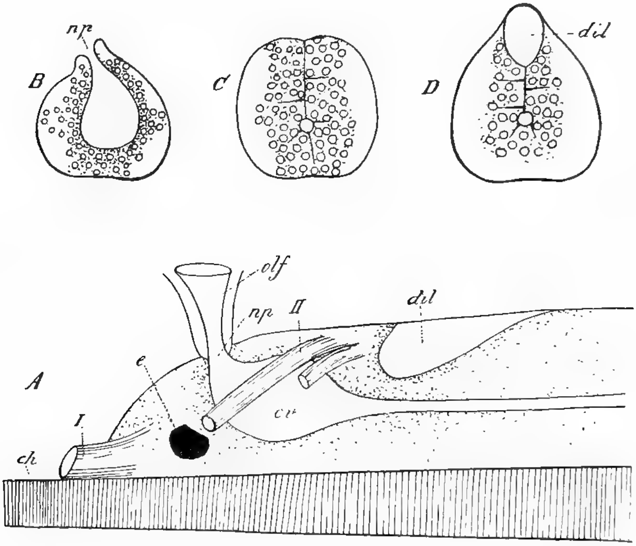

Fig. 45. — *A.* Brain and cranial nerves of a young Amphioxus of 3 mm. length. *B, C, D.* Sections through different portions of brain: *B,* through neuropore and cerebral vesicle; *C,* through the intermediate portion, and *D,* through the dorsal dilatation of central canal. (After HATSCHEK.)

ch. Notochord. *c.v.* Cerebral vesicle. *dil.* Dorsal dilatation (Hatschek's *Fossa rhomboidalis*). *e.* Eye-spot. *np.* Neuropore. *olf.* Olfactory pit.

I, II. First and second cranial nerves.

Behind the cerebral vesicle the lumen of the central canal widens out in its dorsal portion independently of the ventral tube, so as to form a vesicular dilatation covered over by a thin membrane. The region of the nerve-tube, over which this dorsal dilatation extends, has been compared by Hatschek, who discovered it, to the *medulla oblongata* of the craniate Vertebrates, which is similarly roofed in only by membrane. In the fully grown condition, however, it seems to be largely obliterated by the

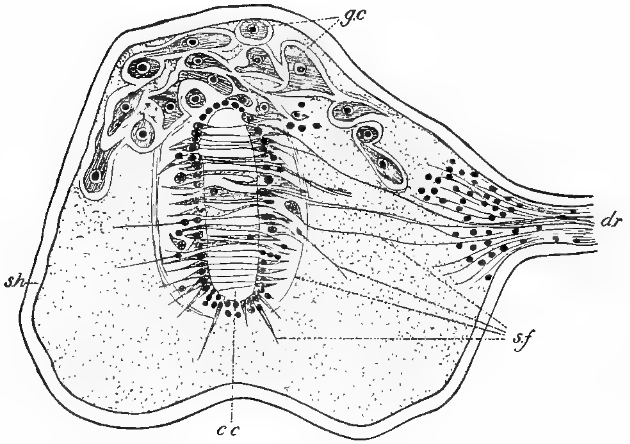

Fig. 46.—Transverse section through the spinal cord between the second and third sensory roots. (After Rohde.)

g.c. Dorsal aggregation of ganglion-cells (extending between the second and fifth pairs of sensory nerves; a somewhat similar group of ganglion-cells occurs on ventral side of nerve-cord below the central canal between the fourth and sixth sensory nerves.)

d.r. Dorsal root. *s.f.* Supporting fibres. *c.c.* central canal; in this case equally wide throughout its entire height, and so all along the spinal cord. *sh.* Sheath of nerve-cord.

development of a mass of large ganglion-cells which extend backwards as far as the fifth pair of sensory nerves (Fig. 46).

All there is of a brain in Amphioxus is shown in Fig. 45. The cerebral vesicle is a plain cavity without any true subdivision into ventricles.[9] In the development of the central nervous system of the higher Vertebrates, a stage is passed through which may be compared broadly with the permanent condition of things in Amphioxus. But in the former the anterior portion of the medullary tube quickly becomes greatly enlarged in contrast to the spinal cord proper, and becomes divided by constrictions into fore-, mid-, and hind-brain, which constitute the three primary divisions of the Vertebrate brain. Then the brain undergoes a flexure round the anterior end of the notochord. This curvature of the primitively horizontal brain-region in the craniate Vertebrates is known as the *cranial flexure*. (Cf. Figs. 23 and 24.)

Among the numerous longitudinal nerve-fibres which compose the bulk of the spinal cord of Amphioxus, there are some which stand out in marked contrast to the great majority on account of their large size. These are the so-called *giant-fibres*, and they form one of the greatest peculiarities in the spinal cord of Amphioxus. According to ROHDE there are no fewer than twenty-six of these giant-fibres present, and each of them arises from a corresponding *giant ganglion-cell*. These so-called giant-cells have many processes, *i.e.* they are *multipolar*, but they each send out one main stem, which is a giant-fibre. The giant-cells lie across the middle of the central canal, and the giant-fibres pass outwards alternately to the right or left of the central canal, and then bend downwards and pass below the central canal and up

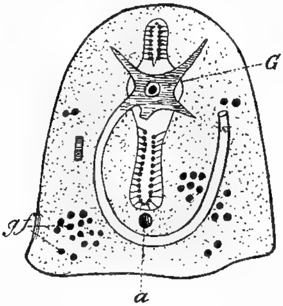

Fig. 47. — Transverse section through spinal cord in region of giant ganglion-cell *G*. (After ROHDE.)
a. Process of giant-cell *A*. *g.f.* Giant-fibres.

to the opposite side of the canal, where they continue their course in the longitudinal direction (Fig. 47). The giant-fibre belonging to the most anterior giant-cell differs in several respects from the other giant-fibres. It is much larger than the others, and, whereas the latter lie on either side of the nerve-cord, the fibre in question lies in the middle line immediately below the central canal (Figs. 43 and 47).

These giant-fibres traverse the spinal cord almost throughout its entire length, stopping short at some distance from its anterior and posterior ends. The giant-cells are arranged one after the other in two groups, one group lying in the anterior third of the spinal cord, the fibres from which run backwards, and the other group occupying the posterior third of the cord, the fibres from which run forwards (Fig. 48).

The giant-fibres are in no direct connexion with the outgoing nerves, but the giant-cells usually occur opposite a sensory (*i.e.* dorsal) root (Fig. 49).

In the spinal cord of Petromyzon giant-fibres are present in considerable numbers,

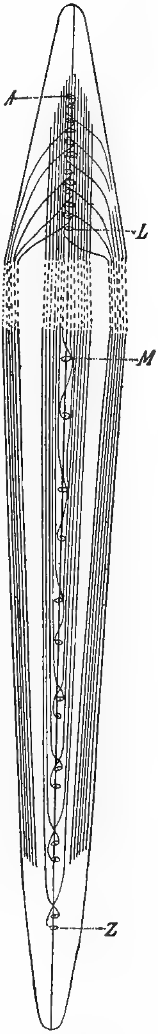

Fig. 48.

Fig. 48.—Scheme illustrating the course of the giant-fibres and their origin from the giant-cells *A–Z* in the spinal cord of Amphioxus. (After ROHDE.)

A–L. Giant ganglion-cells whose giant processes traverse the spinal cord from before backwards. *A* is about at the level of the sixth sensory root, counting from the first cranial nerve. *M–Z.* Giant ganglion-cells whose giant processes traverse the spinal cord from behind forwards. *M* is about at the level of the fortieth sensory root.

while in the higher Fishes and tailed Amphibia, as well as in the tadpoles of the anourous Amphibia, the giant-fibres are represented by the so-called fibres of *Mauthner*.*

They are not found in the spinal cord of adult tailless Amphibia, Birds, and Mammals.[10]

Their occurrence in such large numbers in Amphioxus is therefore the symbol of an archaic organisation.

Giant-fibres form a very striking feature in the ventral nerve-cord of many Invertebrates. Here, however, they appear often to lose their nervous function, and serve rather as elastic supporting rods for the nerve-cord. They are enclosed in thick sheaths of connective tissue, and have been found to originate in giant ganglion-cells. When the enclosed nerve degenerates, they become hollow tubes containing a coagulable fluid. (Eisig.)

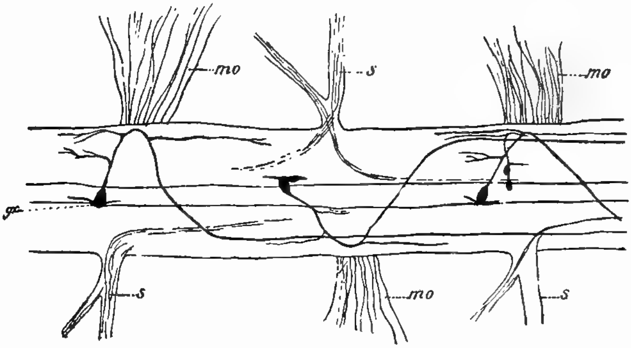

Fig. 49.—Part of spinal cord seen from above; from a preparation stained with methylene-blue. (After Retzius.)

g.c. Giant ganglion-cell lying across central canal. *mo.* Motor root. *s.* Sensory root.

With regard to the internal origin of the nerves which pass out from the spinal cord, our knowledge only extends to the dorsal roots. At the base of the ventral roots the

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* Also known as Müllerian fibres.

fibres appear to stop, and in their place a peculiar granular structure of unknown significance is found (Fig. 49).

The fibres which constitute a dorsal root are derived from two sources. Part of them are continuations or branches of the longitudinal fibres on the same side of the nerve-cord, on which a given dorsal root may be, while the other moiety appears to arise largely from groups of small bipolar ganglion-cells in the neighbourhood of the central canal, which send one process each in the direction of the dorsal root, and another process from the opposite pole of the cell to join in with the longitudinal fibres of the other side of the spinal cord (Fig. 50).[11]

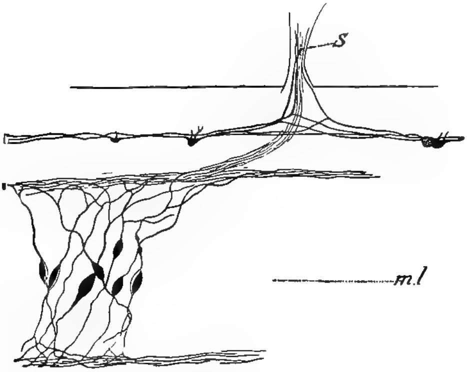

Fig. 50. — Diagram illustrating the internal origin of the nerve-fibres of a sensory root. (Combination of two figures of RETZIUS.)

The cells giving rise to the processes lying on the same side as a sensory root *S*, which divide into a T at the base of the root, are naturally in contiguity with the central canal, but are displaced for the purpose of the diagram. *m.l.* Middle line.

We will now compare, or rather contrast, the central nervous system of Amphioxus with that of an Annelid such as the common earthworm. The type of nervous system presented by the latter is common to a vast proportion of the Invertebrates. It consists essentially of three very sharply defined parts (Fig. 39); namely, (i.) the *cerebral* or *supraœsophageal* ganglion, which is situated dorsally over the buccal cavity; (ii.) a *longitudinal solid nerve-cord* composed of two more or less distinct halves, running along the whole length of the *ventral* side of the body below the alimentary canal; (iii.) the *circumœsophageal nerve-ring* or *commissure* which encircles the buccal tube and connects the cerebral ganglion with the *subœsophageal* ganglion at the anterior extremity of the ventral nerve-cord.

Viewed from above (as in Fig. 39), the ventral nerve-cord presents a series of constrictions which are in some forms very pronounced. The wider portions occur in the middle of the body-segments, and constitute the ventral ganglia, which are strung together by the intervening nerves (connectives) in the form of a ganglionic chain. From the ganglia, paired nerves pass out to the organs of the body.

One of the greatest peculiarities in the type of nervous system above described lies in the fact that the alimentary canal passes through and is surrounded by a portion of the central nervous system; namely, the circumœsophageal commissure. This fact has been one of the most serious difficulties which the upholders of the Annelid-theory have had to contend with.

In the Chordata the alimentary canal does not pierce the central nervous system in any sense whatever.* Nevertheless, there have been many conjectures as to a possible equivalent of the circumœsophageal nerve-collar in the Vertebrates, although it is safe to say that nothing of the kind really exists.

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* Balanoglossus might be said to offer an exception to this rule (see Chap. V.).

The ventral nerve-cord of the Annelids is no doubt in part physiologically equivalent to the spinal cord of the Vertebrates; but since the two structures lie on opposed sides of the body, it is difficult to regard them as morphologically equivalent. Those who defend the Annelid-theory have postulated the occurrence of a half-revolution of the body in the supposed Annelid-like ancestors of the Vertebrates, as a result of which they acquired the habit of performing their locomotion, perhaps swimming, on their backs so that the ventral surface was turned uppermost. In this way, we are to suppose the original dorsal and ventral surfaces became reversed. This phylogenetic acrobatic feat with all its consequences is hard to imagine, and there are other alternatives which make it an unnecessary assumption. (See below, V.)

The chief fundamental differences between the dorsal spinal cord of Amphioxus and of Vertebrates generally, and the ventral ganglionic chain of the Annelids, may be summed up as follows:—

	Amphioxus.	*Annelids.*
1.	Nerve-cord is hollow.	Nerve-cord is solid.
2.	“ “ dorsal.	“ “ ventral.
3.	“ “ unconstricted.	“ “ constricted.
4.	“ “ single.	“ “ double.
5.	Ganglion-cells lie inside the fibrous layer.	Ganglion-cells lie outside the fibrous layer.

As for the resemblances, in both cases nerves are given off segmentally, and also giant-fibres are present, whose function, however, is apparently very different in the two cases.[10]

NOTES.

1. (p. 49.) LANKESTER has made the suggestion that there are not distinct capillaries and cœlomic space around the hepatic cœcum, but that the space itself is capillariform. This view is in accordance with what one observes in transverse sections.

2. (p. 50.) The fullest account of the contractile blood-vessels of Amphioxus, as observed in the living animal, is that given by JOHANNES MÜLLER. He observed the peristaltic contractions of the branchial artery (which is filled with a perfectly colourless blood), beginning from its hinder end, where it is joined by the hepatic vein (which also undergoes peristaltic contraction from before backwards along dorsal side of cœcum) and extending to the front end of the pharynx. The intervals between the successive contractions last about a minute. Immediately succeeding upon the contraction of the branchial artery, the bulbils, which occur at the base of the primary or forked gill-bars, contract too. He says that the heart-like "aortic arch" which occurs to the right of the velum (he thought there was one on the left side as well) contracts from below upwards, and that its contraction enabled him to discover it. As mentioned in the text, van Wijhe states that it has no communication with the branchial artery. Johannes Müller also observed the peristaltic contraction of the sub-intestinal (portal vein), and states that it extends to the anterior end of the cœcum. It should be remembered that his observations were made on young transparent individuals, and the statement as to the extent of the contraction of the sub-intestinal vein is open to doubt.

3. (p. 51.) A *genital artery* running longitudinally above the gonadic pouches has been figured by Langerhans, Rolph, Schneider, Lankester, and Boveri, but its relations to the rest of the vascular system have not been made out. It is doubtful whether its presence is constant.

4. (p. 58.) The "brown funnels" were discovered by LANKESTER in 1875, and were subsequently compared by BATESON with the collar-pores of Balanoglossus. (See Chap. V.) This comparison was made on the supposition that the posterior free oper-

cular fold of the so-called collar in Balanoglossus is of the same nature as the atrium of Amphioxus; but this is somewhat doubtful.

5. (p. 70.) For an admirable critical and historical account of our knowledge of the development of the excretory system in the different groups of Vertebrates, the reader may be referred to the report on the "*Entwickelung der Excretionsorgane,*" by Professor RÜCKERT, in Merkel and Bonnet, *Ergebnisse der Anatomie und Entwickelungsgeschichte,* Band I., 1891. It will be sufficient to note here that the ectodermic origin of the pronephric duct, as briefly described in the text, only holds for the Selachians and Mammals. It was first discovered in the latter by GRAF SPEE in 1884, and confirmed later by FLEMMING. In the former it was discovered independently by VAN WIJHE and RÜCKERT (1886–8). On the contrary, in Petromyzon, Amphibia, Reptiles, and Birds, the duct does not arise from the ectoderm.

Van Wijhe denied the *segmental* fusions with the ectoderm of the pronephric tubules in Selachians as described by Rückert. The account given by the latter author has, however, been indirectly confirmed by the observations of FELIX on the chick, where the pronephric outgrowths were found in some cases to undergo a transitory fusion with the ectoderm.

BOVERI has attempted to show how the origin of the pronephric duct can be imagined to have been gradually transferred from the ectoderm to the mesoderm. Finally, it may be noted that, whereas RÜCKERT compared the pronephric tubules with the Annelid nephridia, SEMPER and others employed the mesonephric tubules for the comparison. The fallacy of the latter comparison was first pointed out by FÜRBRINGER.

6. (p. 74.) In 1887 PAUL MAYER discovered that the subintestinal vein in the Selachian (Pristiurus) embryo communicated with the dorsal aorta, by a series of six segmental vessels which passed up around the intestine on the right side only. Corresponding to them on the left side he found short, blind outgrowths from the dorsal aorta similar to those figured in the text in connexion with the pronephros of Ichthyophis. Paul Mayer's connecting vessels soon become aborted with the exception of one which enlarges and forms the proximal portion of the umbilical artery. In the following year it was shown in a brilliant manner by

Rückert that these vessels occur in the same segments as the rudimentary pronephric tubules, and give rise to rudimentary glomeruli at the level of the tubules. (Cf. Fig. 35 *B.*) There can be no doubt that these vessels are homologous with the vessels which run through the primary branchial bars of Amphioxus, and, as shown by Boveri, assist in forming glomeruli at the level of the excretory tubules.

The morphological importance of these facts is very great and has been strongly emphasised by Boveri. Whether Paul Mayer's connecting vessels indicate the former existence of gill-slits in that region is not so certain, since it is difficult to decide whether the indefinite number of gill-slits in the adult Amphioxus is a palingenetic (ancestral) feature or not. It should also be remembered that Paul Mayer found numbers of connecting vessels, between sub-intestinal vein and dorsal aorta, in the *tail.*

7. (p. 78.) Boveri found that the epithelium of the pronephric duct of Myxine was of a glandular nature, comparable in this respect to the atrial epithelium of Amphioxus.

8. (p. 86.) As shown in Fig. 43, Rohde was inclined to follow Schneider in the belief that the fibres of the ventral spinal nerves were directly continuous with the muscle-plates and, moreover, exhibited the same striation as the latter. It has recently been shown by Gustav Retzius that this appearance of continuity is an illusion, as in so many other cases where nerves have been wrongly supposed to enter into direct continuity with peripheral end-organs. By employing Ehrlich's method of staining nervous tissue, *intra vitam*, with methylene blue, Retzius has proved that the motor fibres of Amphioxus pass with a somewhat winding course between the muscle-plates, and simply end on the surface of the plates. Rarely they branch dichotomously, but there is no special end-apparatus as in the higher forms. Their connexion with the muscle-plates is, therefore, one of intimate contiguity, but not of continuity.

9. (p. 91.) The cerebral vesicle of Amphioxus was discovered in 1858 by Leuckart and Pagenstecher. Owsjannikow (1868) thought it represented the fourth ventricle of the vertebrate brain. Stieda (1873) was the first to homologise the cerebral vesicle of Amphioxus with the entire brain of the higher forms, and to regard

it as representing the latter in its simplest form without any trace of subdivision. This view has very generally been adopted. Stieda also recognised the dorsal and ventral groups of ganglion-cells (of which the former is shown in section in Fig. 46) as belonging to the hinder portion of the brain. Rohde's conception of the brain of Amphioxus agreed very closely with that of Stieda, but he made a more detailed study of its histological character, and defined its limits more precisely. He concludes that the beginning of the spinal cord proper, in the absence of any outward mark of distinction from the brain-region, would lie at the point marked by the appearance of the first of the giant ganglion-cells, which he denotes by the letter A. (Cf. Fig. 48.)

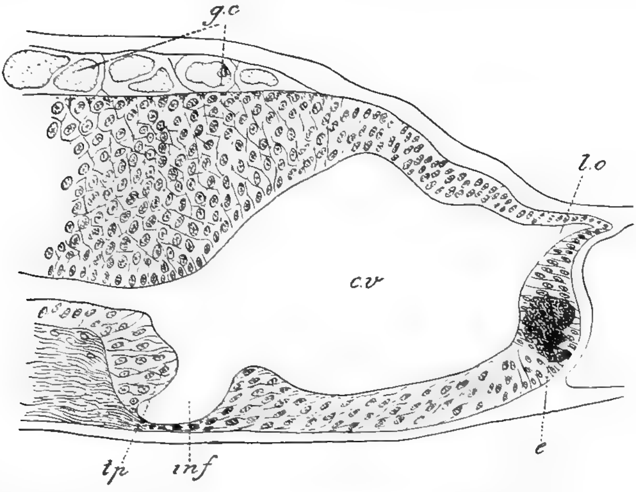

Fig. 51.—Sagittal section through the cerebral vesicle of Amphioxus. (After KUPFFER.)

c.v. Cavity of cerebral vesicle. *e.* Eye-spot. *g.c.* Dorsal group of ganglion-cells (cf. Fig. 46). *inf.* Infundibular depression. *l.o.* Lobus olfactorius impar. *tp.* Tuberculum posterius.

Quite recently the attempt has been made by Professor VON KUPFFER to determine in detail the delimitation of the cerebral vesicle of Amphioxus (Fig. 51). The slight outpushing of the wall of the vesicle towards the base of the olfactory pit has been mentioned in the text. It was discovered by LANGERHANS in

1876, who called it the *lobus olfactorius*. Kupffer has succeeded in finding a similar structure in the embryos of other Vertebrates, notably in *Acipenser sturio* (the sturgeon). He calls it the *lobus olfactorius impar*, and shows that it indicates the point where the medullary tube remained for the longest and last time in direct connexion with the external ectoderm, precisely as is the case in Amphioxus. There is thus at least one fixed point common to the cerebral vesicle of Amphioxus and the brain of the craniate Vertebrates. But Kupffer has found another. While it is obvious that the anterior wall of the vesicle containing the pigment which constitutes the eye-spot is homologous with the primary optic tract (*recessus opticus*) of the higher Vertebrates, in which pigment is, in many cases, deposited in the embryo, Kupffer states that he is able to detect an infundibular depression in the floor of the cerebral vesicle of Amphioxus. Immediately behind this depression there is a prominence in the wall of the vesicle, which Kupffer calls the *tuberculum posterius*. This point is also to be identified in the brains of the higher Vertebrates.

The dorsal dilatation of the central canal, which Hatschek discovered and compared with the fourth ventricle of the vertebrate brain, whose roof is similarly membranous and not nervous (Fig. 45), is certainly a very curious, and apparently constant, feature in young individuals, as I can affirm in confirmation of Hatschek. The conclusion come to by Hatschek, however, that the lobus olfactorius of Langerhans is the homologue of the infundibulum of the higher forms, would appear to be untenable in the light of Kupffer's researches.

It is beyond the scope of this book to discuss the difficult problem of the origin of the paired eyes of the Vertebrates, but it may be pointed out that there is no difficulty in identifying a stage in the embryonic development of the optic tract in the Craniota corresponding to the permanent condition of things in Amphioxus. This fact was first demonstrated by WILHELM MÜLLER in 1874. On account of its position in front of and below the cerebral vesicle, it is doubtful whether the eye-spot of Amphioxus is homologous with the eye of the Ascidian tadpole. (See below.)

10. (p. 94.) It is a significant fact that giant nerve-fibres appear

to be present in the spinal cord of all those Vertebrates whose tail serves as an important organ of locomotion. Thus, they occur in fishes, tailed Amphibia, in the tadpoles of tailless Amphibia, and, finally, they have been recently discovered by MAX KÖPPEN in the caudal region of the spinal cord of the lizard. In the frog and higher forms they do not occur. From these considerations Köppen thinks that there is a causal relationship between the occurrence of giant-fibres in the spinal cord and the presence of a locomotor tail. The caudal locomotion, characterised by the rapid swaying motion of the tail, is not confined to the post-anal region in Amphioxus, but involves the whole body.

Contrary to the observations of EISIG, both NANSEN and ROHDE are of opinion that the giant-fibres of Annelids (Polychæta) have the same physiological significance for the central nervous system as those of Amphioxus.

Some of the older authors mistook the giant nerve-fibres for capillary blood-vessels. As a matter of fact no blood-vessels traverse the central nervous system of Amphioxus. It may be added, also, that there are no *medullated* nerve-fibres.

11. (p. 95.) Several suggestions have been made as to possible representatives of the spinal ganglia of the dorsal roots of the Craniota in Amphioxus.

Omitting earlier, and obviously erroneous, suggestions, ROHDE (1888) regarded the nuclei, which he found imbedded in the dorsal roots, as a collection of "nervous nuclei," comparable to the spinal ganglia of the higher Vertebrates (Fig. 46). According to RETZIUS (1890) these nuclei are not of a nervous nature (probably belong to supporting-cells), and he tentatively suggests that the spinal ganglia are represented by groups of bipolar ganglion-cells which occur inside the spinal cord at fairly regular intervals in two longitudinal rows, one on each side of middle line. The main process (axis-cylinder) of these cells divides in T-form, and one of the branches of the T passes into the dorsal root. (Cf. Fig. 50.)

Finally, Hatschek (1892) finds the homologues of the spinal ganglia at the points where the dorsal nerves divide into *ramus dorsalis* and *ramus ventralis*.

III.

DEVELOPMENT OF AMPHIOXUS.

As an introduction to the study of embryology, and as an indispensable aid to a reasonable appreciation of the value of embryological facts, the life-history of Amphioxus provides an object which, for its capability of application to almost every branch of zoölogical discussion, is perhaps unrivalled. It is alike useful in a text-book of human embryology, and in one of invertebrate zoölogy.

The reason for this obviously lies in the fact that in Amphioxus everything has its own definite line of demarcation, all the fundamental structures of the body are laid down with schematic clearness, there are no massive agglomerations of cells forming complicated tissues, but all the organs are of simple epithelial origin and constitution.

Whereas in many of the higher and lower animals the greatest difficulty is often experienced in deciding to which of the primary layers of the body this or that structure owes its origin, in Amphioxus there is no such difficulty. With these advantages it is, therefore, no wonder that Amphioxus should serve as a refuge to the perplexed embryologist.

It is not an exaggeration to say that the researches both of KOWALEVSKY and of HATSCHEK, on the development of Amphioxus, will always rank among the classics of embryological literature; while it is a familiar fact that Kowalevsky's earlier work (1867) on the development of the

Ascidians and of Amphioxus marks a distinct epoch in the progress of the science of embryology.

EMBRYONIC DEVELOPMENT.

Fertilisation and Segmentation of the Ovum.

The breeding-season of Amphioxus extends, in the Mediterranean, from spring to autumn.

The gonadic pouches become very much distended by the ripening of the ova and spermatozoa in the respective sexes, and finally burst, discharging their contents into the atrial cavity, whence they reach the exterior through the atriopore.[1] At the time of complete sexual maturity the gonads become so large that the atrium is used up to its utmost capacity, and its walls become stretched to such an extent that the metapleural folds are flattened up against the sides of the body.

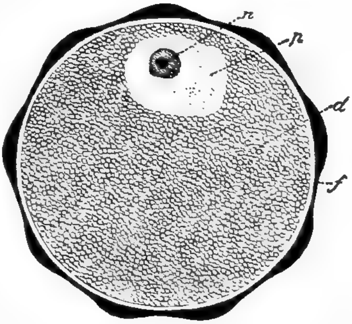

Fig. 52.—Unfertilised ovum of Amphioxus. Magnified about 750 diameters. (After LANGERHANS.)

d. Yolk granules. *f.* Follicle. *n.* Nucleus (germinal vesicle), with nucleolus. *p.* Protoplasmic area, free from yolk granules, surrounding the nucleus.

The ovum is semi-opaque, contains granules of yolk equally distributed throughout its substance, and is surrounded by a cellular membrane known as the *follicle* of the egg, and sometimes less accurately spoken of as the *vitelline membrane* (Fig. 52).

Spawning, when it occurs, invariably takes place at sundown,—*i.e.* between five and seven o'clock in the evening,—and never, so far as is known, at any other time.

Ova and spermatozoa are discharged simultaneously by male and female individuals into the water, and fertilisation is effected in the latter medium.

The final stages in the maturation of the ovum of Amphioxus are very imperfectly known, and the extrusion of the so-called *polar bodies*, preparatory to the process of fertilisation, has not been properly studied, only one such body having been observed, whereas from the analogy of all other sexually reproducing animals we should expect two polar bodies (directive corpuscles) to be given off before the egg was fully mature. As soon as an ovum has been fecundated by the entrance of a spermatozoön, the vitelline membrane springs away from the body of the egg-cell, leaving a wide space between the latter and the former (Fig. 53). This expansion of the vitelline mem-

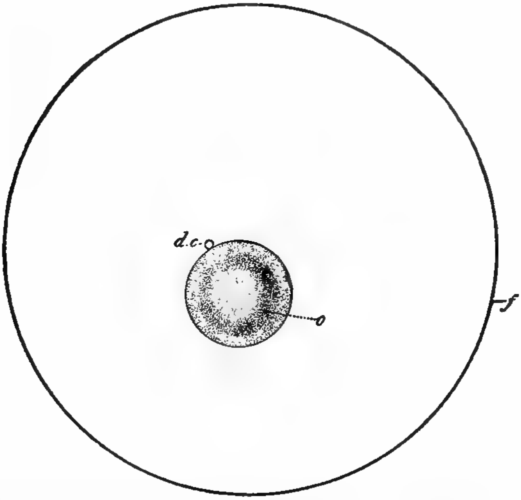

Fig. 53. — Fertilised ovum of Amphioxus. Highly magnified. (From a drawing kindly lent by Professor E. B. WILSON.)
d.c. Directive corpuscle or polar body. *o.* Ovum. *f.* Follicle.

brane is the first outward and visible sign of the accomplishment of the process of fertilisation.

About an hour later, — that is to say, at about 8 P.M., — the egg becomes flattened at its two poles, and a depression appears at the animal pole, the latter being indicated by the polar body. The depression deepens and extends as a meridional furrow round the egg. Finally, the division of the egg into two halves or *blastomeres*, which remain attached to one another, is completed, and the first stage in the segmentation of the egg is accomplished (Fig. 54).

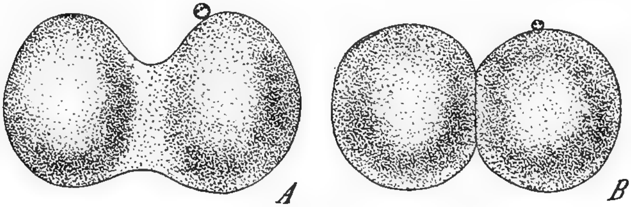

Fig. 54. — Division of ovum into the first two blastomeres. The polar body marks the animal pole. (After HATSCHEK.)

As it is beyond the scope of this book to discuss the mechanics of cell-division, the description of the segmentation stages will be very brief.

The first meridional cleavage which divides the egg into two *blastomeres* is followed by another one at right angles to it, dividing each of the two blastomeres again into two. In this way the stage with four equal blastomeres in one plane is produced. Next follows an *equatorial cleavage*, by which eight blastomeres are produced, the four upper cells at the animal pole being some-

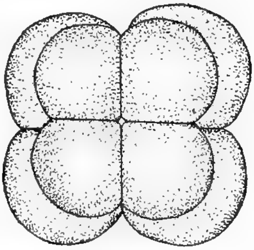

Fig. 55. — Eight-cell stage seen from the upper (animal) pole. Four small blastomeres (micromeres) lie upon four larger blastomeres (macromeres). Radial type of cleavage. (After E. B. WILSON.)

what smaller than the four lower cells at the vegetative pole, since the latter contain a greater quantity of the yolk-spherules (Fig. 55).

The next cleavage giving rise to an embryo of sixteen cells is meridional. Then the eight upper and the eight lower cells become respectively divided by equatorial cleavages, and so the thirty-two cell stage is reached (Fig. 56).

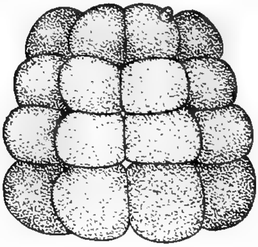

Fig. 56.—Thirty-two cell stage, consisting of four rows of eight cells, each ranged around a central segmentation cavity (blastocœl). The polar body is still visible at the animal pole. (After HATSCHEK.)

The embryo is now known as a *blastula*, and consists of a mulberry-like mass of cells surrounding a central cavity called the *segmentation-cavity* or *blastocœl*.

From this point of the development the blastomeres go on dividing with more or less regularity, until the wall of the blastula consists of a great number of cells arranged in a single layer about the central cavity.

The segmentation of the egg of Amphioxus, however, by no means follows the uniform and stereotyped plan that has been hitherto supposed. It has recently been discovered by Professor E. B. WILSON that Amphioxus presents an example of a *polymorphic* cleavage. Instead of following one type, it follows three types of cleavage; namely, a *radial type* (Figs. 55 and 56), a *bilateral type* (Fig. 57), and a *spiral type* (Fig. 58). These three types of cleavage are reducible to a common basis, and are connected together by all possible intermediate gradations. Wilson points out that in the bilateral type of cleavage Amphioxus shows a close correspondence with the Ascidian embryo.

The segmentation or cleavage of the ovum results in the formation of a spherical blastula, closed at all points, and consisting of some 256 cells surrounding a spacious cavity, the blastocœl.

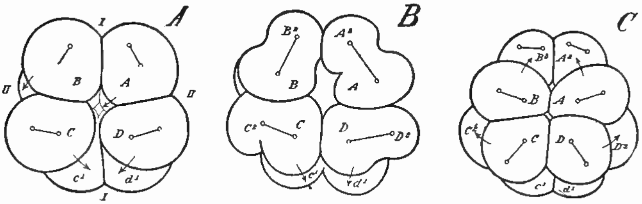

Fig. 57. — Three stages in the segmentation of the ovum, according to the bilateral type. From the lower pole. (After E. B. Wilson.)

A. Eight-cell stage. *A, B, C, D.* The four macromeres, above which are seen portions of the four micromeres.

I–I. Plane of first cleavage, with respect to which the cells divide in such a way as to become arranged in a bilaterally symmetrical manner.

II–II. Plane of second cleavage.

B. Transition to the sixteen-cell stage.

C. Sixteen-cell stage. The line in each cell indicates the direction in which the next division of the cell would take place.

The stages of development leading up to the blastula are known as the *segmentation stages.* At their completion, although, of course, cell-division continues to take place actively, yet other processes supervene which render the mere division of the individual cells of minor morphological importance.

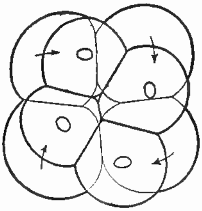

Fig. 58. — Eight-cell stage from the upper pole, illlustrating the spiral type of cleavage. (After E. B. Wilson.)

Gastrulation.

The next phase of the development is known as the *gastrulation* of the embryo. The cells forming the lower or vegetative side of the blastula remain, throughout the segmentation stages, somewhat larger than the rest of the blastula-wall. This side now becomes flattened, as shown in Fig. 59 *A*. Next, the flattened side of the blastula becomes gradually tucked up or invaginated into the blastocœl (Fig. 59 *B*) until, finally, the segmentation cavity is completely obliterated, and the invaginated layer of cells becomes tightly fitted up against the outer layer (Fig. 59 *C*).

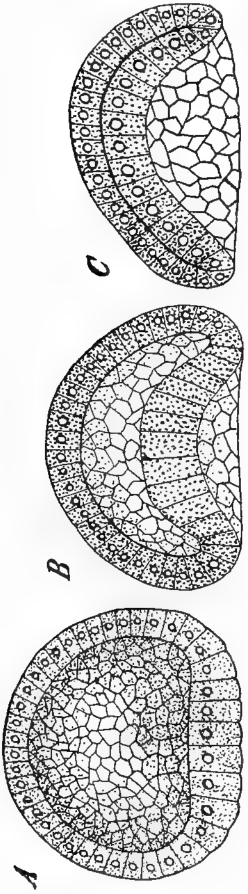

Fig. 59. — Three stages in the gastrulation of Amphioxus, seen in optical section. (After Hatschek.)
A. Blastula with flattened vegetative surface; optical transverse section.
B. Lower pole becomes invaginated into the blastocœl; optical transverse section.
C. The invagination is completed and the blastocœl is obliterated; optical longitudinal section.

The embryo, now known as the *gastrula*, is a double-layered sac, the cavity of which was produced by invagination, and is known as the *primitive gastral cavity*, or *archenteron*. This cavity is widely open to the exterior by the orifice of invagination, or *blastopore*, which in German is designated by the expressive term *Urmund*. The two layers of cells which constitute the wall of the gastrula are the *primitive germ-layers*; the outer layer is the *primitive ectoderm*, and the inner layer, surrounding the gastral cavity, is the *primitive endoderm*; the two layers are continuous with one another round the margin of the blastopore.

The blastopore is at first a very wide oval opening, but it soon becomes narrowed down to a small aperture by the continued deepening of the archenteric cavity (Fig. 60).

It is now a well-established fact that all multicellular animals (Metazoa) pass through a gastrula-stage in the course of their development, although the form of the gastrula is often extremely modified and difficult to recognise. The significance of this fact, as was long since pointed out by Huxley, Haeckel, Lankester, and others, is very great when it is remembered that the embryonic characteristics of the gastrula are essentially identical with the permanent features of the organisation of the Cœlenterata (Hydra, etc.).

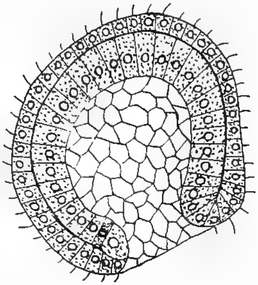

Fig. 60. — Optical longitudinal section of later gastrula. Cilia (flagella) have been protuded from the ectoderm cells, and the embryo at this stage begins to rotate within the follicle. (After HATSCHEK.)

Returning to the gastrula of Amphioxus, in the course of the further differentiation which goes hand in hand with the progressive growth and development, we shall find that the primitive ectoderm gives rise to (1) the *central nervous system* and (2) the *definitive ectoderm;* the primitive endoderm gives rise to (1) the *mesoderm,* which is usually regarded as a third or intermediate germ-layer; (2) the *notochord;* and (3) the *definitive endoderm,* which forms the lining mucous epithelium of the alimentary canal; finally, the primitive gastral cavity or archenteron will become subdivided into (1) the *body-cavity* or *cœlom,* and (2) the *definitive gut* or *alimentary canal.*

The embryo shown in optical section in Fig. 60 represents the stage reached at midnight of the first night of development. It will be noticed that one side is convex, while the opposite side is flattened; this is an indication that dorso-ventral differentiation has taken place, since the flattened side marks the dorsum or back of the embryo, while the convex side is ventral. It may be seen further that the blastopore is inclined towards the dorsal side of the embryo. The dorsal inclination of the blastopore is eminently characteristic of the vertebrate gastrula from the Ascidians up to the highest craniate forms. In the Invertebrates (Annelids, Molluscs, etc.) the blastopore acquires a ventral inclination.*

At the stage represented in Fig. 60 the embryo commences to rotate within the vitelline membrane, each ectodermic cell being now provided with a vibratile cilium.

The embryo next begins to elongate, and the blastopore becomes still narrower (Fig. 61).

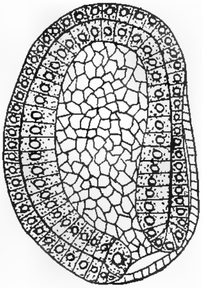

Fig. 61. — Elongated gastrula. Optical longitudinal section. The cilia are omitted from the ectoderm. (After HATSCHEK.)

A comparison of the accompanying figures will show that the narrowing of the blastopore is effected by the downward and backward growth of its dorsal border, while the ventral lip remains stationary. The dorsal ectoderm, which is converted into the *medullary plate,* now shows indications of a shallow longitudinal groove. This is the beginning of the medullary groove which leads on to the formation of the central nervous system.

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* For a discussion of the phylogenetic relation of the blastopore or protostoma (Hatschek) to the mouth and anus, the following works should be consulted: ADAM SEDGWICK, *On the Origin of Metameric Segmentation, etc.,* Quarterly Jour. Micro. Sc., XXIV., 1884, and by the same author, *Notes on Elasmobranch Development, Ib.* Vol. XXXIII., 1891–92.

Finally, BERTHOLD HATSCHEK, *Lehrbuch der Zoologie,* Jena, 1888–91.

Growth of Free-swimming Embryo.

Between 4 and 5 A.M. in the first morning of development, *i.e.* at about the eighth hour, the embryo has reached the stage represented in Fig. 62, and it now bursts through the vitelline membrane and becomes free, swimming by means of its cilia at the surface of the sea, or aquarium.

The fact that Amphioxus has a free-swimming, ciliated embryo is important as providing a general connecting link between the Vertebrates and the Invertebrates, since the possession of a ciliated ectoderm is very common among Invertebrate embryos, but entirely unknown among the craniate Vertebrates.

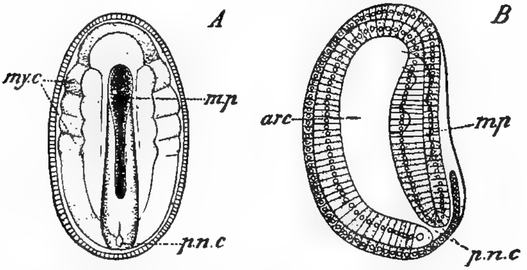

Fig. 62.—Embryo of Amphioxus at the stage at which it ruptures the follicle and becomes free-swimming.

A. Seen from above as a semi-opaque object. (After KOWALEVSKY.)

B. Seen in sagittal (optical) section. (After HATSCHEK.)

arc. Archenteron. *m.p.* Medullary plate. *my.c.* Myocœlomic pouches of archenteron. *p.n.c.* Posterior neurenteric canal.

The medullary plate is now being closed off from the outer surface. This is effected by the co-operation of two factors. The ectoderm which bounds the medullary plate laterally, grows over it, and simultaneously the ectoderm of the posterior or ventral lip of the blastopore grows forward over the medullary plate so as to shut in the blastopore from the exterior (Fig. 62 *A* and *B*). The archenteric cavity therefore no longer opens by the blastopore to the exterior, but it communicates with the medullary tube. The blastopore has, in fact, become converted into the *neurenteric canal*, joining the canal of the central nervous system with the cavity of the alimentary system. This remarkable condition of things was first discovered by KOWALEVSKY, who also found it in the Ascidians and in a number of the higher Vertebrates. It has since been found to occur in all classes of Vertebrates, including man.

Hitherto the body-wall of the embryo has consisted of only two primary germ-layers, *ectoderm* and *endoderm*. At the stage now under consideration, a third intermediate layer, the *mesoderm*, has begun to put in its appearance. The mesoderm arises in the first instance as a series of paired lateral pouches of the archenteron. In Fig. 62 the first two or three archenteric pouches are distinctly visible. Before proceeding, however, to a more detailed account of the origin of the nervous system and of the mesoderm, we will trace briefly the changes in external appearance which the embryos undergo up to the time of the formation of the mouth.

As the embryos are very transparent, the external appearance necessarily involves a good deal of the internal structure.

The period of *embryonic* development may be defined as commencing with the first cleavage of the ovum, and ending with the perforation of the mouth, thus comprising approximately the first thirty-six hours. During this period the embryo does not take up independent nourishment, but lives on the original food-yolk which was contained in the egg.

During the first few hours of its pelagic or free-swimming existence, the embryo keeps rigidly to the surface of the water.

After its escape from the vitelline membrane, it grows rapidly in length. Fresh archenteric pouches are added to those already formed, one after the other, in metameric order. The medullary plate (*i.e.* the fore-cast of the nerve-tube) becomes completely closed in beneath the superficial ectoderm except at its anterior extremity, where it remains open to the exterior in the mid-dorsal line by an aperture known as the *neuropore* (Fig. 63 *A*, *B*, *C*). Finally, the notochord becomes differentiated from the primitive endoderm.

According to Hatschek the number of *mesodermic somites* which arise as diverticula from the archenteron is fourteen pairs. Those which are subsequently added to these arise at the hinder end of the body by proliferation from the cells which lie behind, and at the sides of the neurenteric canal, or in that region, so that they never appear as actual outgrowths from the archenteron.[2]

In Fig. 63 *C* the embryo has undergone some radical changes in form. Its body, previously cylindrical, has become laterally compressed, the ectoderm cells of the hinder end of the body have begun to elongate so as to form the rudiment of a provisional caudal fin, and the front end of the body has grown out into the shape of a snout. In connexion with the latter there are two remarkable structures which arise as a pair of outgrowths from the anterior region of the archenteron, and were first described by Hatschek as a pair of *anterior intestinal diverticula.* These we shall return to later.

Near the front end of the alimentary canal a curious sac-like structure has appeared (Fig. 63 *C*). It arose as a transverse groove in the floor of the gut in the region of the first myotome, extending from the right side underneath to the left side of the body. (Cf. Figs. 63 *A* and 71.) The groove deepened, and its margins coalesced, and so it

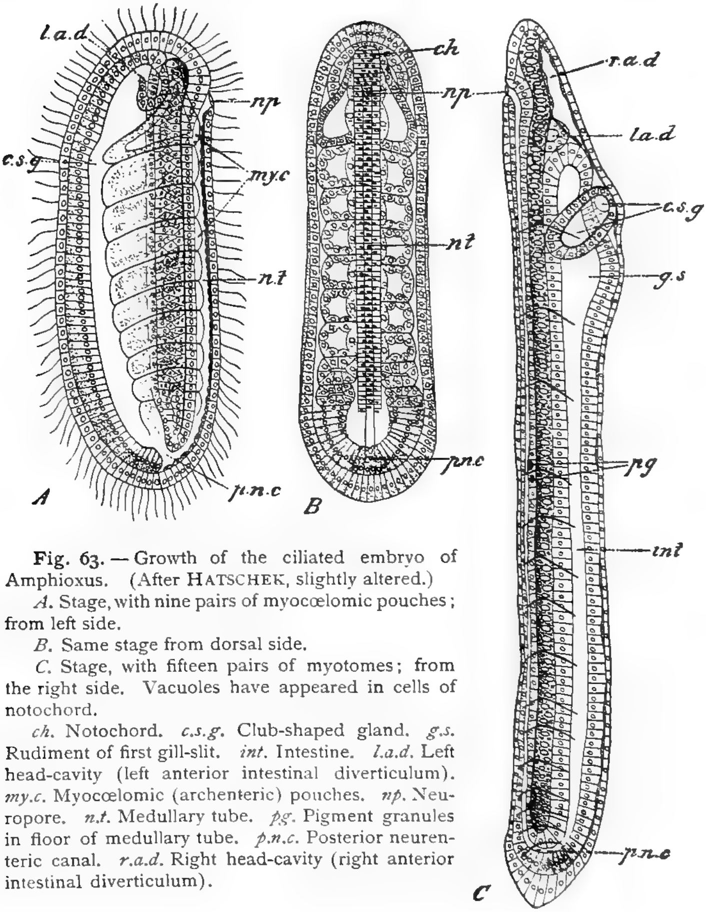

Fig. 63. — Growth of the ciliated embryo of Amphioxus. (After HATSCHEK, slightly altered.)

A. Stage, with nine pairs of myocœlomic pouches; from left side.

B. Same stage from dorsal side.

C. Stage, with fifteen pairs of myotomes; from the right side. Vacuoles have appeared in cells of notochord.

ch. Notochord. *c.s.g*. Club-shaped gland. *g.s*. Rudiment of first gill-slit. *int*. Intestine. *l.a.d*. Left head-cavity (left anterior intestinal diverticulum). *my.c*. Myocœlomic (archenteric) pouches. *np*. Neuropore. *n.t*. Medullary tube. *pg*. Pigment granules in floor of medullary tube. *p.n.c*. Posterior neurenteric canal. *r.a.d*. Right head-cavity (right anterior intestinal diverticulum).

became constricted from the gut, and now forms a hollow sac closed at present at both ends. It is known as the *club-shaped gland*. Immediately behind it, in Fig. 63 *C*, is seen a shallow depression in the floor of the gut. This is the indication of the first gill-slit which becomes perforated at this point later.

From this stage it is an easy transition to the stage which marks the close of the embryonic and the commencement of the *larval* period of development.

In the embryo shown in Fig. 64, the mouth appears as an oval aperture placed asymmetrically on the left side. At its first origin it is relatively much smaller than shown in the figure. A disc-shaped thickening of the ectoderm appears on the left side, in the region of the first myotome. The subjacent endoderm fuses with the thickening, and then the centre of the disc becomes perforated, and so the mouth is formed.

The club-shaped gland has acquired an opening to the exterior immediately below the mouth, on the left side; while the body of the gland lies on the right side.

Behind the club-shaped gland on the

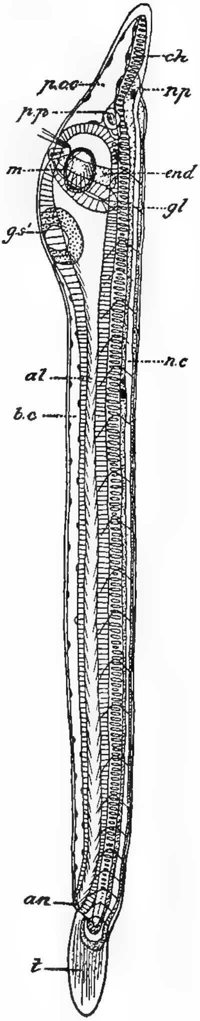

Fig. 64.

Fig. 64.—Stage in which the external apertures of the body, præoral pit, mouth, first gill-slit, and anus have become perforated. Age about 36 hours. From the left side. (After HATSCHEK.)

al. Alimentary canal. *an.* Anus. *b.c.* Body-cavity. *ch.* Notochord. *end.* Endostyle. *gl.* Club-shaped gland, which has acquired an opening to the exterior on the left side below the mouth. *g.s'.* First primary gill-slit. *m.* Mouth. *n.c.* Nerve-tube; the neurenteric canal has closed up, but the nerve-tube still curves round the hinder end of the notochord. *np.* Neuropore. *p.o.c.* Præoral cœlom (right head-cavity). *p.p.* Præoral pit (left head-cavity). *t.* Provisional caudal fin.

right side is the first gill-slit, opening directly to the exterior. At the time of its actual perforation it lies near the mid-ventral line of the body, but as it increases in size it becomes shifted up to the right side.

The neurenteric canal is closed up, and the nerve-tube ends blindly behind, being curved round the hinder end of the notochord. Immediately in front of and below the point where the neurenteric canal formerly existed, the *anus* has now made its appearance, approximately, if not exactly, in the mid-ventral line * (Fig. 64).

We will now return to consider more closely the exact development of the mesodermic somites, the notochord, and the nerve-cord.

Development of Central Nervous System.

As in the craniate Vertebrates, so in Amphioxus the medullary plate arises as a median unpaired longitudinal specialised portion of the dorsal ectoderm. The way in which it becomes separated from the superficial ectoderm has already been indicated above, but it can best be studied in transverse sections.

In the sections shown in Figs. 65 and 66, the separation of the medullary plate from the ectoderm, and its subsequent conversion into a closed tube, is so clearly illustrated, that further description is unnecessary. A unique feature in connexion with the formation of the central nervous system of Amphioxus is, that the medullary plate sinks below and becomes covered over by the superficial ectoderm before it takes on the form of a closed tube, so that for some time it exists as a half-canal open dorsally

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* According to Hatschek, the anus breaks through slightly to the left of the middle line.

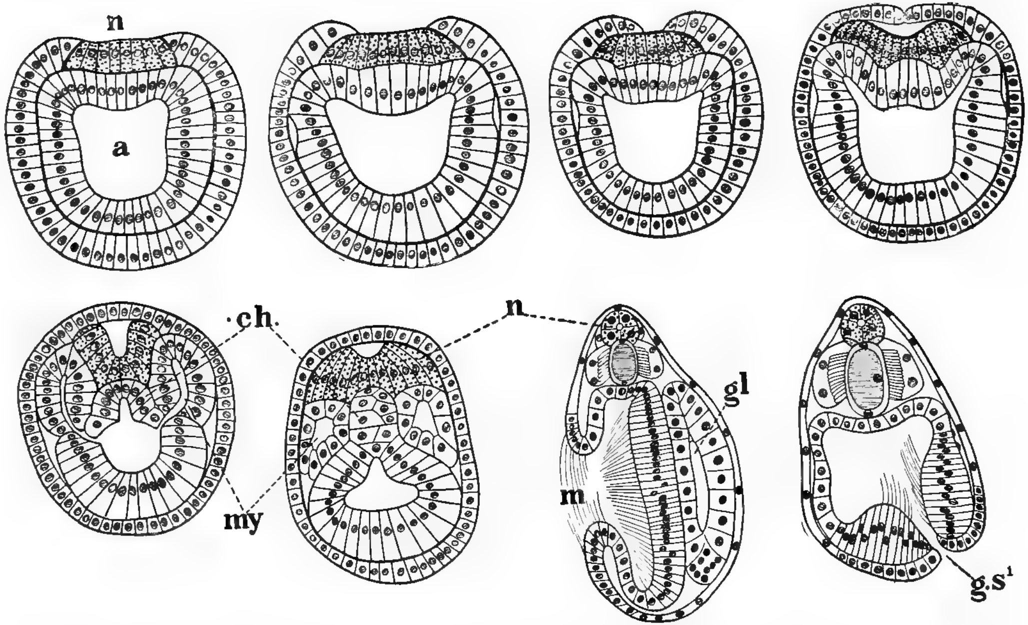

Fig. 65.—Transverse sections through embryos of different ages, illustrating the mode of formation and relations of the medullary tube, notochord, mesodermic somites, etc. (After HATSCHEK.)

The figures should have been lettered consecutively from *A* to *H* (they are thus referred to in the text), but the letters were accidentally omitted. *a*. Archenteron. *ch*. Notochord. *gl*. Club-shaped gland. *g.s*¹. First primary gill-slit. *m*. Mouth. *my*. Myocœlomic pouches (mesodermic somites). *n*. Medullary plate and tube.

N.B.—In the last two figures the nuclei of the cœlomic epithelium, which has become extremely flattened, are not well indicated. The nuclei are scarce enough, but not quite so scarce as would appear from the figures.

against the ectoderm. Later the dorsal margins of this half-canal meet and fuse in the middle line, and so produce the medullary tube * (Fig. 66).

Origin of Mesoderm and Cœlom.

In consequence of the flattening and incurving of the medullary plate, pressure is brought to bear on the dorsal wall of the archenteron, and the dorso-lateral borders of the latter acquire the form of two longitudinal grooves (Figs. 65 *A* and *B*). It is from these grooves that the archenteric pouches are split off. The grooves deepen, and in doing so become divided up into a series of pouches. Eventually the pouches become shut off from the archenteron gradually from before backwards, and then appear as closed cavities on either side of the notochord, which has, in the meantime, been developing (Fig. 65 *F*).

In the higher Vertebrates the mesoderm arises as two solid, lateral, longitudinal bands, which are split off from the primitive endoderm. These mesodermic bands are at first unsegmented, and might be taken to correspond with the longitudinal grooves of the archenteron of Amphioxus, as described above. Later, only the dorsal portion of the mesodermic bands undergoes segmentation, while the ventral portion, which becomes hollowed out to form the general body-cavity, is never segmented in the craniate Vertebrates. (Cf. Fig. 33.) In Amphioxus the whole of the mesoderm is contained in the archenteric pouches, and is, therefore, at first entirely segmented.

As soon as the pouches have lost their primitive con-

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* In the Ascidian embryo the formation of the medullary tube takes place after the manner typical of craniate Vertebrates (see below, IV.).

nexion with the archenteron, they commence to extend dorsally and ventrally between the ectoderm and the internal organs (Fig. 66). Meanwhile the cells forming the inner or visceral wall of the pouch adjacent to the notochord elongate transversely and longitudinally, and begin to form the plate-like muscle-fibres of the myotome. The cells producing these fibres are arranged in such a way that each of them gives rise to a muscle-fibre extending from the anterior to the posterior limit of a myotome.* The muscles are at first closely approximated to the notochord and project freely into the cavity of the pouch. The latter gradually grows downwards, until it meets its fellow of the other side; the two fuse together, and so the cavity is made continuous from side to side, below the intestine.

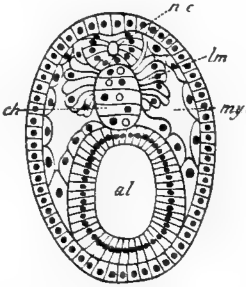

Fig. 66. — Transverse section through the middle of the body of an embryo, with ten pairs of somites, to show the closure of medullary tube and the dorsal and ventral extension of the mesodermic somites. (After HATSCHEK.)

al. Alimentary canal. *ch.* Notochord, in the cells of which vacuoles have commenced to form. *l.m.* Commencing formation of longitudinal muscle-plates from the cells forming the inner wall of the somite. *my.c.* Myocœlomic cavity.

When this occurs, the primarily single cavity of each archenteric pouch becomes divided into two portions; namely, a dorsal portion, the *somite* proper or *myocœl*, and a ventral portion, the *cœlom*, by a transverse partition, which arises through a fusion between the parietal and

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* Already in the embryo shown in Fig. 63 *C*, and even at a somewhat earlier stage, the muscles are so far developed that the body can be bent and jerked. By the time the mouth has broken through, *muscular locomotion* effectually replaces the primitive *ciliary locomotion*, although the cilia persist to a late stage.

visceral walls of the cavity, at about the level of the base of the notochord (Fig. 67).

The dissepiments between the myotomes are formed from the contiguous walls of the successive pouches, but ventrally, in the region of the cœlom, they break down, so that the latter then becomes a continuous unsegmented cavity. On account of the fact that the archenteric pouches give rise both to the cavity of the somites (*myocœl*) and to the general body-cavity (cœlom proper or *splanchnocœl*), they are often spoken of as the *myocœlomic* pouches. The cavity of the original archenteric pouches is known as the *primitive cœlom*, the epithelial walls of which constitute the *mesoderm.*

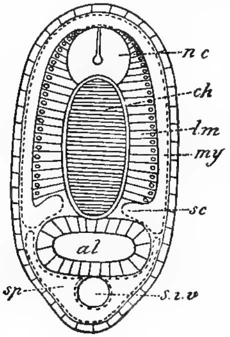

Fig. 67. — Scheme of a transverse section through the body of a larva with five gill-slits, to show the division between myocœl and splanchnocœl. (After Hatschek.)

n.c. Spinal cord (medullary tube). *ch.* Notochord. *l.m.* Muscles. *my.* Myocœl. *sc.* Rudiment of sclerotome. *al.* Alimentary canal. *s.i.v.* Sub-intestinal vein. *sp.* Splanchnocœl.

As differentiation and organogeny proceed, the mesoderm gives rise to (1) the *musculature*, (2) the *connective tissue*, (3) the *blood-vessels*, (4) the *reproductive organs*, (5) the *cœlomic epithelium* or lining of body-cavity, also called the *peritoneum*, and (6) the *excretory tubules.* The development of the last-named structures has, however, not yet been worked out in Amphioxus.

The parietal layer of the mesoderm applies itself closely against the ectoderm, and gives rise to the cutis of the body-wall.

The connective tissue-sheath of the notochord and nerve-cord, together with the internal sheath or *fascia* of the muscles of the myotome, arises from the walls of a pouch-like diverticulum of myocœl which grows up between the muscles and the notochord and nerve-cord. (Cf. Figs. 67 and 68.) The myocœl also grows downwards between the somatic layer of the peritoneum and the ectoderm (Fig. 68). According to Hatschek the dorsal and ventral fin-spaces are also derived from the myocœl.[3]

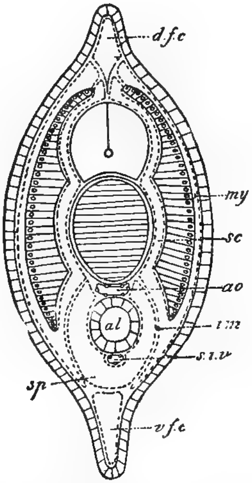

Fig. 68. — Scheme of a transverse section through region between atriopore and anus, of a young Amphioxus shortly after the metamorphosis. (After HATSCHEK.)

d.f.c. Dorsal fin-space. *my.* Myocœl. *sc.* Sclerotome. *ao.* Aorta. *al.* Intestine. *i.m.* Intercœlic membrane. *s.i.v.* Sub-intestinal vein. *sp.* Splanchnocœl. *v.f.c.* Ventral fin-space.

The diverticulum of the myocœl which has just been described is known as the *sclerotome*, since it gives rise to the fibrous sheath of the notochord and nerve-cord, which (*i.e.* the sheath) in most of the higher forms becomes replaced by cartilage, and finally by bone. In the craniate Vertebrates the sclerotome arises as a solid proliferation of cells from the visceral wall at the base of the somite. This solid proliferation is undoubtedly a modification of a hollow diverticulum, involving, as it does, only the visceral wall of the somite, precisely as we find it in Amphioxus.[4] (Cf. Fig. 33.)

On their outer surface the muscles of the myotomes are not provided with a sheath of connective tissue (fascia), standing, in this respect, in contrast to the condition which obtains in the Craniota.

Origin of the Notochord.

The notochord is formed from the endodermic cells which lie between the mesodermic pouches and constitute the dorsal wall of the archenteron. The dorsal wall of the archenteron at an early stage becomes converted into a shallow longitudinal groove whose concavity is turned towards the archenteric cavity (Fig. 65 *D*). This groove gradually deepens (Fig. 65 *E*), and eventually its walls become closely appressed to one another so as to obliterate the lumen (Fig. 65 *F*). Finally the adjoining cells of the archenteric wall grow across the gap occasioned by the formation of the notochord, and joining together, shut off the latter from any participation in the enteric wall (Fig. 66). In this way is the notochord separated from the endoderm gradually from before backwards. Posteriorly it remains for a considerable time fused with the endoderm at the point where the anterior wall of the neurenteric canal becomes continuous with the dorsal wall of the archenteron.

We have indicated above that the differentiation of the notochord takes place from before backwards. At its anterior extremity a very noteworthy exception to this rule is presented. In the region of the first myotome the notochord retains an open communication with the archenteron after its lumen has already been obliterated behind this point. Moreover, in the embryo, with eight pairs of myocœlomic pouches (Fig. 68 *bis*), the front end of the notochord lies some distance behind the front end of the body, while the anterior portion of the archenteron extends beyond the notochord. Eventually the notochord is continued to the front end of the body by becoming constricted off from the dorsal wall of the anterior section of the archenteron in the usual way. This retarded growth of the notochord anteriorly indicates that its extension to the tip of the snout is a secondary phenomenon. Ancestrally we are bound to assume it did not extend so far forwards. The forward extension of the notochord is, as noted above, obviously useful to Amphioxus in rendering its pointed snout sufficiently resistant to enable it to burrow in the sand. When it wants to bury itself in the sand, it has not to take pains to dig a hole, but darts in in the fraction of a second.

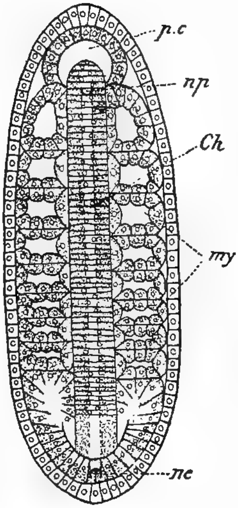

Fig. 68 *bis.*—Embryo of Amphioxus, with eight pairs of somites to show the primary relations of the anterior end of the notochord. From above. (After Hatschek.)

p.c. Præchordal portion of archenteron, which becomes converted into the head-cavities. *n.p.* Neuropore. *ch.* Notochord; over which lies the neural tube. *my.* Myocœlomic pouches. *ne.* Neurenteric canal.

N.B.—In this and other figures of Amphioxus embryos here reproduced after Hatschek, the so-called mesodermic pole cells have been omitted in accordance with the observations of Wilson and Lwoff.

The histological differentiation of the notochord commences soon after the sides of the chordal groove have come together so as to obliterate the lumen. The cells composing the notochord are, at the first approximation of the walls of the groove, placed end to end, but soon begin to interlace with one another across the middle line (Fig. 65 *F*), and finally each cell comes to occupy the whole width of the notochord (Fig. 66). Meanwhile vacuoles begin to appear in the cells (Fig. 66).

The *vacuolisation* of its component cells is an extremely characteristic feature of the notochordal tissue throughout the group of the Vertebrates. It is carried on to such an extent in Amphioxus as to obscure the original cellular structure of the notochord. The cells anastomose with one another in the longitudinal direction, and so produce a reticulum the meshes of which represent the vacuoles whose first origin is shown in Fig. 66. Most of the nuclei become eventually displaced from the centre of the notochord, and are, in the adult, almost exclusively confined to its dorsal and ventral aspects (Fig. 69).

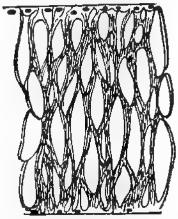

Fig. 69.—Median sagittal section of notochord of a young Amphioxus of 8 mm., to show the vacuolar character of the notochordal tissue and the displacement of the nuclei to the dorsal and ventral borders. (After Lwoff.)

The Præoral "Head-cavities" of Amphioxus.

Before leaving the embryonic period of the development it is necessary to consider the origin and fate of what may be called the *head-cavities* of Amphioxus as made known to us by the work of Hatschek.

They arise symmetrically as a pair of diverticula from the anterior portion of the archenteron, which lies at first partly in front of the notochord (Fig. 68 *bis*) and completely in front of the myocœlomic pouches (Fig. 70).

They begin to appear at the stage in which some eight pairs of pouches are already present. Their origin therefore, in point of time and the subsequent modifications which they undergo, show that they do not belong to the metameric series of the mesodermic pouches, but are structures *sui generis.*

The archenteron extends at first to the front end of the body. Its anterior portion, after the formation of several mesoblastic somites, becomes marked off from the hinder region by a slight constriction, which gradually becomes deeper and deeper (Fig. 70), until finally the whole of this portion of the archenteron is divided into two separate sacs, which eventually lose all connexion with the archenteron (Fig. 71). The alimentary canal now no longer reaches to the anterior extremity of the body. Very soon after their separation from the archenteron these sacs enter upon a series of changes by which their originally symmetrical disposition is entirely destroyed.

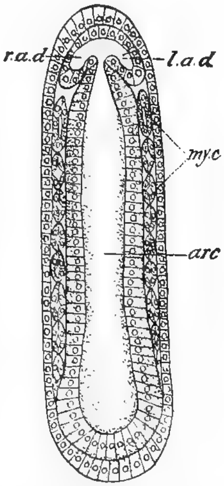

Fig. 70. — Embryo, with nine pairs of primitive somites, seen in optical section from the ventral surface, to show the origin of the head-cavites. (After HATSCHEK.)

r.a.d. Right head-cavity. *l.a.d.* Left head-cavity. *my.c.* Myocœlomic pouches (primtive somites). *arc.* Archenteron.

Already in Fig. 71 it can be noticed that the right sac is becoming larger than the left, and the epithelium lining its walls is losing its original cubical character, the inner ends of the cells are rounding off, and in fact it is being converted from a cubical to a flattened pavement epithelium (Figs. 63 *C* and 64). The left sac, on the contrary, retains its original form and dimensions for a long time. During the asymmetrical changes affecting the two sacs, which take place coincidently with the formation of the snout, the left one comes to lie transversely below the notochord, while the right sac becomes greatly enlarged and constitutes the cavity of the snout lying below the notochord (Fig. 63 *C*).

Shortly after the breaking through of the mouth the left sac acquires an opening to the exterior on the left side of the body (Fig. 64). The right sac becomes the *præoral body-cavity* or cœlom of the "head," while the left sac is known as the *præoral pit.* It is necessary to emphasise the fact that these two structures which are so different in their fully formed condition are at first perfectly similar and symmetrical and form a pair of "head-cavities." Ultimately, as we have seen, only one of them actually persists as a head-cavity; namely, the right one.

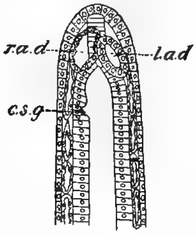

Fig. 71. — Anterior portion of embryo, with thirteen primitive somites, from the ventral side in optical section. (After HATSCHEK.)

r.a.d. and *l.a.d.* Right and left head-cavities. *c.s.g.* Rudiment of club-shaped gland.

The entire conversion of the left sac into the præoral pit is probably to be regarded as a secondary or cenogenetic phenomenon, but the acquirement of an opening to the exterior is probably not secondary, since a similar opening (the *proboscis-pore*) occurs in Balanoglossus.

In addition to the above-described peculiarities which sufficiently distinguish the head-cavities from the myocœlomic pouches, must be mentioned the fact that at no point of their epithelial walls are muscles developed.

It is probable that the præoral head-cavities of Amphioxus are homologous with the *præmandibular cavities* of the higher Vertebrates, from the walls of which the greater number of the eye-muscles are developed.* This view is

* This is also the opinion of Kupffer. Singularly enough van Wijhe has advanced the view that only the right head-cavity of Amphioxus is to be

strongly confirmed by the mode of development of the præmandibular cavities in the Cyclostomes.

In these fishes, von Kupffer has shown that they actually appear in the form of a pair of diverticula from the anterior extremity of the archenteron (Fig. 72). If a comparison be made between Figs. 70 and 72, it will be at once manifest how close the correspondence is between the mode of development of the head-cavities in Amphioxus and in Ammocœtes. In the Selachians the similarity is hardly less striking.[5]

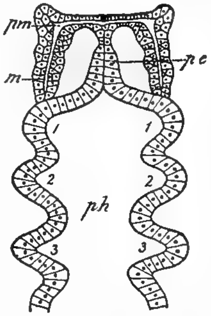

Fig. 72. — Horizontal projection of pharynx and præoral endodermic extension of a young *Ammocœtes planeri* of 3½ mm., reconstructed from a series of transverse sections. (After Kupffer.)

p.e. Præoral endodermic extension (præorale Endodermtasche). *pm.* and *m.* Præmandibular and mandibular portions of head-cavities. *ph.* Cavity of pharynx. *1, 2, 3.* First three pairs of gill-pouches.

N.B.— Kupffer considers it probable that the mandibular as well as the præmandibular cavities arise from the single pair of endodermic diverticula. In the course of the following pages I have referred chiefly to the præmandibular cavities alone so as to avoid complications.

Endostyle and Pigment Granules.

In Fig. 64 there is to be noticed a vertically placed structure lying in front of and contiguous with the club-shaped gland. It is a tract of very high cylindrical cells forming part of the right wall of the alimentary canal in

homologised with the præmandibular cavity (see below, V.). Kupffer regards the præmandibular and mandibular head-cavities as rudimentary or metamorphosed gill-pouches. This deduction is entirely foreign to the standpoint which I have adopted. The conclusion may seem plausible from the conditions observed in Acipenser alone; but when these are regarded from a comparative point of view, the deduction is, to my mind, unjustified. It should be added that Kupffer has shown that the head-cavities (præmandibular and mandibular) of Acipenser also arise as endodermic pouches.

this region. (Cf. Figs. 65 *G* and 75.) I have shown that this epithelial tract is the rudiment of the *endostyle* (*vide infra*).

It is a curious fact that the first trace of pigment to appear in the nerve-tube is not the eye-spot, but that at a constant point in the region of the fifth somite a black pigment-spot is deposited in a cell in the ventral wall of the medullary tube. This is followed by another smaller pigment granule slightly posterior to the first (Fig. 63 *C*). The eye-spot appears at the end of the embryonic period.

LARVAL DEVELOPMENT.

Formation of Primary Gill-slits, etc.

With the establishment of the definite relations of the head-cavities, the mouth, club-shaped gland, first gill-slit, and anus, the embryo enters upon the larval phase of the development.

It is no longer, or only very rarely, to be taken from the surface of the sea, but descends to a depth of several fathoms. When kept in aquaria, the larvæ can often be observed to be suspended vertically, and apparently quite motionless in the water. This suspension is, no doubt, effected by the movement of the long cilia, or flagella, with which the ectoderm is provided, each cell possessing one flagellum.[6]

The principal changes which take place during the early stages of this phase of the development are the addition of new myotomes, the formation of new gill-slits, in metameric order, in an unpaired series on the right side of the larva, to the number of from twelve to fifteen, or even sixteen (the more usual number being fourteen), and the origin of the atrial cavity.

Each gill-slit breaks through in, or slightly to the right of, the mid-ventral line, and then grows well up on the right side of the body. A larva with three gill-slits and the indication of a fourth is represented in Fig. 73. The originally circular mouth has grown to a much larger size, and extends on the left side anterior to the endostylar tract (which is on the right wall of the pharynx) and posterior to the first gill-slit. The oral opening later attains to relatively gigantic dimensions, and forms one of the most striking features of the larva.

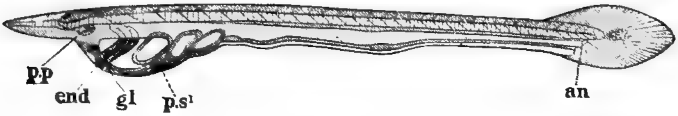

Fig. 73. — Larva of Amphioxus, with three gill-slits and the rudiment of a fourth; from the left side. (After LANKESTER and WILLEY.)

p.p. Præoral pit. *end.* Endostyle lying on right side, seen through the wide lateral mouth. *gl.* Position of external aperture of club-shaped gland. *p.s'.* First primary gill-slit. *an.* Anus.

N.B. — Actual length of larva, nearly 1⅓ mm.

The anus is now displaced from its original ventral position to the left side in consequence of the increased development of the provisional caudal fin. The latter consists of elongated ectodermal cells, in which a certain amount of brown pigment is deposited. Later, when the dermal expansion, which has been described above as the definitive caudal fin, begins to grow out, it pushes the cells composing the provisional fin before it, so that they form a fringe round its border. Eventually the provisional fin disappears entirely.

The gill-slits now go on adding to their number, one after the other, until the larva reaches the stage shown in Fig. 74. In this larva there are fourteen primary unpaired gill-slits, lying, for the most part, on the right side of the pharynx, although the more posterior slits bend under the pharynx, while the most posterior have a median ventral position.

In front the gill-slits still open directly to the exterior, but the right metapleural fold is seen to be hanging over the tops of them; while the hinder slits now open into the partially formed atrium, which has already closed in posteriorly, as described above. The larva is remarkably transparent, so that its internal organisation can be seen as clearly as possible through the outer body-wall.

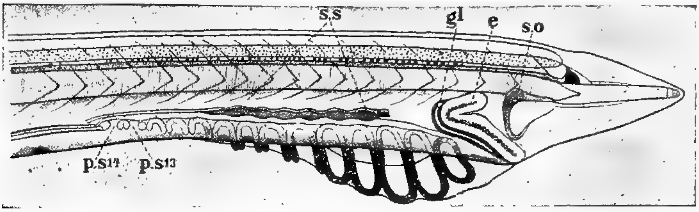

Fig. 74.—Anterior portion of larva, with fourteen primary gill-slits and rudiments of the secondary gill-slits; viewed as a transparent object from the right side. (After WILLEY.)

s.o. Sense-organ of præoral pit (groove of Hatschek). *e.* Endostyle. *gl.* Internal opening of club-shaped gland. *s.s.* Rudiments of secondary gill-slits. $p.s^{13}$, $p.s^{14}$. Thirteenth and fourteenth primary gill-slits. The lower margin of the mouth is seen through the anterior gill-slits.

Total length of larva, nearly 3½ mm.

The long axis of the primary gill-slits is approximately at right angles to the long axis of the body. They are not more numerous than the myotomes in the corresponding region of the body, so that the *branchiomery* at this stage coincides with the muscular *metamery*. In Fig. 73 the first gill-slit was somewhat larger than the second and third. At about that stage, however, its further growth became arrested, and now it is seen to be considerably smaller than those which immediately follow it.

In addition to its external opening on the left side, be-

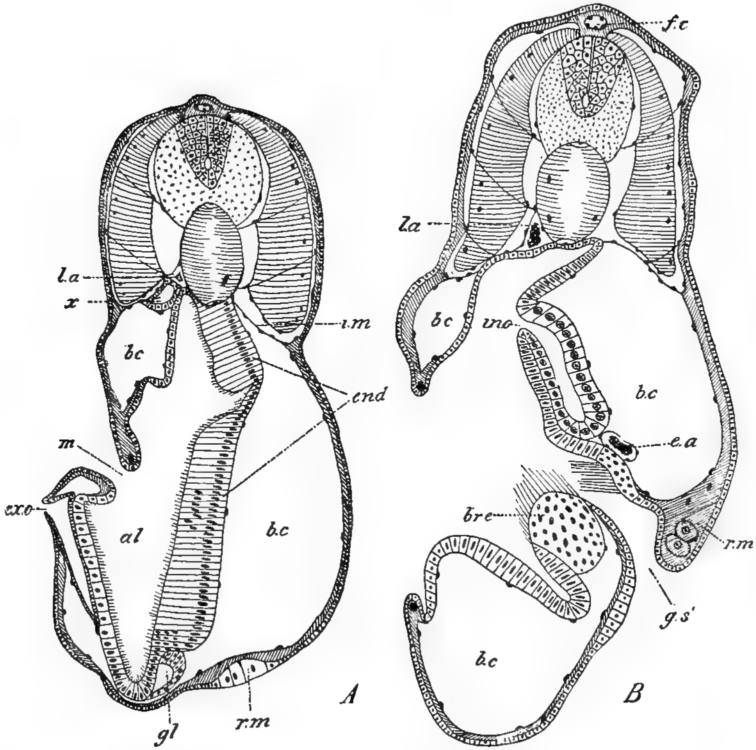

Fig. 75. — Transverse sections through the region of the mouth of larvæ of Amphioxus, to show the endostyle and the external and internal openings of club-shaped gland. (After LANKESTER and WILLEY.)

A. Section passing through the anterior corner of the mouth of a larva, with eleven gill-slits.

B. Section passing through the middle of the mouth of a larva, with twelve gill-slits.

al. Pharyngeal cavity. *b.c.* Cœlom (splanchnocœl). *br.e.* Branchial epithelium. *e.a.* Branchial artery. *end.* Endostyle. *ex.o.* External opening of club-shaped gland. *f.c.* Dorsal fin-space. *gl.* Lower portion of club-shaped gland. *g.s'.* First gill-slit. *i.m.* Intercœlic membrane. *in.o.* Internal opening of club-shaped gland. *l.a.* Left aorta; there is no corresponding right aorta in the larva. *m.* Mouth. *r.m.* Rudiment of right metapleur; a mere ectodermic thickening in *A*; a solid thickening of the cutis in *B*, in which two of the original enlarged ectoderm cells have become imbedded. These curious cells occur over a long stretch of the metapleural folds during this phase of the development, disappearing eventually.

In *B*, the left metapleur is indicated by an ectodermic thickening immediately below the gill-slit. *x.* So-called nephridium of Hatschek.

low the mouth (see Fig. 64), the club-shaped gland has now acquired an opening at its upper extremity, on the right side, into the pharynx.[7] The gland lies, as usual, behind, and closely approximated to, the endostylar tract, which is bent forwards on itself at its upper end (Figs. 75 *A* and *B*).

Pigment-spots are present in great numbers at the base of the neural canal. The pigment is deposited in special

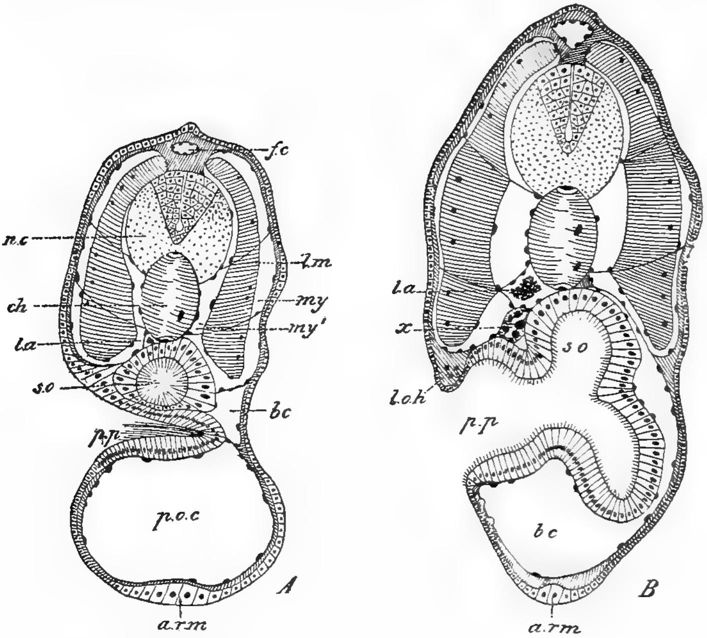

Fig. 76.—Transverse sections through the region of the præoral pit. (After LANKESTER and WILLEY.)

A. Through a larva, with twelve gill-slits and no atrium.

B. Through a larva, in which the atrium was closed in over all the gill-slits except the first two. (Cf. Fig. 38 *C.*)

a.r.m. Anterior median portion of right metapleur. *p.o.c.* Præoral body-cavity (right head-cavity); this cavity becomes much reduced after the metamorphosis, and is largely filled up by gelatinous tissue. *p.p.* Præoral pit. *s.o.* Sense-organ of præoral pit (groove of Hatschek). *l.o.h.* Rudiment of left half of oral hood. *my'.* Sclerotome (diverticulum of myocœl *my*). Other letters as above.

Section *B* is taken through a plane slightly posterior to section *A*.

cells, the *pigment-cells*, which arise as modified epithelial cells of the central canal. These cells send out several branching processes, which lose themselves in the fibrous tract of the spinal cord.

Already in the youngest larva — namely, that shown in Fig. 64 — the præoral pit had become subdivided into two portions, which, however, retained a free communication with one another.

In the course of the changes which the left head-cavity had to undergo in its conversion into the præoral pit it had come to lie transversely below the notochord. Subsequently it extended itself, in the form of an offshoot, dorsally to the right of the base of the notochord.

This offshoot from the præoral pit appears to serve as a special sense-organ lying ultimately, as mentioned above, in the roof of the oral hood, whose function is possibly to test the water as it enters the mouth (Figs. 76 *A* and *B*, and Fig. 74, etc.).

Formation of Secondary Gill-slits.

Above the primary gill-slits in Fig. 74, and like them, on the right side of the body, is to be observed a longitudinal ridge provided with a series of nodal enlargements which alternate with the primary gill-openings, the first of them lying above and between the third and fourth primary slits. Each of these enlargements represents a thickening in the wall of the pharynx, which has undergone fusion with the body-wall beneath the right metapleural fold, in the angle formed by the latter with the body-wall.

These metameric fusions of the pharyngeal wall with the body-wall are the forecast of a second row of gill-slits, whose relation to the primary row will become clear as we proceed. With their appearance, the larva enters upon that phase of its development which has been called the later larval period. It is the period of the metamorphosis of the larva, during which the pronounced asymmetrical arrangement of the parts is exchanged for the partial, but not absolute, symmetry which we have noted in the adult. The metamorphosis, therefore, consists largely in the symmetrisation of the larva.

The simultaneous appearance of the six nodal thickenings in the exact position, shown in Fig. 74, is very constant. Shortly afterwards a minute perforation appears in the centre of each thickening almost simultaneously, except in the case of the first, which usually becomes perforated rather later than the others. The originally small circular openings of the secondary gill-clefts gradually increase in size and become oval in shape, their long axes being parallel to the long axis of the body, instead of at right angles to it as in the case of the primary slits.

Next, the upper borders of the secondary slits begin to flatten, and later to show signs of curving downwards. The changes in shape, which affect the secondary slits at the stages now under consideration, may be expressed by saying that they are at first shaped like a biconvex lens, then like a plano-convex lens with the flat surface directed upwards and the convex surface downwards, and finally like a concavo-convex lens with the concavity directed upwards (Fig. 77).

During these changes, which do not take place in all the secondary slits at the same time, the last one especially retaining for a long time its primitive shape, the walls of the successive slits become sharply rounded off and distinct from one another, and a new perforation makes its appearance in front, above, and between the second and third primary slits. This new slit constitutes the definitive first slit of the secondary series (Fig. 77).

The larva shown in Fig. 77 presents a very different aspect from that shown in Fig. 74: the transition from one stage to the other is, of course, gradual, and all intermediate steps can be observed. In the stage which we are now considering (Fig. 77), the atrial cavity has become completely closed up in front, so that now none of the gill-slits open directly to the exterior.

None of the primary slits now lie entirely on the right side, but they have become bent under the pharynx, and thus extend round to the left side. This bodily migration of the primary slits from one side to the other occurs in correlation with the increase in size of the secondary slits, which, as they continue to grow, push, as it were, the primary slits before them, and so cause the latter to bend under the pharynx in the way described. The peculiar growth by which the primary gill-slits are gradually carried from the right to the left side, may be described as a transverse or rotatory growth affecting the pharynx *in toto* in

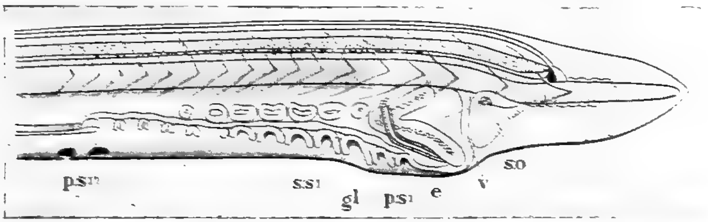

Fig. 77.—Anterior portion of larva, in which the secondary slits have become perforated, and the primary slits are passing round to the left side. From the right side. (After WILLEY.)

so. Sense-organ of præoral pit. *v*. Right half of velum. *e*. Endostyle, growing beyond the club-shaped gland *gl*. *ps*¹. First primary slit much reduced in size. *ss*¹. First secondary slit. *ps*¹². Twelfth primary slit, behind which is to be seen a vestige of the thirteenth slit.

the region of the secondary slits. Such of the primary slits as occur behind this region are not affected by the rotatory method of growth, and retain their original position in the mid-ventral line of the pharynx.

It is to be noted also that there are only twelve primary gill-slits at this stage. Assuming that in the particular larva here figured there were originally fourteen primary slits, the fourteenth has closed up and vanished without leaving a trace, while a vestige of the thirteenth can still be recognised. The actual process involved in the closure and disappearance of a certain number of the primary slits can, as we shall see, be readily observed in the living larva.

Club-shaped Gland and Endostyle.

The internal aperture of the club-shaped gland into the pharynx is exceptionally plain at this stage, and its refringent walls and relatively large size give it a curiously slit-like appearance. We shall find that the gland subsequently atrophies, but the most persistent part of it — that is to say, the last part of it to disappear — is precisely the internal opening with its refringent border.

The endostyle, whose primary position, as we have seen, was immediately in front of the club-shaped gland, now presents a remarkable condition. It has begun to grow backwards and downwards, being probably pulled down, so to speak, by the general rotatory growth of which we have spoken above; and so the club-shaped gland no longer lies behind it, but upon it. The gland itself being disconnected with the wall of the pharynx, except at its upper end where it opens into the latter, is not affected by the complicated changes to which the pharyngeal wall, including gill-slits, mouth, and endostyle, is subjected, so that it forms a convenient *punctum fixum* with relation to which the growth of neighbouring structures, particularly that of the endostyle, can be determined.

The upper and lower limbs of the endostyle are inclined to one another at an acute angle, and may be said to form two unequal sides of a triangle, the apex of which is directed backwards between the rows of secondary and the primary gill-clefts (Fig. 77).

Between the two rows of slits on the right side of the body there is a blood-vessel, representing the anterior continuation of the sub-intestinal vessel, which ends blindly in front above the first primary slit. This is the future ventral branchial artery, with which we are already acquainted. When its final situation in the mid-ventral line below the endostyle is remembered, its position in the larva high up on the right side, as in Fig. 74, will appear very striking.

Continued Migration of Primary Gill-slits.

The secondary slits now go on growing in size, and the primary slits gradually tend to disappear entirely from the right side until, as in Fig. 78, only the original upper por-

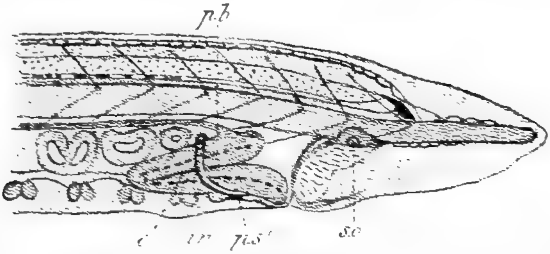

Fig. 78. — Anterior portion of larva from right side to show the backward growth of the endostyle between the primary and secondary gill-slits. (After WILLEY.)

s.o. Sense-organ of præoral pit. *p.s¹.* First primary slit. *io.* Internal opening of club-shaped gland. *e.* Endostyle. *p.b.* Peripharyngeal ciliated band.

tions of them are visible from this side. In some of the secondary slits the dorsal margin, which had previously begun to curve downwards, has now reached the ventral margin and fused with it (Fig. 78, third secondary slit). In this way is the tongue-bar formed, and the primitively simple gill-opening is divided into two distinct halves. The formation of the tongue-bars occurs in the secondary slits considerably in advance of the primary, both actually and relatively, since the latter have existed all through the earlier period of the larval development without a trace of tongue-bars.

Peripharyngeal Bands.

The endostyle has now grown a long distance behind the club-shaped gland, and extends backwards between the two rows of slits as far as the middle of the second secondary slit. From the anterior part of the upper half of the endostyle, which is now nearly equal in length to the lower half, arises an epithelial tract in the wall of the pharynx, which appears in the form of a band of ciliated cells, and proceeds backwards below the notochord to the end of the pharynx. A corresponding ciliated band occurs in the left wall of the pharynx, proceeding from a similar point in the lower limb of the endostyle. In their course below the notochord the two bands take part in forming the hyperpharyngeal (dorsal) groove of the pharynx.

Atrophy of First Primary Gill-slit and Club-shaped Gland, etc.

We have already seen indications of a reduction in the size of the first primary slit. This reduction has advanced considerably in the stage we are now describing (Fig. 78), where the slit in question is only recognisable in side view as a small groove.

The next stage to be considered is characterised above all by the simultaneous atrophy, closure, and disappearance of the club-shaped gland, and the first primary gill-slit (Fig. 79). At this stage the increase in size of the secondary slits has progressed to such an extent that the primary slits have been displaced entirely from their original position, and are no longer to be seen from the right side, except in the case of the hindermost slits of the series, which remain, as mentioned above, in a median ventral position until their disappearance.

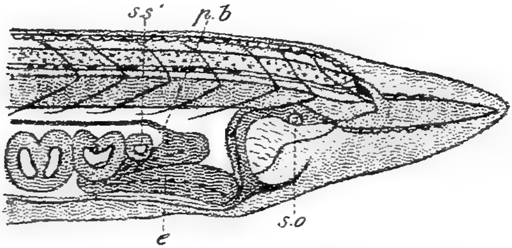

Fig. 79.—Anterior portion of larva from right side after the disappearance of the club-shaped gland. (After WILLEY.)

s.o. Sense-organ. *e.* Endostyle. *p.b.* Peripharyngeal band. *s.s'.* First secondary slit.

A larva seen from below, so as to show the relative positions of the gill-slits and endostyle, etc., at this stage, is represented in Fig. 80.

It is obvious, from what has been said above, that in the passage of the primary slits from their original position on the right side of the body to their final position on the left side, their dorsal and ventral margins are reversed. What was at first the dorsal edge of a primary slit becomes its ventral edge, and *vice versa.* In other words, what is *actually* the dorsal border of the primary slits in Fig. 74 is *morphologically* the ventral border; and conversely, what is *actually* the latter is *morphologically* the former; and it is from the latter, towards the completion of the rotatory growth, which carries the slits from one side to the other, that the tongue-bars arise (Fig. 80).

The vertical and longitudinal axes of most of the slits, both primary and secondary, are now almost equal, but the original difference in this respect, which we noted above, is still to be observed in the case of the foremost and hindmost slits of the two series. (Cf. Fig. 80, $s.s^1$ and $p.s^2$, and $s.s^8$ and $p.s^{10}$.) The first primary slit has now completely closed up, and its former existence is barely indicated by a loose granular appearance at the place it formerly occupied.

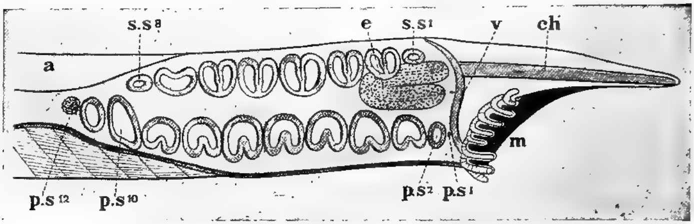

Fig. 80.—Anterior portion of larva of same age as in Fig. 79, seen from the ventral surface. The pharynx is flattened out. (After WILLEY.)

ch. Notochord. *m.* Entrance to mouth. *v.* Velum. $p.s^1$. Vestige of first primary slit. $p.s^2$. Secondary primary slit. $p.s^{10}$. Tenth primary slit. $p.s^{12}$. Vestige of twelfth primary slit. $s.s^1$. First secondary slit. *e.* Endostyle. *s.s.* Eighth secondary slit. *a.* Atrium, pressed aside.

The alternation of the gill-slits of the two series comes out very clearly in Fig. 80. In most of the secondary slits the formation of the tongue-bars is completed; but not so in any of the primary slits, where it is only beginning.

There are now eight secondary slits, an additional one having been added behind, alternating with the ninth and tenth primary slits. Usually the formation of secondary slits stops at this point, no more being formed until the number of primary slits is reduced to the same number; namely, eight.

Since it is usual for the primary slits to break through in the first instance to the number of fourteen, no less than six of them must close up and disappear before the stage with only eight gill-slits on each side of the body is arrived at. The six slits which are to close include the first and the five posterior primary slits. In the larva shown in Fig. 80, the tenth and eleventh primary slits would have to close at a later stage; the twelfth is on the point of closure, and its walls present the characteristic coarsely granular appearance spoken of above, while the thirteenth and fourteenth slits have entirely vanished.

In addition to the fact of the closure of these primary slits, it is important also to emphasise the fact that they disappear without leaving a trace behind. In the higher Vertebrates there are a number of structures not only directly connected at some stage of development with the pharyngeal wall, but also at some distance removed from it, which various morphologists have interpreted as the remnants of ancestral gill-clefts, without sufficiently considering the question whether gill-clefts were in the habit of leaving their mark behind them.[8] In Amphioxus, at all events, they do not.

The Adjustment of the Mouth, etc.

While the gill-slits have been adjusting themselves to their definitive positions, the mouth has also been subjected to a peculiar kind of growth, which results in its bending round the front end of the pharyngeal wall, and ultimately assuming an anterior and median position, as we find it in the adult.

In Fig. 81, a larva corresponding in age approximately to that of Fig. 74 is represented as seen from the left side.

As noted above, the posterior primary slits bend normally under the pharynx at this stage, and some of them extend as much on one side of the body as on the other, being continued across the ventral side of the pharynx. The great feature of this larva is the relatively prodigious mouth, through which the upper portions of the first four primary slits can be seen.

From this side we look into the depths of the præoral pit, having only seen it by transparency in the preceding figures. It is continued backwards into a ciliated groove, which abuts on the dorsal margin of the mouth. Probably most of the food which enters the mouth passes along this groove.

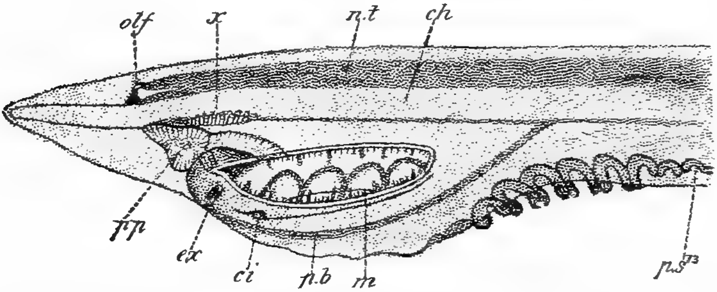

Fig. 81.—Anterior portion of larva, with thirteen gill-slits, from the left side. (After WILLEY.)

olf. Olfactory pit, communicating with neuropore. *x.* "Nephridium" of Hatschek. *n.t.* Spinal cord. *ch.* Notochord. *p.p.* Præoral pit. *ex.* External opening of club-shaped gland. *ci.* Rudiment of buccal cirri. *p.b.* Peripharyngeal band. *m.* Mouth. $p.s^{13}$. Thirteenth primary slit.

Below the pointed anterior extremity of the mouth is to be seen the external aperture of the club-shaped gland, and a short distance behind this is a round, refringent body, which has become differentiated from the gelatinous connective tissue lying below the epidermis, and represents the rudiment of the first element of the cartilaginous skeleton of the buccal cirri.

Running parallel with the lower margin of the mouth, and curving gently upwards to the dorsal wall of the pharynx, is a ciliated band proceeding from the lower limb of the endostyle, and corresponding to the one on the other side, which we found in connexion with the upper portion of the endostyle. Its course on the left side is somewhat different anteriorly from that of the right side, owing to the position and size of the mouth. (Cf. Figs. 78 and 81.)

The so-called olfactory pit, which arose at a much earlier stage as an ectodermic depression above and in connexion with the neuropore, no longer lies in the mid-dorsal line as in Fig. 64, but it has been displaced to the left side by the upgrowth of the dorsal fin (Fig. 81). Here, as in the case of the anus, the development of a median fin has no other effect on the aperture in question than to cause it to forsake its primitively median and symmetrical position and to assume an asymmetrical position on the left side of the body. This is important to bear in mind, as the asymmetrical position of the mouth will be explained below on an analogous basis.

For the present it is sufficient to call attention to the fact that, with the exception of the gill-slits, whose primary unpaired character is due to the retarded or *latent* development of their antimeres, the unpaired openings in the body-wall — namely, neuropore, præoral pit, external aperture of club-shaped gland, mouth, and anus — all lie on the *left* side of the body.

At a slightly later stage than the preceding, the front end of the mouth is found to be no longer pointed, but to have become rounded off, and, moreover, to lie at a deeper level than previously (Fig. 82). The posterior groove of the præoral pit which we described in the last stage, seems to be preparing the way for the mouth to dip inwards towards the right wall of the pharynx, which, in fact, it has actually begun to do.

At a still later stage, corresponding to that shown in Fig. 77, the shape of the mouth has become entirely altered (Fig. 83).

It has now the form of a triangle with the apex directed backwards and the base standing vertically in front. But the apex and the base are not in the same tangential plane, the former being on the left side of the body, and the latter much deeper inwards; in fact, just below the skin on the right side of the body. (Cf. Fig. 77.)

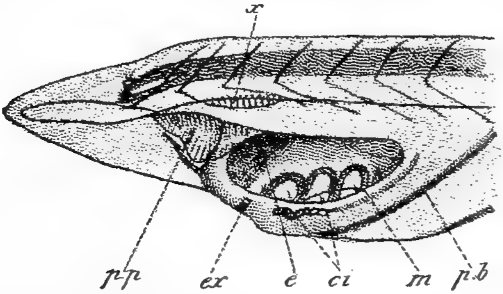

Fig. 82.—Anterior portion of larva somewhat older than preceding, to show commencing adjustment of the mouth. (After Willey.)

e. Endostyle seen through the mouth. Other letters as above.

We see, therefore, that the longitudinal diameter of the larval mouth is gradually shortening. It is eventually reduced to zero when the right and left sides of the mouth or velum come to lie opposite to one another, the velum ultimately attaining a circular form and a median subvertical position underneath the oral hood. When the larva has reached the age to which Fig. 11 refers, the right half of the velum is nearly but not even yet quite opposite to the left half (Fig. 93).

In the preceding stage (Fig. 82) there were several additional buccal cartilages added to the first one which we described. In the present stage these have begun to grow outwards so as to produce small notches in the integument, which is now commencing at this point to form the right half of the oral hood. The left half of the latter arises as a downgrowth of the integument from the upper margin of the præoral pit and its posterior continuation, the above-mentioned ciliated groove. (Cf. Figs. 81, 82, and 83.) The hinder portion of this fold is at first on a level with the dorsal margin of the mouth, and in fact merges into the latter, but subsequently grows over it, extending to its posterior extremity, where it meets the right half of the oral hood.

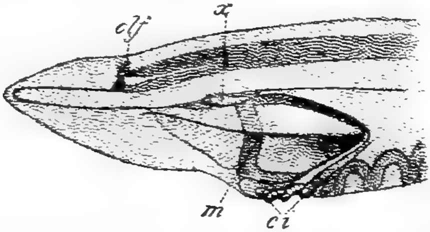

Fig. 83. — Anterior portion of still older larva, from the left side, to show change in shape and position of the mouth. (After WILLEY.)

Letters as above. The left half of the oral hood is now growing down over the mouth and præoral pit.

It is obvious from the above description and figures that a large part of the right wall of the oral hood is derived from the original wall of the snout below the præoral pit, and so an explanation is afforded of the fact noted in the first chapter that the right half of the oral hood is continuous round the anterior extremity of the notochord with the cephalic expansion of the dorsal fin.[9]

The præoral pit itself is absorbed, as it were, into the oral hood, so that it eventually loses its independent existence as a pit, although the sense-organ of the præoral pit persists in the adult as a deep groove in the dorsal wall of the oral hood to the right of the base of the notochord. The remaining ciliated epithelium of the original præoral pit increases in extent, and grows out into the finger-shaped tracts which we have already described as being characteristic of the inner surface of the oral hood, constituting the so-called "Räderogan." (Cf. Fig. 3.)

Equalisation of the Gill-slits.

In the stage next succeeding that of which a ventral view is given in Fig. 80, the first eight primary slits — that is to say, from the original second to the ninth inclusive — have become definitely established on the *left* side, their longitudinal and vertical axes are equalised, and in most of them the tongue-bars are completely formed (Fig. 84). No tongue-bar is formed in the first slit on either side, and this slit apparently remains as a rule simple throughout life.

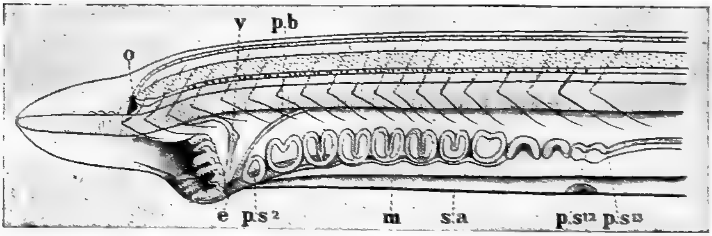

Fig. 84. — Larva toward the close of the metamorphosis, from the left side. (After WILLEY.)

o. Olfactory pit. *v.* Velum. *p.b.* Peripharyngeal band. *e.* Endostyle. $p.s^{2}$. Second primary slit, the first having closed up. *m.* Left metapleur. *s.a.* Floor of atrium. $p.s^{12}$. $p.s^{13}$. Vestiges of the twelfth and thirteenth primary slits.

In Fig. 84 the last indications of the twelfth and thirteenth primary slits are to be observed as slight depressions in the floor of the pharynx in the mid-ventral line. The tenth and eleventh slits would close up later.

It should be pointed out that the closure of the posterior primary slits does not proceed in perfect correspondence with the age of the larva, but takes place sometimes at an earlier and sometimes at a later stage than here depicted.

The gill-slits of both sides now begin to elongate in the vertical direction (Fig. 93), and eventually a very well-marked stage is reached, which is characterised by the presence of eight pairs of gill-clefts. This latter stage would appear to have a considerable duration, and, as it stands on the borderland between the larva and the adult, and forms the commencement of what may be called the *adolescent period* of the development, it may well be regarded as a *critical stage.* By this time the young Amphioxus has given up its free pelagic life in the open sea, and has commenced to burrow in the sand, which it continues to do for the rest of its life.*

Further Growth of Endostyle, etc.

At the point at which we left the endostyle, its two halves were in the relation to one another of upper and lower. During the steps in the metamorphosis which we have recorded above, the upper half of the endostyle is brought down to the same level as the lower half on the right side of it, and so the definite form of the endostyle is established by the conjunction of its right and left halves. It then proceeds to grow backwards along the

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* The duration of the larval development of Amphioxus may be estimated at about three months.

base of the pharynx between the two rows of gilt-slits, but does not reach the posterior end of the pharynx until a much later period.[10]

The features in the development of the endostyle which ought to be especially emphasised are, firstly, its direction of growth from before backwards, and secondly, its primary anterior position in the wall of the pharynx in front of all the gill-slits.

In connexion with the modification in the shape and position of the mouth, as described above, it is important to insist on the fact that the mouth of the larva is directly converted into the velum of the adult, while the oral hood which grows over the mouth is a new formation.

During the period of the metamorphosis the larva does not increase in length. It is rather a readjustment of parts which is then taking place than an increase in bulk which is the symbol of active growth. From the time of the first indication of the secondary slits (Fig. 74) till after the completion of the passage of the primary slits from the right to the left side of the body, the average length of the larva may be taken as approximately 3.5 mm.

The *adolescent period* is essentially the period of active growth in bulk and maturity. The increase in length during this period does not, however, depend on the addition of new myotomes to those already formed, but merely on the progressive growth in size of the latter. The full complement of myotomes was developed during the early larval period, and is present in the larva represented in Fig. 74.

Development of Reproductive Organs.

One of the most interesting events which we have now to chronicle is the development of the reproductive organs. This commences when the young Amphioxus has reached the length of about 5 mm.

Our knowledge of the details of the processes involved in the formation of the genital organs is again due to the work of Boveri, who has made the discovery that the primitive sexual cells arise in the cavity of the myotome by differentiation of certain of the epithelial cells lining the myocœl.

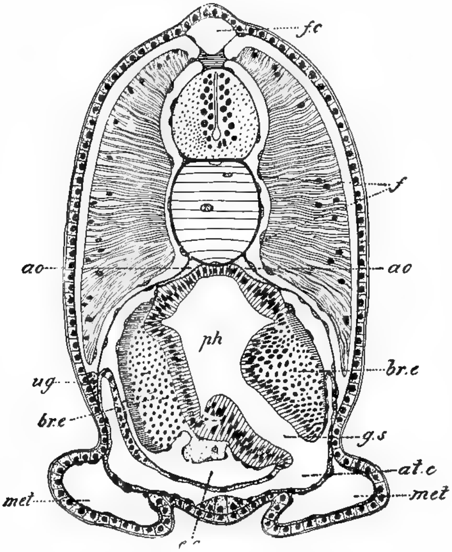

Fig. 85. — Transverse section through the pharyngeal region of a young individual of 5 mm., to show place of origin of sexual elements. (After Boveri.) *f.* Fascia. *e.c.* Portion of cœlom, which will form the endostylar cœlom. *ug.* Primitive sexual cells in the lower angle of the myocœl. Other letters as above.

It had previously been assumed that they were derivatives of the peritoneal epithelium lining the general body-cavity. The fact that they arise in the way shown by Boveri is one of great morphological importance.

In a transverse section of a young individual 5 mm. in length, the primitive sexual cells are to be recognised as a closely packed group of cells, with large nuclei in the lower angle of the myotome; that is, in the angle formed by the membrane which divides the myocœl from the splanchnocœl, which we may call the *intercœlic membrane,* with the cutis (Fig. 85). Since the myotomes of one side alternate with those of the other, so do the centres of formation of the primitive sexual cells, and in a given section, as in Fig. 85, only one such centre is to be observed on the right or left side of the section, as the case may be. Its actual position in the longitudinal aspect of the myotome is shown in Fig. 86 *A*, *B*, and *C*. The formative centres of the primitive sexual cells lie at first in the angle mentioned above, but applied to the posterior faces of the dissepiments between the myotomes (Fig. 86 *A*).

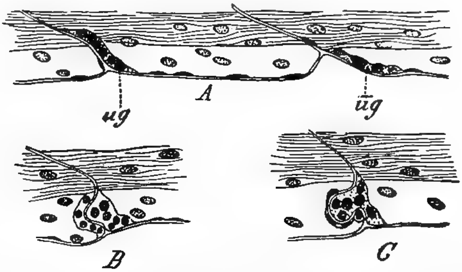

Fig. 86.—Longitudinal views of the developing gonads, obtained by dissecting out the ventral borders of the myotomes. (After BOVERI.)

u.g. Primitive sexual cells arising from the myocœlic epithelium; the nuclei scattered about the surface of the preparations also belong to the myocœlic epithelium.

At a somewhat later stage, having slightly increased in bulk, they begin to push the dissepiments before them so as to make a projection into the myocœl in front (Fig. 86 *B*, *C*). This projection of the primitive gonad into the myocœl next in front of that to which it originally belonged, is gradually carried to such an extent that the gonad becomes entirely shut off from its original myocœl and hangs freely into the next one, being connected by a short stalk with the *anterior face* of the dissepiment and surrounded by a membrane which is obviously derived from, and for some time continuous with, the original dissepiment (Fig. 87). In correlation with the increase in size of the primitive gonad, an evagination of the basal wall of the myocœl in which it now lies, takes place, and by the time the young Amphioxus has attained a length of 13 or 14 mm. there is, in connexion with each primitive gonad, a wide rhomboidal expansion of the lower portion of each corresponding myocœl projecting into the atrial cavity (Fig. 88).

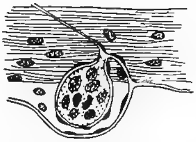

Fig. 87. — Similar preparation as the preceding, showing a later stage in the development of the primitive gonad. (After BOVERI.)

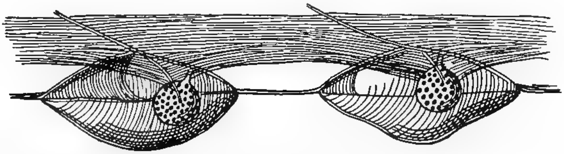

Fig. 88. — Preparation showing the rhomboidal pouches of the myocœl which project into the atrial cavity. (After BOVERI.)
This condition is found in individuals of 13–14 mm.

The cavity of these sacs, to the wall of which the gonads are at this stage still united by a stalk, constitutes the so-called *perigonadial cœlom*,[11] or cavity of the gonadic pouches, which, at the time of sexual maturity, is entirely filled up by the sexual elements.

The gonadic pouches next become gradually constricted off from the myocœlic spaces, and eventually lose all communication with them. In the midst of the at first solid mass of primitive sexual cells a cavity subsequently appears, and the gonad becomes a hollow sac (Fig. 89).

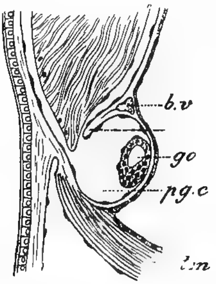

Fig. 89. — Portion of transverse section through an individual of 13 mm., to explain the conditions observed in preceding preparation. (After Boveri.)

b.v. Blood-vessel. *go.* Gonadic sac. *p.g.c.* Perigonadial cœlom (gonadic pouch). *t.m.* Transverse muscles. The index line to which there is no letter indicates the fold by which the gonadic pouch becomes constricted off from the myocœl.

In the course of its further growth the gonadic sac (not to be confused with the gonadic pouch in which it lies) grows out into a number of lappets, and so becomes a racemose reproductive gland (Langerhans).

The primitive sexual cells remain for a considerable length of time in an absolutely indifferent condition, and it is impossible to distinguish the male from the female.

According to Langerhans, sexual differentiation does not begin to take place until the individuals have reached a length of 17 mm., and sometimes it does not occur until a much later period. It is inaugurated by the commencement of the processes of spermatogenesis and ovogenesis. There are no accessory sexual characters in Amphioxus, and the sex can only be determined by an examination of the reproductive glands.

The segmental arrangement of the formative centres of the reproductive organs at the base of the myotomes is again met with in the embryonic development of the Selachians, as shown by Rückert (Fig. 90). Here, also, the primitive sexual cells make their first appearance in the segmented area of the trunk at the base of the somites. Later on, by differential growth, they come to lie on the dorsal wall of the unsegmented peritoneal cavity, and their primitive segmental origin is entirely obscured; while in Amphioxus the primitive segmentation of the gonads is maintained throughout life.

This forms another most interesting example of the way in which the adult Amphioxus, in the details of its organisation, essentially resembles the embryos of the higher types.

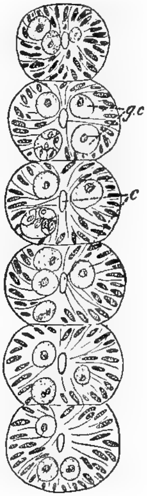

Fig. 90. — Horizontal section through the ventral portion of six consecutive mesodermic somites of an embryo of Pristiurus, to show the segmental origin of the sexual elements. (After RÜCKERT). *c.* Cavities of somites. *g.c.* Sexual cells.

This observation of Rückert's has recently been doubted, with how much justice it is difficult to say, by MINOT (*Gegen das Gonotom.* Anat. Anz. IX. 1894. pp. 210–213).

GENERAL CONSIDERATIONS.

We will now pass on to give a general interpretation of some of the principal phenomena which are presented to us in the development of Amphioxus.

Larval Asymmetry.

By far the most prominent feature of the fully formed larva is its astounding asymmetry, and it is extremely important, from a morphological point of view, to form a just conception of it.

The phenomenon of asymmetry manifests itself in the larva of Amphioxus under several very different aspects, and is occasioned by various causes. For convenience we may classify the forms of asymmetry which we have to consider under three main divisions, according to the type of organs involved.

1. *Median Asymmetry.*—This relates to such structures as lie normally in the middle line, whether dorsal or ventral, but which have been mechanically or correlatively displaced from their primitive position by the differential growth of neighbouring parts. Such are the olfactory pit and neuropore, the anus, the mouth, and the endostyle. All these are essentially and primordially median and unpaired structures. We have already dealt with the neuropore and anus, while the mouth and endostyle will be considered below.

2. *Bilateral Asymmetry.*—This refers to the alternation of paired structures, such as myotomes, spinal nerves, gill-slits, and gonads, which we have already noted in the adult organisation. Primarily the organ of one side lies opposite to its antimere of the other side. By a secondary displacement it comes to alternate with it.*

3. *Unilateral Asymmetry.*—Next to the asymmetrical mouth, this is perhaps the most striking form of asymmetry which the larva of Amphioxus exhibits. It relates to those structures which belong to the category of paired organs, but which, in the course of the larval development, appear unpaired on one side of the body. Such are the

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* When the myocœlomic pouches first appear in the embryo they are placed symmetrically. At an early stage, however (see Fig. 63 *B*), the alternation sets in. This involves such later-appearing structures as the spinal nerves and gonads, so that they alternate from the time of their first origin. The alternation of the gill-slits would seem to be independent of that of the myotomes.

gill-slits and the præoral pit. As described in the foregoing pages the asymmetry of the præoral pit is a secondary occurrence, since it arises at first as one of a pair of symmetrically disposed head-cavities, or anterior intestinal diverticula, while the unilateral asymmetry of the gill-slits is ontogenetically primary. The unilateral gonads of the species of Amphioxus from the Bahamas and Torres Straits also belong to this category.

Although, on account of their essentially azygous nature, the mouth and endostyle have been separated from the gill-slits in the above classification, it is obvious that their asymmetrical position in the larva must be ascribed to one and the same cause. In the succeeding pages we shall endeavour to demonstrate what this cause was.

Explanation of Asymmetry of Mouth and Gill-slits.

It is quite evident that the primary gill-slits which appear on the right side of the larva belong primitively, or ancestrally, to the left side, to which, in fact, they are eventually transferred. Meanwhile, the left side of the larval pharyngeal region is largely occupied by the huge oral aperture.

We may figure to ourselves the primitively left-side gill-slits being carried over to the right side by a semi-rotation from left to right of the pharyngeal wall. The primitive right side of the pharynx would thus be crowded out, so to speak, and the right-side gill-slits would be temporarily obliterated owing to lack of room, while the original mid-ventral line would be carried high up on the right side, where, in point of fact, it is plainly indicated by the branchial artery, which lies actually above the primary gill-slits in the larva (Fig. 74, etc.).

Thus the actual topographical conditions in the larva do not by any means coincide with the morphological relations of parts, since the morphological mid-ventral line of the pharynx lies high up on the right side of the body. It should be carefully noted that the form of asymmetry which we are now considering only affects the anterior portion of the larval body.

The same semi-rotation of the pharyngeal region which converted the primitive left side of the larva into the actual right side caused the primitively median mouth to take up its position on the actual left side. But since, as we have noted, the rotation occurred from left to right, the mouth must have been originally situated in the median dorsal line.

In postulating a virtual semi-rotation of the ancestral pharynx, we do not, of course, mean to suggest the probability of an actual movement in bulk about the longitudinal axis, but merely that the formative centres of the various structures belonging to this region of the body (gill-slits, mouth, endostyle, etc.) have, by the correlated interaction of their component cell-groups, been diverted from their ancestral relations through the intercalation, in the course of the progressive evolution of the organism, of a new and disturbing element.

We are now in a position to say what this disturbing element is. It is the secondary forward extension of the notochord beyond the limits of the dorsal nerve-tube to the tip of the snout. As already stated, there is direct evidence to show that this is a secondary and not an ancestral feature, inasmuch as in the young embryo (Fig. 68 *bis*) the notochord is removed from the anterior extremity of the body by a very appreciable interval, which is occupied by that portion of the archenteron which gives rise to the head-cavities. Moreover, as was pointed out above, the dorsal groove of the archenteron, which gives rise to the notochord, remains open into the archenteric cavity in the region of the first myotome, and even somewhat behind the level of the neuropore, for some time after its walls have approximated to form the solid notochord behind this region.

The forward extension of the notochord in Amphioxus is, therefore, *de facto*, to a large extent an ontogenetic phenomenon, although, from the very beginning, it shows what may be described as a precocious tendency to extend beyond the nerve-tube. We shall also find that there is every reason to suppose that it is a cenogenetic, and not a palingenetic, feature.[12]

Since we know for an actual fact that the primary gill-slits of the larva belong ancestrally to the left side, it follows as an absolute topographical necessity that the mouth has been brought to one side from an originally *median dorsal position*, by the same semi-rotation of the pharynx (in the sense explained above) which has demonstrably carried the primitive left-side gill-slits under the pharynx up to the right side of the larva. But this is not the only criterion by which we can judge of the ancestral position of the mouth.

In the larvæ of the Ascidians, the nearest existing relatives of Amphioxus, there is a præoral lobe and a neuropore, which opens at first to the exterior in the mid-dorsal line, just as in Amphioxus. But in contrast to the latter form the notochord does not extend forwards into the region of the præoral lobe, but it stops short behind the cerebral vesicle.

Immediately in front of the neuropore, in the Ascidian larva, the wall of the pharynx comes into contact with the ectoderm and fuses with it, and then at the point of fusion a perforation takes place, and the mouth is established in the mid-dorsal line. During the formation of the mouth the neuropore temporarily closes up, but subsequently it reopens — *into the mouth.*

In Amphioxus we can only assume that in correlation with the forward extension of the notochord, the mouth was compelled to forsake its primitive relations to the neuropore and to move to one side so as to make way for the notochord. The growth of the latter to the front end of the body obviously prevents the wall of the pharynx from coming into contact with the ectoderm in the mid-dorsal line, while it leaves the neuropore unaffected, since the nerve-tube is essentially dorsal to the notochord, and the pharynx, on the other hand, essentially ventral to it.

This explains the fact that the hypophysis (olfactory pit) of Amphioxus opens dorsally directly to the exterior instead of into the mouth as it does in the Ascidian.

The secondary gill-slits — that is, those belonging to the primitive right side of the body — present an interesting instance of *retarded* or *latent* development. This is due to the fact that their own side of the body is at first usurped by their primitive antimeres, the so-called primary slits, as a result of which they have themselves been temporarily crowded out as mentioned above. In consequence of their retardation, when they do appear to inaugurate the process of symmetrisation, they do not conform to the method in which metameric structures are normally produced, but most of them — namely, from the second to the seventh inclusive — arise simultaneously while the first and the eighth arise somewhat later.

Larval Asymmetry not Adaptive and not Advantageous; Forward Extension of Notochord Adaptive and Advantageous.

The conclusion to be drawn from the above considerations is that the remarkable asymmetry of the larva of Amphioxus, in respect of the pharynx and the parts connected with it, is of no specific advantage whatever to the larva, but is merely a stage, which has been preserved in the ontogeny, of a topographical readjustment of parts necessitated by the removal of the mouth from its primitive mid-dorsal position in consequence of the secondary forward extension of the notochord, which has thus caused a virtual semi-rotation of the pharyngeal region of the body. On the other hand, the forward extension of the notochord is a distinct advantage in later life, since, by giving resistancy to the snout, it enables the animal to burrow its way into the sand with such astonishing facility, while the fact that it grows to the front end of the body at a very early stage in the embryonic development, long before it comes to be put to this definite use, must be regarded as an instance of *precocious* development of which there are numerous and otherwise inexplicable examples in the field of comparative embryology.

The larval asymmetry of Amphioxus is therefore a purely secondary or cenogenetic feature, and has no directly ancestral or palingenetic significance, although, as we have shown above, it serves indirectly as a clue to what the ancestral condition was. At the same time it is a primary feature in the actual ontogeny; that is to say, the asymmetrical structures (mouth and gill-slits) arise *in situ*, and are not removed in the individual development from a primary symmetrical to a secondary asymmetrical position, as is the case, for instance, with the neuropore.

It may appear paradoxical, but is nevertheless correct, to say that in the ontogeny the mouth and gill-slits appear *primarily* in a *secondary* position.

It is quite evident that the asymmetry of the larva of Amphioxus is of a totally different character to the well-known asymmetry of the flat-fishes or *Pleuronectidæ* (turbot, sole, plaice, halibut, flounder, etc.). The latter are hatched as perfectly symmetrical larvæ with eyes quite opposite to one another. Then, in adaptation to a life at the bottom of the sea, after a short pelagic existence they turn over on one side, in some species the right side, and in others the left, and the eye of that side moves over the snout, sometimes even through the snout, to the other side, and so the eyes come to lie on the same side. In this case, therefore, the asymmetry, which is secondary in every sense of the word, is the result of a special adaptation to a particular habit of life, and is accordingly of the greatest advantage to the fishes which possess it.

On the other hand, its extraordinary asymmetry is of no conceivable advantage to the larva of Amphioxus, and does not represent an adaptation to any peculiar mode of existence whatever.

It is rather the mechanical, incidental, accessory, and subsidiary accompaniment of another organic change which is both advantageous and adaptive, namely, the forward extension of the notochord; and while the excessive asymmetry is indifferent to the pelagic larva, it would be positively detrimental to the adult.

Thus in all respects the larval asymmetry of Amphioxus is the precise converse of the adult asymmetry of the Pleuronectidæ.[13]

AMPHIOXUS AND AMMOCŒTES.

We will now pass on to consider what new light the larval development of Amphioxus throws on its relationship to the craniate Vertebrates.

As a type of the latter with which to make the comparison, we will select *Ammocœtes*, the larva of the lamprey, Petromyzon, which is the nearest relative of Amphioxus among the Craniota.

Nervus Branchialis Vagi.

Although Ammocœtes possesses an organisation which, especially in virtue of its nervous system and sense-organs, entitles it to an undoubted place among the craniate Vertebrates, yet, on the whole, its structural elements remain in such a relatively simple condition of elaboration that it readily adapts itself to a comparison with Amphioxus.

At the same time the system of ganglia and peripheral cranial nerves indicated in Fig. 91 will show what a great gap there is between the two forms. Nevertheless, a nerve corresponding to that which lies over the gill-slits in Fig. 91, the *nervus branchialis vagi*, has recently been discovered in Amphioxus by VAN WIJHE, so that there need be no difficulty in comparing the pharyngeal tract of Ammocœtes with that of Amphioxus.

It may be added here that the nerve-supply of the pharynx of Amphioxus was described as a branchial plexus by ROHON and FUSARI, but the origin of the nerves which gave rise to the plexus was not satisfactorily determined, beyond the fact that they arose from the rami viscerales of the dorsal spinal nerves. VAN WIJHE also was not able to determine the precise origin of the longitudinal nerve discovered by him. This nerve, which lies on either side at the place where the ligamentum denticulatum passes into the gelatinous lamella derived from the intercœlic membrane, gives off the branches which form the "branchial plexus." Van Wijhe states that the origin of the "ramus branchialis vagi" of Amphioxus is to be sought in the eighth to the tenth dorsal spinal nerves.

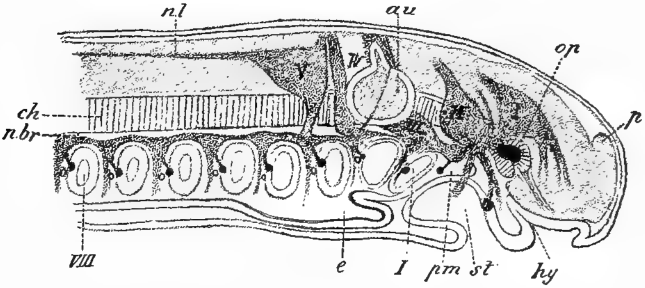

Fig. 91.—Anterior portion of young Ammocœtes of 4 mm., to show extension of brain, origin of endostyle (thyroid), relations of branchial nerves, etc. (After KUPFFER.)

I, II, III, IV. The so-called "Hauptganglia." *I* and *II.* Trigeminus. *III.* Acustico-facialis. *IV.* Glossopharyngeus. *V.* Vagus.

au. Auditory capsule. *ch.* Notochord. *e.* Endostyle (hypobranchial groove, thyroid). *hy.* Hypophysis, in front of which is the nasal groove. *n.l.* Nervus lateralis. *n.br.* Nervus branchialis. *o.p.* Eye. *p.* Pineal body (epiphysis). *p.m.* Præoral endodermic pouch (median portion of præmandibular cavity. *st.* Stomodœum. *I, VIII.* First and eighth gill-pouches; the small circles behind the gill-pouches indicate the positions of the external openings of the gill-pouches, which will become perforated later. The small black spots in front of the (later appearing) external openings represent the so-called *ganglia prætrematica.*

He found that the nerve curved ventralwards in front and passed downwards through the intercœlic membrane until it reached the level of the ventral transverse muscles in front of the visceral branch of the eleventh spinal nerve. He was unable to follow it further in the complex nerve-plexus which lies on the surface of the muscles. It is probable, however, that the branchial nerve arises from the visceral branch of the eighth, ninth, or tenth spinal nerve.*

Stomodæum, Hypophysis, and Gill-slits.

It is a common fact that the time and order of formation of corresponding parts differ greatly in the development of different species. Thus in Ammocœtes, at the stage shown in Fig. 91, the definitive mouth, corresponding to the velum in Amphioxus, has not yet formed, but the equivalent of the oral hood is already present in the form of a deep in-pushing of the ectoderm which, at its blind end, is closely applied to the anterior endodermic wall. The mouth will break through later in the middle of the area of contact between ectoderm and endoderm.

This ectodermic invagination, whose cavity is probably the homologue of the vestibule formed by the oral hood which leads into the mouth in Amphioxus, is known as the *stomodæum.* Immediately in front of the stomodœum is another ectodermic involution which is in contact with the front of the brain, and is known as the *hypophysis* or *pituitary body.*[14]

It will appear later that this is the probable equivalent of the so-called olfactory pit of Amphioxus.

In the wall of the pharynx of Ammocœtes there are, at this stage, the indications of eight pairs of gill-slits. They have not yet, however, broken through to the exterior, but consist of a succession of hollow outgrowths of the pharynx stretching towards the ectoderm with which they will eventually fuse (Fig. 92 *A*, *B*, *C*).

In the case, however, of the first pair of gill-pouches,

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* It is not impossible that many of the rami viscerales may send up branches to the branchial plexus, as was indeed described by Rohon. In this case, Van Wijhe's nerve would be of the nature of a *collector*.

it does not come to a fusion with the ectoderm; but instead they begin to undergo a retrogressive development and eventually flatten completely out (Fig. 92 *B*). They are thus shown to be rudimentary structures, morphologically representing the first pair of gill-clefts, but never achieving their full development.

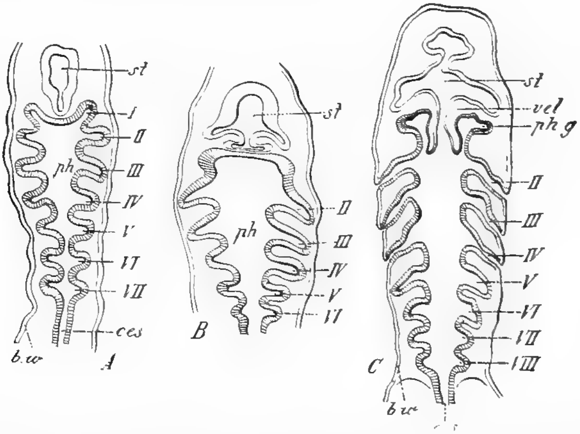

Fig. 92. — Horizontal sections through the pharyngeal region of Ammocœtes, to show the relation of the first pair of gill-pouches to the peripharyngeal grooves. (After Dohrn.)

A. Two days after hatching; first pair of gill-pouches well developed.

B. Six days after hatching; first pair of gill-pouches flattened out.

C. Nine days after hatching; appearance of peripharyngeal grooves.

I–VIII. Gill-pouches. *b.w*. Body-wall. *oes*. Œsophagus. *ph*. Pharynx. *ph.g*. Peripharyngeal groove. *st*. Stomodœum. *vel*. Velum.

As to their position, they occupy the extreme anterior angles of the pharynx formed by its lateral walls with the anterior transverse wall against which the stomodœum is applied. Whatever may be the reason for it, the atrophy of the first pair of gill-pouches in Ammocœtes is of precisely the same nature as the atrophy of the first gill-slit in Amphioxus, with the distinction that the latter actually opens to the exterior for a time.

Endostyle or Hypobranchial Groove.

At a stage in the development of Ammocœtes which precedes the flattening out of the anterior gill-pouches, a median depression occurs in the extreme anterior region of the ventral wall of the pharynx between the first pair of gill-pouches. In its production the wall of the pharynx at this region projects itself ventrally and slightly forward. This groove, which is known as the *hypobranchial groove*, develops in the direction from before backwards, and eventually extends backwards as a longitudinal groove as far as the fifth pair of gill-pouches (Fig. 91).

WILHELM MÜLLER showed that it was the homologue of the *endostyle* of Ascidians and Amphioxus, and he has been amply confirmed by DOHRN. It agrees with the latter structure in its origin at the anterior extremity of the pharynx and subsequent growth backwards and in its histological structure, the most marked feature of the latter being the four longitudinal rows of gland-cells which were noted above in the endostyle of Amphioxus. (Cf. Fig. 13.) Like the latter, also, it is a slime-secreting gland.

In Ammocœtes the hypobranchial groove becomes largely shut off from the cavity of the pharynx by the gradual ingrowth of a diaphragm-like lamella which proceeds from the angle made by the groove in front with the anterior wall of the pharynx (Fig. 91). Subsequently a similar diaphragm grows in from the posterior margin of the groove, and finally the latter only communicates with the pharynx by a small aperture in the mid-ventral line between the fourth pair of gill-pouches.

Peripharyngeal Ciliated Bands of Ammocœtes.

Corresponding with the right and left peripharyngeal ciliated bands which we described as proceeding from the anterior borders of the endostyle in Amphioxus there is a pair of ciliated grooves in the pharyngeal wall of Ammocœtes which proceed from the anterior lip of the hypobranchial groove after the latter has become to a large extent shut off from the pharynx by the above-mentioned diaphragm. These grooves curve forwards and upwards in front of the gill-clefts (after the obliteration of the first pair of gill-pouches), and then proceed backwards on either side of the dorsal middle line of the pharynx as far as the commencement of the œsophagus. Here they appear to curve downwards again, and uniting together, extend forwards as a median ventral groove to the posterior lip of the hypobranchial aperture.

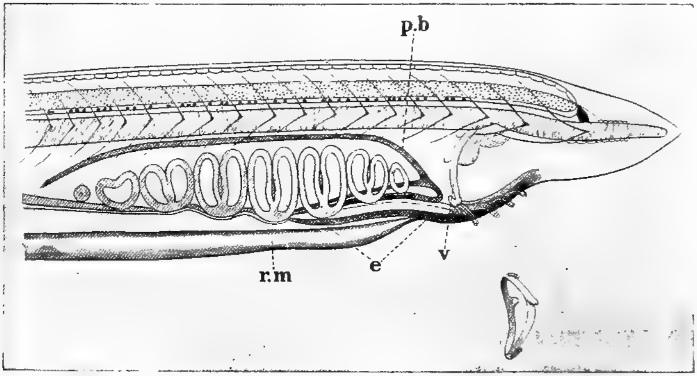

Fig. 93.—Young Amphioxus, after the metamorphosis, having eight gill-slits on each side. From the right side. (After WILLEY.)

p.b. Peripharyngeal band. *v.* Velum; shown separately below the main figure, with rudiments of four velar tentacles. *e.* Endostyle, extending backwards to the level of the fourth gill-slit. *r.m.* Right metapleur.

The last-mentioned median ciliated groove would appear to be unrepresented in Amphioxus, but the downward curvature of the ciliated bands of the latter behind the gill-slits can be observed (Fig. 93).

In Ammocœtes the ciliated peripharyngeal grooves, where they curve upwards in front along the anterior wall of the pharynx, apparently occupy the same position which was previously occupied by the first pair of gill-pouches. Since the latter have already entirely disappeared, there is nothing in the way of their occupying this position (Fig. 92 *C*). In Amphioxus, where the corresponding gill-slit remains open for a long time, the peripharyngeal band exists without connexion of any sort with the portion of the wall occupied by the slit, and when the latter closes up, it leaves no trace behind.[15]

Thyroid Gland.

When the metamorphosis of Ammocœtes into Petromyzon takes place (which happens after a larval existence of some two years' duration), the hypobranchial groove loses all connexion with the pharynx and becomes broken up by the ingrowth of connective tissue into a number of separate capsules which collectively constitute the *thyroid gland* of Petromyzon.

The thyroid gland is one of those enigmatical ductless glands which form such a curious and constant feature of the Vertebrate organisation.

There is considerable doubt as to the specific physiological function which it has to perform, but at the same time it is a necessary factor in the Vertebrate economy, and is of great importance from a pathological point of view.

In the higher forms it is attached to the lower side of the larynx, and appears to have received its name on account of its close proximity to the thyroid cartilage of the latter, the older anatomists assuming a functional relation between the two structures.

We know perhaps more about the morphological than about the physiological significance of the thyroid gland, since it is the vestige of the very actively functional endostyle or hypobranchial groove of the Ascidians, Amphioxus, and Ammocœtes.

Morphology of Club-shaped Gland of Amphioxus.

In describing above the formation of the second row of gill-slits in Amphioxus, we found that the first secondary slit paired with the second primary slit. It now remains to consider what has become of the antimere of the first primary slit.

The probability is that, unlike the antimeres of the succeeding primary slits, that of the first has not suffered a retardation of development, but is present from the very beginning of the larval development, although in a somewhat modified form. I refer to the *club-shaped gland.*

The club-shaped gland fulfils the requirements of a gill-slit in so far as it opens at one end into the pharynx, and at the other to the exterior. Since, as we have shown, the morphological mid-ventral line lies high up on the right side, immediately above the primary gill-slits, it is evident that its anterior continuation would pass through the endostyle precisely at the point where the latter is redoubled upon itself. But the internal opening of the club-shaped gland lies above the upper limb of the endostyle, and therefore it is placed not only on the actual right side of the larva, but in opposition to the first primary slit, on the morphological right side as well.

It must be supposed that the original gill-slit, from which the club-shaped gland is derived, acquired, for some reason or other, a tubular form.

A familiar precedent for gill-slits being drawn out into elongated tubes, the effect of which is to separate the internal from the external opening by a long interval, is presented by the hag-fish, *Myxine*. Myxine also shows us that, in correlation with the canalisation of the gill-slits, their external apertures may enter into new relations differing considerably from the primitive condition. As is well known, the elongated tubular gill-clefts of Myxine do not open separately to the exterior, but fuse together at their distal extremities, so as to give rise to a longitudinal duct on each side, which opens to the exterior some distance behind the gill-region.

It is only on some such supposition as this — namely, that the external aperture of the gill-slit represented by the club-shaped gland of Amphioxus has assumed new topographical relations in correlation with the canalisation of the original slit — that its position on the opposite (left) side of the body to the internal opening of the gland is rendered intelligible. The position of the internal opening furnishes the criterion by which to judge of the primitive relations of the original gill-slit.

With the above point of view, therefore, we may signalise the following facts to prove that the club-shaped gland is the antimere of the first primary gill-slit.

1. They arise simultaneously in the embryo as grooves in the ventral wall of the pharynx.
2. They come to lie on opposite sides of the morphological median line — the first gill-slit entirely so, and the club-shaped gland in respect of its internal opening into the pharynx.

3. They atrophy and disappear simultaneously during the metamorphosis of the larva.
4. No secondary gill-slit ever arises to pair with the first primary slit.

As the stage represented in Fig. 64 marks such a vital turning-point in the development of the individual, being the stage at which the embryo becomes a larva and the struggle for existence in obtaining independent nourishment genuinely sets in, it is important to be able to define it accurately. In view of the above considerations, we arrive at the conclusion that the larva is at this stage possessed morphologically of a pair of gill-slits.

It should be pointed out that this opening stage of the larval development appears to be of the nature of a *resting phase*, during which the larva accumulates energy for future growth.

Præoral "Nephridium" of Hatschek.

In the larvæ of Amphioxus there is a structure lying at the base of the notochord on the left side, immediately above the præoral pit, which we have not yet considered. (Cf. Figs. 81 and 82, *x*.) According to Hatschek, who first described it, it arises in the larva as a mesodermal, ciliated funnel and canal in front of the mouth, in the region of the first metamere. It lies in a narrow division or prolongation of the body-cavity, beneath the left aorta. (Cf. Fig. 76 *B*.) At its hinder end it opens into the pharynx. Hatschek interprets this structure as a nephridium. Its true physiological, and especially its morphological, significance is, however, very perplexing and requires further study.

Ancestral Number of Gill-slits.

The unlimited number of gill-slits in the adult Amphioxus has led to a good deal of controversy as to the approximate number present in the ancestral Vertebrate, some authorities being of the opinion that Amphioxus presents the primitive condition in this respect, and others that the multiplication of gill-slits in this form was a secondary phenomenon.

Sometimes as many as fourteen pairs of gill-clefts are found in a remarkable cyclostome fish from the Pacific, allied to Myxine, and called *Bdellostoma.** With this exception, no true fishes, recent or fossil, are known which possess more gill-slits than the existing sharks belonging to the family of the *Notidanidæ.* Of these the genus *Heptanchus* possesses eight gill-clefts (*i.e.* seven plus the spiracle) on each side, and *Hexanchus* seven. In Ammocœtes, as we have seen, there are at one time indications of eight pairs of gill-slits. The first pair of these, however, never breaks through to the exterior, and eventually disappears, but Dohrn has shown that the primary relation in which the seventh pair of cranial nerves stands to it, indicates that it is the homologue of the *spiracle* of the higher forms.

Moreover, in the larval development of Amphioxus several facts combine to produce the impression that the indefinite number of gill-slits in the adult is a secondary acquirement. First of all, there is the series of primary gill-slits which, while varying within narrow limits, usually numbers fourteen. Their unpaired unilateral character is merely incidental, as explained above, and it may be stated

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* For a recent account of Bdellostoma, consult HOWARD AYERS, No. 69, bibliography.

that they are potentially paired, the first of them in all probability being actually paired (with the club-shaped gland).

In the second place, after the closure of a number of the primary slits, the so-called *critical stage* occurs with eight pairs of gill-slits. This is another resting phase in the development, and marks the turning-point from the larval to the adolescent period. Subsequently the addition of new gill-slits behind those already present commences and goes on indefinitely throughout life.

Counting in the first pair of slits (*i.e.* first primary slit plus club-shaped gland) which is destined to atrophy, we must regard it as probable that the proximate common ancestor of Amphioxus and the higher Vertebrates was characterised by the presence of from *nine to fourteen* pairs of gill-clefts, although it is also probable that there was a variable tendency to add to this number by fresh perforations.

NOTES.

1. (p. 105.) It is unaccountable how there can have been conflicting statements as to the ejection of the genital products (male and female) through the atriopore. It was first observed by DE QUATREFAGES in 1845, and his observations have since been fully confirmed by PAUL BERT, A. WILLEY, and E. B. WILSON. On the other hand, both KOWALEVSKY and HATSCHEK affirm that they are discharged through the mouth. It is to be regretted that two such eminent observers should have committed this error, since it is difficult to eradicate it from the text-books.

2. (p. 115.) The primitive endoderm cells in the neighbourhood of the neurenteric canal apparently retain an undifferentiated character, until the completion of the myotome-formation. In the young embryo they are to be observed in transverse section in process of division, numbers of karyokinetic figures being present. But the cells divide without regard to the median plane of sym-

metry, and the recent researches of E. B. WILSON and LWOFF lead to the conclusion that the so-called *mesoblastic pole-cells*, which were described by HATSCHEK, have no real independent existence.

3. (p. 123.) Whether the dorsal and ventral fin-spaces are actually derived from the original myocœl, as described by Hatschek, or do not rather arise by a splitting of an originally solid thickening of the gelatinous connective tissue which surrounds them, must remain doubtful. The cavity of the metapleural folds certainly arises as a *schizocœl, i.e.* by a hollowing out of a solid thickening. Even in case the fin-spaces also arise as schizocœls, Hatschek's interpretation of their morphological significance might still hold good.

4. (p. 123.) A transitory pouch-like diverticulum of the myocœl has been observed in connexion with the formation of the sclerotome in the Selachian embryo by RABL and H. E. ZIEGLER.

5. (p. 129.) Since the work of BALFOUR on the development of Elasmobranch fishes (Selachians), it has been known that the paired præmandibular head-cavities communicate with one another across the median line in the embryo. The important results obtained by the researches of KUPFFER (Petromyzon, Acipenser), KASTSCHENKO (Selachian), and JULIA PLATT (Selachian), not only established the fact that the præmandibular cavities arose essentially as anterior archenteric pouches (cf. Fig. 72), but also that the median cavity which effected their communication across the middle line, from side to side, arose by constriction from the front end of the archenteron (using the latter term with some latitude), and that, therefore, the *union of the right and left præmandibular cavities in the embryo of the craniate Vertebrates is primary, and not secondary, as was previously supposed.*

For an excellent historical and critical summary of our knowledge of the origin of the head-cavities in the craniate Vertebrates, the reader may consult FRORIEP. (See bibliography.)

6. (p. 130.) The ciliation of the ectoderm in the larva of Amphioxus continuing, as it does, long after the muscles have been fully differentiated, and when the cilia are therefore no longer required for purposes of locomotion, should be especially noted as evidence of a very archaic organisation.

We shall find in the last chapter that the possession of a ciliated ectoderm is a prime characteristic of *Balanoglossus* and many of the lower worms (e.g. *Nemertines*). In none of the craniate Vertebrates is the ectoderm at any time ciliated.

7. (p. 134.) The exact stage at which the club-shaped gland reopens into the pharynx must remain an open question. It is, very probably, subject to a good deal of variation in this respect, occurring now earlier, now later. Experiments to determine the physiological rôle of this gland are much needed.

8. (p. 143.) In accordance with Dohrn's conception of the principle of the change of function (*Das Princip des Functionswechsels*), the number and nature of the organs of the Vertebrate body, which have been interpreted as modified gill-clefts, are truly astonishing. First and foremost, Dohrn supposed that the Vertebrate mouth arose by the fusion of two gill-slits across the middle line, the old Annelid-mouth, which perforated the central nervous system, having been lost. A great many forcible arguments have been brought forward in support of this hypothesis. Dohrn himself would probably admit that it is only tenable on his further hypothesis that Amphioxus is a form which has undergone a retrogressive evolution from the craniate Vertebrates. This was a better hypothesis than that of Semper, who, perceiving that Amphioxus would not fall in with the Annelid-theory, declared, "er sei kein Wirbelthier; also, auch kein Fisch."

Besides the mouth, many other structures have similarly been referred back to modified gill-slits, among which may be mentioned the nose, hypophysis, thyroid gland, lens of the eye, and the anus. None of these comparisons is supported by the facts of development and anatomy of either Amphioxus or the Tunicates, while most of them would appear to be definitely disproved by these facts.

9. (p. 147.) Since the right metapleural fold bends round to the median ventral line of the snout, as shown in Fig. 38, and since, further, at a later period, the right half of the oral hood is similarly continued round the front end of the body into the dorsal fin, it is clear that the right half of the oral hood must arise essentially in continuity with the right metapleur. On the contrary, the left half of the oral hood arises entirely independently of the left metapleur. It is possible that this discontinuity of

development of the left half of the oral hood and the left metapleur has been secondarily brought about.

10. (p. 150.) The study of transverse sections has led me to the conclusion that the backward extension of the endostyle is effected by interstitial growth, and not by the conversion of the cells which form the primary floor of the pharynx into endostylar elements. These cells are probably disintegrated and absorbed by the endostyle as it grows backward.

11. (p. 153.) For a comparison between the perigonadial cavities of Amphioxus and the mesonephric tubules of the craniates the reader should consult Boveri's original memoirs. (See bibliography.)

12. (p. 159.) The following definition of the so-called biogenetic law of recapitulation (Haeckel's biogentisches Grundgesetz) will explain the meaning of Haeckel's terms "cenogenesis" and "palingenesis." According to this law: The development of the individual (*ontogeny*) is a compressed summary of the gradual modifications which have resulted in the evolution of the species, or type (*phylogeny* = Stammesgeschichte); this recapitulation (summary, or Auszug) of the phylogenetic stages in the ontogeny is the more perfect according as the ancestral development (Palingenesis, Auszugsentwicklung) has been the less disturbed or falsified through secondary or "recent" adaptation (cenogenesis, Störungsentwickelung) of the embryo or larva to a new environment.

13. (p. 162.) The explanation of the asymmetry of the larva of Amphioxus given in the text was first suggested by me in 1891. It may be well to state that it has not as yet received very general recognition in the more recent literature on the subject. It was, however, fortunate enough to receive the endorsement of the late Professor MILNES MARSHALL in his text-book of Vertebrate Embryology. When the pelagic larvæ of Amphioxus are confined in glass jars, after a certain lapse of time they sink to the bottom, like all other pelagic organisms. When they arrive at the bottom, they fall over on to one side, owing to a physical impossibility to rest in any other position, just as was described above for the adult. It ought not to require to be emphasised that their incidentally lying on one side is not due to a pressing desire or

instinct to assume that position, but rather because they cannot help it. It is apparently in consequence of a misunderstanding of this observation that KORSCHELT and HEIDER ascribe the larval asymmetry of Amphioxus to the same causes which brought about the asymmetry of the Pleuronectidæ. Another, and, as it appears, a still more impossible view, has recently been expressed by VAN WIJHE. According to van Wijhe, the left-sided mouth occupies its normal and primitive position in the larva of Amphioxus, and in that position it represents a gill-slit, whose antimere is the club-shaped gland. Van Wijhe arrived at this view as a result of his very important discoveries as to the musculature and innervation of the adult mouth. These discoveries may be summarised as follows: —

1. The outer muscle of the oral hood represents the anterior continuation of the *left half only* of the transverse and subatrial muscles.
2. The inner nerve-plexus of the oral hood is formed on both sides, exclusively from nerves which arise from the left side of the central nervous system.
3. The velum is innervated entirely from nerves of the left side.

From these observations van Wijhe concludes that the mouth of Amphioxus, even in the adult, is essentially an organ of the left side, and is neither homologous with the Ascidian nor with the craniate mouth.

It would seem, however, that the more obvious and justifiable interpretation of these facts is that the asymmetrical musculature and innervation described by van Wijhe are merely the partial persistence in the adult of the more complete asymmetry of the larva.

Van Wijhe's observations, therefore, do not affect the question of the cause of the asymmetry in any degree.

14. (p. 165.) As first shown by Dohrn, the hypophysis of Ammocœtes first arises from the roof of the stomodœum, from which it is subsequently removed to the dorsal surface of the head by the enormous development of the upper lip.

15. (p. 169.) The ciliated tracts in the pharynx of Ammocœtes were first described and figured by ANTON SCHNEIDER in

1879. In 1886 DOHRN thought he had proved that the anterior portion of them, which bends upwards on either side of the pharynx and forms the *peripharyngeal grooves*, represented the last traces of the aborted first pair of gill-clefts. Although they appear at the place which was formerly occupied by these rudimentary gill-pouches, yet, according to Dohrn's own account, they do not appear until after the gill-pouches have *completely flattened out.* Under these circumstances, but above all, in view of the relations of the homologous peripharyngeal bands in Amphioxus which exist both before and after the disappearance of the first pair of gill-clefts (*i.e.* first primary gill-cleft and club-shaped gland), it must be assumed that Dohrn's interpretation, though most natural, was nevertheless somewhat at fault.

IV.

THE ASCIDIANS.

The Ascidians, Tunicates, or sea-squirts, as they are indifferently called, constitute one of the most clearly defined and yet most heterogeneous groups of animals which it is possible to imagine. There is a great variety of families, genera, and species occurring all the world over, and in all depths of the ocean from the tide-marks to the profoundest depths.

Most of them are sedentary animals, remaining fixed all their lifetime on one spot, whether attached to rocks, stones, shells, or sea-weeds, from which they are incapable of moving. There are, however, several very extraordinary genera of Ascidians which swim or float about perpetually in the open ocean, and have become adapted in the extremest manner to a purely pelagic environment. These pelagic Ascidians have become so modified in adaptation to their oceanic existence, and their development diverges, as a rule, so much from the normal, that they will hardly enter at all into the present discussion, with the exception of one family, the *Appendiculariæ.*

Just as there are two kinds of sessile Ascidians, *simple* and *compound* or *colonial*, so there are two analogous kinds of pelagic Ascidians. In some of the latter, however, where there is an alternation of generations, one generation, namely, the asexual generation, is a solitary form, while the sexual generation is a colonial form, as, for example, the *solitary Salpa* and the *chain-Salpa.*

For convenience, the Ascidians, as a whole, may be arranged as follows:—

SESSILE ASCIDIANS.

SIMPLE.	COLONIAL.
e.g. *Ascidia.*	e.g. *Clavelina.*
Phallusia.	*Botryllus.*
Ciona.	*Amaroucium.*
Molgula.	*Distaplia.*
Cynthia.	*Didemnum.*

PELAGIC ASCIDIANS.

SIMPLE.	COLONIAL (or capable of producing a colony by budding).
e.g. *Appendicularia.*	e.g. *Pyrosoma.*
	Salpa.
	Doliolum.

The compound sessile Ascidians consist of colonies of individuals or *ascidiozooids* produced by budding from a parent individual. Such colonies are often brilliantly coloured and of massive proportions, as *Amaroucium* and *Fragarium.* Others form thin encrusting expansions on the surfaces of marine plants and shells, as *Botryllus* and *Leptoclinum.* In others, again, the individuals are entirely separate, except at the base, where they are connected together by a common creeping stolon from which new buds are periodically produced, as *Clavelina* and *Perophora.*

STRUCTURE OF A SIMPLE ASCIDIAN.

Test, Mantle, Atrium, Branchial Sac.

The simple or solitary Ascidians which do not produce buds, present hardly less striking differences among the different families than do the compound, but their general shape is much more uniform.

An average simple Ascidian, as *Phallusia* or *Cynthia*, has been aptly compared to a leather bottle provided with two spouts. The spouts occur in the form of two funnel-like prominences projecting from the surface of the body and bearing at their free extremities the *incurrent* or *buccal* and *excurrent* or *cloacal* apertures respectively, the latter usually occurring at a lower level than the former.

The most prominent and, apart from the two apertures, the only external feature of a simple Ascidian, is the characteristic *tunic* or *test* which surrounds the whole body. As a rule, all Ascidians of whatever kind possess this external tunic, and it is one of their chief diagnostic characters.

According to the species this test may be of a cartilaginous, coriaceous, fibrous, or membranous consistency, usually opaque, but sometimes hyaline and transparent, as in *Corella*, *Salpa*, etc. Its outer surface may be smooth, wrinkled, or rough, capillated, papillated, or mammillated. In 1845 KARL SCHMIDT made the discovery that the test of the Ascidians was largely composed of the substance which forms the cell-walls in plant tissues; namely, *cellulose.* When treated with the proper chemical reagents, it gives the cellulose-reaction. This is interesting as showing the fundamental identity of protoplasm whether it occurs in animal- or in plant-cells, since in both cases it is capable of depositing cellulose.

Judging by external appearances an ordinary Ascidian resembles nothing so little as Amphioxus, and yet it is probably more closely related to the latter than is the lamprey larva, Ammocœtes, whose external resemblance to Amphioxus is incomparably greater.

It is only in its internal organisation that we meet with structures which remind us strongly of corresponding parts in Amphioxus.

A schematic representation of a dissection of a typical Ascidian after Professor W. A. HERDMAN, whose reports on the Ascidians collected during the voyage of H. M. S. Challenger have done so much to advance our knowledge of the group, is given in Fig. 94. The greater part of the thick cartilaginoid test (also called tunic, outer mantle, or cellulose mantle), *t*, is supposed to be removed from the right side, and its cut edge can be traced all the way round. Below the test comes the inner or muscular mantle, *m*, which is the true body-wall, to which the external tunic is secondarily superadded.[1] The muscular mantle is limited externally (below the test) by the epidermis, and beneath the latter are the interlacing muscle-fibres which compose the bulk of the mantle.

Beneath the mantle is an extensive cavity surrounding to a large extent the viscera. This is the *peribranchial* or *atrial cavity* which communicates with the exterior by the atrial or cloacal aperture, *at.s.*

The mouth, *or.s*, leads into the *pharynx* or *branchial sac*, *ph*, which is of surprising dimensions, and stretches nearly to the posterior end of the body. The walls of the branchial sac are perforated by innumerable gill-openings, the so-called *stigmata*, arranged in successive transverse rows, through which the water which enters at the mouth passes out of the sac into the atrial cavity.

Dorsal Lamina, Endostyle, and Peripharyngeal Band.

On cutting through its right wall we open into the cavity of the branchial sac along the dorsal side of which a fold is seen projecting freely into the cavity, the so-called *dorsal lamina* corresponding to the dorsal groove in the pharynx of Amphioxus, while along its ventral side is a

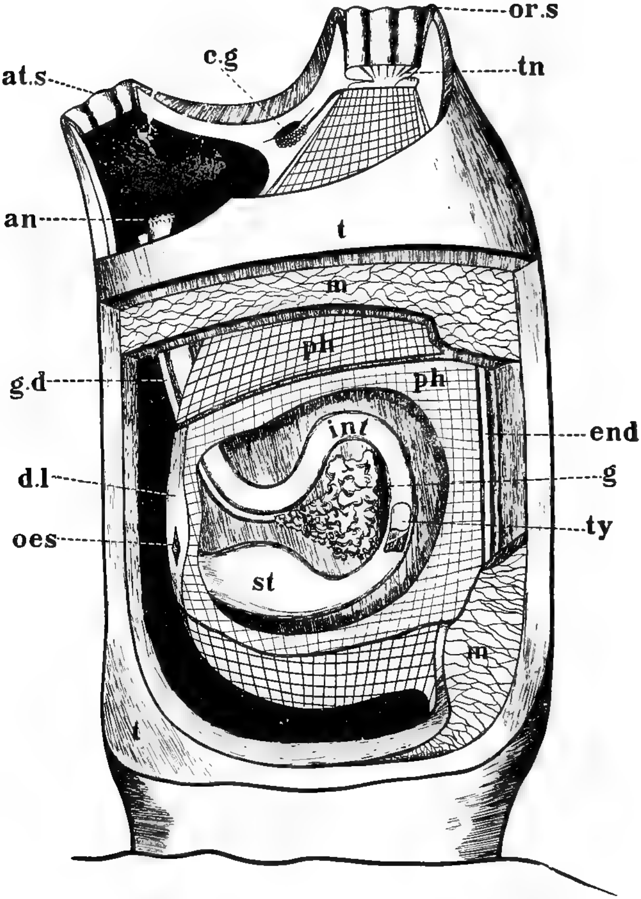

Fig. 94. — Diagram of a dissection of *Ascidia*, from the right side. (After HERDMAN.)

The peribranchial cavity is indicated by the black shading.

an. Anus. *at.s.* Atrial siphon. *c.g.* Cerebral ganglion, beneath which is the subneural gland and its duct. *d.l.* Dorsal lamina. *end.* Endostyle. *g.* Gonad. *g.d.* Genital duct. *int.* Intestine. *m.* Muscular mantle. *oes.* Aperture, leading from branchial sac into œsophagus. *or.s.* Buccal siphon. *ph.* Branchial sac. *st.* Stomach. *t.* Test or cellulose mantle. *tn.* Buccal or coronary tentacles. *ty.* Typhlosole; internal fold of intestinal wall, to increase the digestive surface.

well-defined groove with white glistening walls, which is the *endostyle.* The groove of the endostyle is deeper here than in Amphioxus, but its epithelial walls have the same histological differentiation, with the two rows of gland-cells on each side of the middle line, the latter being occupied by a median group of cells carrying very long cilia. The food which enters the mouth together with the water does not pass out of the pharynx into the atrial chamber, but is caught up by the slime secreted by the endostyle and is then carried *forwards* along the endostyle, and, having arrived at the anterior extremity of the latter at the base of the buccal tube, is carried round along a circular ciliated groove which surrounds the base of the mouth at the entrance to the branchial sac, until it reaches the dorsal side of the animal, when it is led backwards by the ciliary action of the cells of the *dorsal lamina* in the form of a cord of slime in which the food-particles (microscopic organisms, vegetable *débris*) are imbedded.

The ciliated groove round the base of the buccal tube connecting the anterior extremity of the endostyle with the dorsal lamina is known as the *peripharyngeal band* or *pericoronal groove.* We have already made the acquaintance of the homologue of this structure both in Amphioxus and in Ammocœtes. It forms a complete circle round the base of the buccal tube and is indicated in Fig. 94 by the black line which limits the pharyngeal wall anteriorly. It is still better shown in Fig. 96, which represents a young individual of Clavelina.

The cord of slime containing the food passes backwards along the dorsal lamina to the opening of the œsophagus, which lies near the posterior end of the branchial sac, in the dorsal middle line, through which it passes into the stomach. The dorsal lamina is continued to one side of the œsophageal aperture, as a low ridge, which joins the posterior extremity of the endostyle.*

Visceral Anatomy.

Except in its most anterior region, the dorsal border of the pharynx lies freely in the atrial chamber. On the contrary, along its ventral border, throughout the whole length of the endostyle, it is attached to the muscular mantle. In other words, the right and left halves of the atrial cavity are continuous round the dorsal side of the pharynx, but are separated from one another ventrally by the concrescence of the endostyle with the mantle. (Cf. Fig. 95.) In Amphioxus, as we have seen, the opposite condition obtains. There, the dorsal wall of the pharynx is closely applied to the notochord, while the endostylar tract

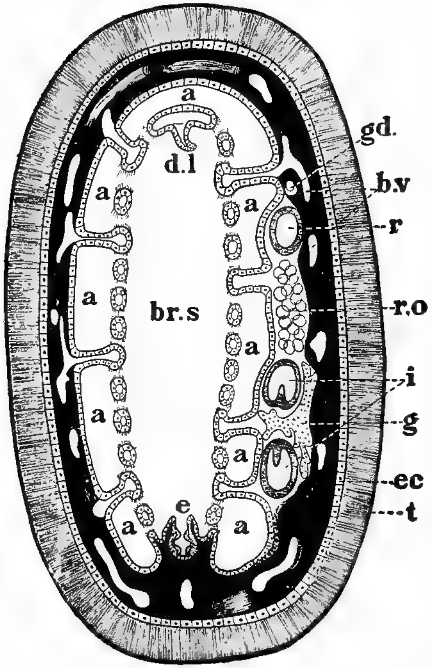

Fig. 95. — Diagrammatic transverse section through the middle of the body of *Ascidia.* (After HERDMAN.) The muscular mantle is indicated by the black shading.

a. Peribranchial cavity traversed by numerous vascular trabeculæ, through which the blood flows into the branchial bars. *br.s.* Branchial sac. *b.v.* "Blood-vessels." *d.l.* Dorsal lamina. *e.* Endostyle. *ec.* Ectoderm. *g.* Gonad. *gd.* Double genital duct. *i.* Intestine, with typhlosole. *r.* Rectum. *r.o.* Renal vesicles. *t.* Test.

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* Compare the above with the description of the course of the ciliated tracts in the pharynx of Ammocœtes, given on p. 168.

is free, so that the right and left halves of the atrial cavity are continuous ventrally, instead of dorsally.

In order to see the stomach and intestine, it is necessary to cut through the left wall of the pharynx, since the viscera lie, at least in the genus Ascidia (or Phallusia), on the left side of the pharynx. It should be pointed out that the topographical arrangements vary considerably among the different genera of Tunicates. In Clavelina, for example, the viscera lie behind the pharynx, as shown in Fig. 96.

On the left side of the pharynx (Fig. 94) the short œsophagus leads into the dilated stomach, which again narrows down to the looped intestine, and finally the latter bends sharply forwards into the rectum, which opens by the anus into the atrial cavity, the excrement being carried to the exterior by the constant stream of water which flows out through the atrial or cloacal aperture.

Instead of being straight, as in Amphioxus, the alimentary canal is here doubled round upon itself. This U-shaped character of the alimentary canal of Ascidians is shown with great clearness in the case of Clavelina (Fig. 96), where there are no secondary convolutions in the course of the intestine.

The Ascidians are one and all *hermaphrodite*, and the reproductive glands frequently lie between the loops of the intestine, while two ducts, *oviduct* and *vas deferens*, which often present the appearance of a single duct with a double lumen, proceed forwards by the side of the rectum, to open into the cloacal region of the atrial cavity near the anus (Fig. 94, *g* and *gd*).

The ovary and testis, though quite separate in the adult, originate, according to the account given by the Belgian zoölogists, ÉDOUARD VAN BENEDEN and CHARLES JULIN, from a common centre of formation, which subsequently undergoes a division into two portions, one of which becomes the ovary, and the other the testis. Similarly the oviduct and vas deferens are derived by division of a primarily single structure, which arises in continuity with, and in fact as an outgrowth from, the primitive sexual gland.

In spite of their hermaphroditism, it would appear that not all the Ascidians are self-fertilising, although many, if not most of them, are. In some cases it is supposed that in different individuals the male and female organs attain maturity at different times, so that in a given individual, when the ovary is ripe the testis is unripe, so that it must be fertilised from another individual, in which the testis is ripe, but the ovary unripe, and so on.

Nervous System and Hypophysis.

(*Neurohypophysial System.*)

The central nervous system of an Ascidian usually bears a ridiculously small proportion to the bulk of the organism. Its main constituent is a ganglion which lies imbedded in the thickness of the mantle, between the oral and the atrial siphons, the two latter structures being innervated by nerves proceeding from the ganglion. As belonging to the central nervous system must also be mentioned a solid nerve-cord which runs along the dorsal border of the branchial sac from the cerebral ganglion to the visceral region (Fig. 96). This was discovered by van Beneden and Julin, and is derived from a persistent portion of the central nervous system of the larva.

Beneath the cerebral ganglion is a lobulated glandular organ known as the *subneural gland.* It is provided with a duct which runs forward and opens at the end of a ciliated funnel-shaped dilatation into the branchial sac at the base of the buccal tube (Figs. 94, 96, and 97) in front of the peripharyngeal band.

The branchial opening of the duct of the subneural gland appears primarily as a simple circular orifice, but it does not usually retain this character in the adult.

Generally it assumes a crescentic form by the incurving of its anterior or posterior lip, and then in many cases the horns of the crescent so formed become coiled over and over concentrically, and usually in approximately the same plane, so that the lips of the aperture assume a very complicated appearance and constitute the so-called *dorsal tubercle* (Fig. 97).

It has taken a long time and the work of a great many zoölogists to achieve our present knowledge (which is by no means complete) of the subneural gland of Ascidians and its duct.

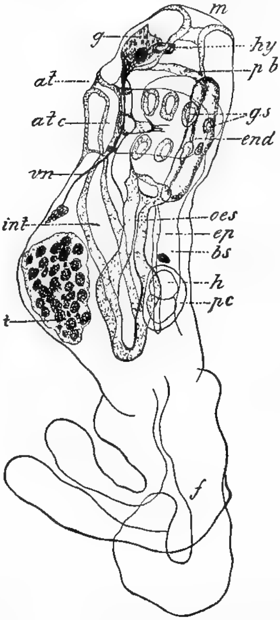

Fig. 96. — Young Clavelina, shortly after the metamorphosis, from the right side. (After VAN BENEDEN and JULIN.)

at. Atrial opening. *at.c.* Atrial cavity. *b.s.* Blood-sinus. *end.* Endostyle. *ep.* Epicardium; outgrowth from branchial sac behind endostyle, which grows down into the creeping stolon, forming a septum in the latter, and being the chief element in the production of buds. *f.* Lobes of the fixing organ, which give rise to the creeping stolon. *g.* Ganglion. *g.s.* Stigmata. *h.* Heart. *hy.* Hypophysis (dorsal tubercle). *int.* Intestine. *m.* Mouth. *oes.* Œsophagus. *p.b.* Peripharyngeal band. *pc.* Pericardium. *t.* Remains of tail, withdrawn into the body. *v.n.* Visceral nerve.

The dorsal tubercle was discovered by the celebrated Savigny in 1816, and was for a long time supposed to be an independent sense-organ of an olfactory nature. The subneural gland was detected not as a gland, but as an enigmatical structure lying below the brain by the English naturalist Hancock in 1868. Its glandular character was demonstrated by Nassonoff and Ussow in 1874–75, the last-named author showing its connexion by means of the duct with the dorsal tubercle. In 1881 Julin produced an admirable memoir on the subneural gland and its duct, and strongly urged its homology with the pituitary body or hypophysis cerebri of the higher Vertebrates. The same suggestion was made in a more tentative form in the same year by Balfour. We shall have to consider this question later. Suffice it to say at present that Julin's suggestion has been accepted to

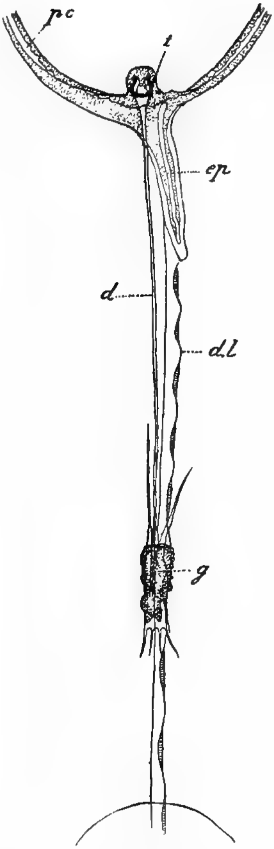

Fig. 97. — Hypophysis of *Phallusia mentula*, prepared out and seen from the inside. (After Julin.)

g. Subneural gland, above which may be seen the outline of the ganglion and its nerves. *d.* Duct of the subneural gland. *t.* Dorsal tubercle, the opening of the hypophysis into the branchial sac. The actual opening is indicated in black. *pc.* Peripharyngeal groove. *ep.* Epibranchial groove. *d.l.* Dorsal lamina, slightly displaced, to show the duct of the subneural gland above it.

N.B.—In this species, the atrial and buccal siphons are widely separated, and the duct of the subneural gland is very long.

the extent that the subneural organ of the Ascidians is frequently spoken of as the *hypophysis.*

Circulatory System.

With regard to the circulatory system the Ascidians differ markedly from Amphioxus in the possession of a well-defined *heart* which lies in a distinct *pericardium.* The heart lies ventrally and usually in the neighbourhood of the stomach. (Cf. Fig. 96.) Its wall is muscular, but consists only of a single layer of cells whose deeper portions (*i.e.* towards the cavity of the heart) are drawn out into striated muscular fibres, while the outer portions of the cells containing the nuclei project into the cavity of the pericardium.

There is therefore no true endothelial lining to the heart, and the cells which build up its wall offer a most interesting example of epithelio-muscular tissue, as was first pointed out by Édouard van Beneden. This type of muscular tissue, in which the muscle-fibres occur as basal prolongations of cells which still retain their epithelial character, is found, as is well known, in the case of the body-muscles of the Nematode or thread-worms, and is above all characteristic of the Cœlenterata (Hydroids and Medusæ).

There are no true blood-vessels in Ascidians, but the passages along which the blood percolates are merely lacunæ in the connective tissue and musculature of the body and between the viscera. They are not lined by an endothelium, and are more correctly described as *blood-sinuses.* They are often irregular in their outline, as shown in the transverse section represented in Fig. 95, but often again they simulate the appearance of true blood-vessels, as in the case of those branches which pass from the mantle into the substance of the test, as well as the tubes which traverse the wall of the branchial sac in every direction.

In the second chapter it was pointed out that the Vertebrate heart arose as a specialisation of a portion of the primitive sub-intestinal blood-vessel whose calibre was originally uniform throughout, and that in Amphioxus the cardiac region of the vascular system retains its primitive tubular character.

Very different is the actual origin of the Ascidian heart; although it is simply a dilated tubular structure, yet it arises entirely independently of and prior to the rest of the vascular system at a time, in fact, before the formation of the muscular mantle and before the atrial cavity has so far extended itself as to almost entirely replace the original body-cavity. The blood-sinuses of the Ascidians are remnants of the latter.

With the formation and growth of the atrial cavity, the perforation of the stigmata, and the development of the muscular mantle, the original body-cavity becomes reduced to a system of narrow canal-like spaces which constitute the above-mentioned blood-sinuses. The general distribution of the blood-sinuses can be made out from Fig. 95. There are two main longitudinal sinuses, one below the endostyle and another above the dorsal lamina, while others are scattered irregularly in the muscular mantle; others again lie in amongst the viscera forming the interspaces between the various parts; and finally the branchial bars between the stigmata are all hollow, and their cavities are placed in communication with the system of sinuses at intervals as shown in Fig. 95.

The periodic contraction of the heart of Ascidians takes place on a highly characteristic and unique plan. Each systole occurs as a peristaltic wave of contraction passing from one end of the heart to the other; but the chief peculiarity in connexion with it is, that after a certain number of contractions in one direction the heart makes a brief pause and then commences to contract again in the *opposite* direction, and so it goes on contracting now in one direction and now in the other. This phenomenon of the periodic reversal of the direction of contraction of the Tunicate heart is known as the *recurrent action* of the heart, and was discovered in 1824 by VAN HASSELT. The discovery was first made in the case of Salpa, but it has since been found to hold good for all Tunicates.

When the heart contracts from its posterior to its anterior extremity, — that is to say, in the postero-anterior direction, — the blood is thereby propelled forwards into the blood-sinus which lies below the endostyle, and from this it passes into sinuses which run transversely into the branchial bars. In the basket-work formed by the intercrossing of the branchial bars, the blood has a complicated and irregular course, and is finally collected into the dorsal sinus which lies above the dorsal lamina. Here it flows backwards, and after passing in amongst the viscera arrives back to the heart. (Other branches of the sinuses pass into the test, where they end in curious knob-like dilatations.)

On the contrary, when the heart contracts in the reversed or antero-posterior direction, the blood which has already been oxygenated in its passage through the branchial bars is sent to the viscera direct, and from there it collects into the dorsal sinus, from which it is distributed over the branchial sac, and so into the sub-endostylar or ventral sinus, in which it flows backwards to the heart.

On account of the above peculiarities relating to its independent origin, the histological structure of its wall, and its recurrent action, the Tunicate heart would appear to be a unique organ peculiar to the group of the Ascidians and analogous but not homologous, or only incompletely so, with the heart of the Vertebrates.

Again, the vascular system of an Ascidian is only functionally comparable to that of Amphioxus, since true vessels provided with an endothelial lining are entirely absent, their place being taken by sinuses which arose by reduction from the original body-cavity.

Renal Organs.

The renal organs of the Ascidians have no apparent morphological relation to those of Amphioxus, and therefore need not detain us. They consist of a group of bladder-like vesicles with cellular walls lying around the intestine. The products of excretion (uric acid, etc.) are deposited inside the vesicles in the form of solid concretions. There is no excretory duct. In *Molgula,* there is a single large cylindrical renal sac closed at both ends and lying on the right side of the body, behind the heart, known as the *organ of Bojanus.*

Comparison between an Ascidian and Amphioxus.

Having sketched in rough outline the organisation of an adult Ascidian, we are now in a position to consider in what respects it resembles and in what it differs from that of Amphioxus. We shall see that some of the most fundamental differences will be made good by the structure of the larva,—such as the absence of a dorsal nerve-tube and of a notochord.

Let us first consider the resemblances between an adult Ascidian and Amphioxus.

In both cases the pharynx is perforated by a great number of *gill-apertures* (gill-slits, stigmata), converting it into a *branchial sac* and opening into an *atrial* or *peribranchial* cavity instead of directly to the exterior. At the base of the pharynx there is a longitudinal gland consisting of a groove open throughout its whole length towards the cavity of the pharynx, and known as the *endostyle*, whose histological character is closely similar in the two cases. From the anterior extremity of the endostyle a ciliated band of columnar cells passes round the wall of the pharynx on each side, in front of the gill-openings, and abuts on the dorsal border of the pharynx, along which it is continued backwards in connexion with the *dorsal lamina* in the one case and the *hyperpharyngeal groove* in the other. This band forms a circlet round the pharynx behind the velum, and is the *peripharyngeal band.** We shall find also that the Ascidian *hypophysis* is essentially homologous with the *olfactory pit* of Amphioxus.

In the Ascidians there are sphincter muscles round the buccal and atrial siphons, and inside the former, in front of the peripharyngeal band (pericoronal groove), there is a circlet of tentacles corresponding perhaps to the velar tentacles of Amphioxus. (Cf. Fig. 94, *tn.*)

The differences between the structure of an adult Ascidian and of Amphioxus may appear to outweigh the resemblances, but it must be remembered that they are all correlated with and accessory to the one great difference in the mode of existence of the respective types.

An Ascidian is sessile; Amphioxus is free. The former, as it were, builds its house upon a rock and is immovable; the latter lives in the shifting sands, and is capable of extremely active locomotion.

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* As mentioned above, this band is usually grooved in the Ascidians.

In correlation with this sessile habit of existence we find that the Ascidians, in contrast to Amphioxus, are hermaphrodite,—an almost universal condition among sessile organisms of every description. They are unsegmented, the muscles not being divided up into myotomes ; and none of their organs (gonads, renal organs, etc.) are metamerically repeated, unless we regard the successive transverse rows of stigmata in the wall of the branchial sac as evidence of metamerism. It is, however, of a totally different nature from the metamerism of the gill-slits of Amphioxus, and we shall see that only in the earlier stages of their development can the stigmata of the Ascidians be compared with the former.

Another of the most characteristic accompaniments of a sessile mode of life is the U-shaped alimentary canal. Instead of being a straight tube with a posteriorly directed anus as in Amphioxus, the alimentary canal of the Ascidians is doubled up upon itself, the rectum is directed forwards, and the anus opens into the atrial cavity. The absence of a dorsal nerve-tube and notochord in the adult Ascidian has been indicated above.

In spite of these great differences, the presence of the endostyle and the perforated wall of the pharynx in the adult, and above all the features in the embryonic and larval development, entitle the Ascidians to be defined as more or less *Amphioxus-like* creatures which have become adapted to a sessile habit of existence.

DEVELOPMENT OF ASCIDIANS.

The first accurate and detailed account of the embryonic development of Ascidians was the classical memoir published in 1867 by Kowalevsky in the Mémoires de l'Académie impériale des Sciences de St. Pétersbourg.

The Ascidian larva was known long before this time, and the external features of its metamorphosis were described in 1828 jointly by Audouin and Milne-Edwards, to whom the discovery of the free-swimming larva is due. Furthermore, the internal structure of the tailed larva, and even the histological structure of the axial rod of the tail, was described with some accuracy by Krohn in 1852, but in ignorance of the details of the embryonic development, he was unable to give the right morphological interpretation to the various parts, and did not identify the axial rod with the notochord of the higher forms.

Segmentation and Gastrulation.

The segmentation of the egg, the formation of a hollow one-cell-layered blastula, and the flattening and subsequent invagination of one side of the blastula to form the two-cell-layered gastrula, take place on a plan so essentially similar to what has been described above for Amphioxus that it is not necessary to dwell at length upon them here. Suffice it to point out that the segmentation of the Ascidian egg takes place typically, according to van Beneden and Julin, on a strictly bilateral plan. That is to say, when the ovum has divided into two blastomeres, right and left, each blastomere represents and will give rise to the corresponding half of the larval body, and the descendants of the first two blastomeres can be distinguished for a remarkably long time on each side of the middle line of the embryo, — a fact which is highly characteristic of Ascidian development.

After the gastrula has begun to elongate, and the blastopore has been narrowed down by the approximation of its lips to a small aperture situated at the posterior dorsal extremity of the embryo, the formation of the medullary plate occurs.

Formation of Medullary Tube and Notochord.

Here, as in Amphioxus, the dorsal wall of the embryo flattens, while the ventral remains convex, and the ectodermic cells on the dorsal side become marked off from the rest by their larger size and columnar shape. The medullary plate extends nearly to the front end of the embryo, while posteriorly its cells form a ring round the blastopore.

In the formation of the medullary tube, however, there is an important difference, and the Ascidian embryo conforms in this point more to the mode of development which is typical of the higher Vertebrates than does Amphioxus. In the latter the medullary plate sinks bodily below the level of the surrounding ectoderm, which then grows over it. Subsequently while underneath the ectoderm the medullary plate assumes the form of a half-canal open towards the ectoderm, and eventually its margins come together and so form a complete tube.

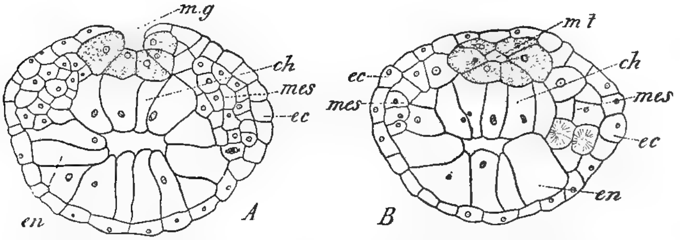

Fig. 98.—Transverse sections through embryo of *Clavelina Rissoana*, to show mode of formation of medullary tube and mesoderm. (After DAVIDOFF.)

A. Through anterior region of embryo, with medullary groove still open.

B. Through posterior region, with closed medullary tube.

ch. Rudiment of notochord. *ec.* Ectoderm. *en.* Endoderm. *mes.* Mesoderm. *m.g.* Medullary groove. *m.t.* Medullary tube.

In the Ascidian embryo the overgrowth of the surrounding ectoderm and the folding up of the margins of the medullary plate occur simultaneously, so that when the latter has the form of a half-canal it is not closed over by a layer of ectoderm, but is open to the exterior (Fig. 98).

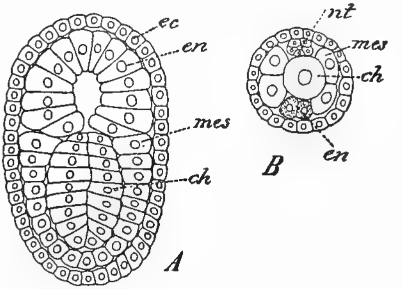

Fig. 99. — *A.* Embryo of *Phallusia mammillata* seen in optical section from above, to show notochord.

B. Section through tail of older embryo of *Phallusia mammillata.* (After KOWALEVSKY.)

ch. Notochord. *ec.* Ectoderm. *en.* Endoderm. *mes.* Mesoderm. *nt.* Medullary tube.

At a somewhat later stage the two *medullary folds* meet together and fuse in the middle line (Fig. 98 *B*), and this, combined with a slight forward growth of the posterior lip of the blastopore, leads to the inclusion of the latter in the medullary tube, so that we arrive at the condition already described for Amphioxus, in which the nerve-tube opens in front to the exterior by the *neuropore* and behind into the archenteron by the blastopore, which has now become converted into the *neurenteric canal.*

Meanwhile the cells forming the dorsal wall of the archenteron in its posterior two-thirds begin to gather themselves together to form the notochord (Figs. 98 and 99). The cells forming the notochord are at first arranged end to end (Fig. 99), and subsequently interlace in the manner described above for Amphioxus.

Origin of Mesoderm.

At about the same time in which the formation of the medullary tube and notochord is going on, the mesoderm begins to put in its appearance, and this is the first event in the development in which there is an important difference between the Ascidian and Amphioxus. The mesoderm in the Ascidian embryo does not arise as a series of archenteric pouches, but is produced on each side by a solid proliferation of cells from the primitive endoderm which lines the archenteric cavity. This solid proliferation begins in the middle region of the embryo near the anterior limit of the notochord, and extends backwards (Figs. 98 and 100). It takes place from the dorso-lateral cells of the endoderm, in a position corresponding to that at which the mesoblastic pouches of Amphioxus grow out from the archenteron. The mesoderm of the Ascidian embryo therefore agrees with that of the embryo of Amphioxus in being derived from the primitive endoderm, but differs in being solid and unsegmented.*

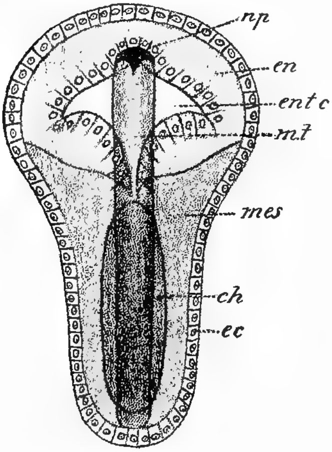

Fig. 100. — Embryo of *Clavelina Rissoana* seen from above, to show the relation of parts. (Simplified after VAN BENEDEN and JULIN.)

np. Neuropore. *en.* Endoderm. *ent.c.* Enteric cavity. *m.t.* Medullary tube. *mes.* Mesodermic band. *ch.* Notochord. *ec.* Ectoderm.

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* For a recent and elaborate discussion of the origin of the mesoderm in the Ascidians see VON DAVIDOFF'S *Untersuchungen zur Entwicklungsgeschichte der Distaplia magnilarva, etc., II. Allgemeine Entw. der Keimblätter.* Mitth. Zool. Stat. Neapel, IX. 1891. pp. 533–651.

As shown by van Beneden and Julin in *Clavelina*, the primary mesoderm of the Ascidian embryo can be detected at a much earlier stage of development than in Amphioxus.

I have studied the origin of the mesoderm in *Cynthia papillosa* and found that the primary mesoderm cells are to be distinguished, by their poverty in food-yolk, from the remaining endoderm, at the commencement of gastrulation (at the so-called *plakula-stage*). They occur in the form of a crescent round the posterior margin of the blastopore, and are carried in by the invagination, and then increase in number by mitotic division. In Cynthia, these

We thus have two solid longitudinal mesodermic bands inserted between the ectoderm and endoderm. Anteriorly the mesodermic bands consist of several layers of cells superimposed one above the other (Fig. 98), but farther back they consist of only one layer of cells. Both portions of the mesoderm—namely, the anterior two- or three-layered and the posterior one-layered portions—arise in continuity with one another, but they have different fates, the former eventually breaking up into loose cells which float about in the body-cavity and constitute the so-called *mesenchyme*, the latter, on the other hand, becoming converted into the musculature of the tail; whence the former is spoken of as the *gastral* and the latter as the *caudal mesoderm.*

Outgrowth of Tail.

In Amphioxus, at the stage corresponding to that of which we have been speaking—namely, when the embryo has an oval or sub-elliptical shape—it bursts through the vitelline membrane inside which it has already been rotating for some time by means of the cilia of the ectoderm, and escapes into the open sea. This is not the case, however, with the Ascidian embryo. The latter is never ciliated externally, and it remains enclosed within the follicular membrane throughout the whole of the *embryonic* period of development.

After the stage in question, the growth in the length of the embryo is accompanied by a *ventral curvature*, owing to the confined space in which it is contained. Moreover, the increase in length is not due to a simple elongation of the entire body of the embryo, as is the case with Amphi-

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primary mesoderm cells appear to give rise almost exclusively to the *caudal mesoderm*, while the *gastral mesoderm* appears to be added in front by proliferation from the primitive endoderm as described above.

oxus, but it is merely due to the outgrowth of the tail from the body of the embryo (Fig. 101).

The structures involved in the outgrowing tail are the dorsal nerve-tube, the notochord, the caudal mesoderm, which lies on each side of the notochord, and will give rise to the muscles of the tail, and finally a solid cord of endoderm consisting of two rows of cells placed side by side below the notochord (Fig. 99 *B*). As soon as the tail begins to grow out, the neurenteric canal becomes obliterated, and shortly afterwards the anterior neuropore closes up temporarily. At a later period, as we shall see, it reopens; not, however, to the exterior, but into the buccal tube.

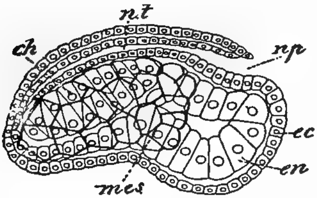

Fig. 101. — Embryo of *Phallusia mammillata* in side view, to show commencing outgrowth of tail. (After Kowalevsky.)

ch. Notochord. *ec.* Ectoderm. *en.* Endoderm. *mes.* Mesoderm; the cells indicated by dark outlines, beneath which may be seen the notochord and caudal endoderm. *n.p.* Neuropore. *n.t.* Medullary tube.

As the tail grows in length, it becomes coiled round about the body of the embryo, attaining two or three times the length of the latter.

The cord of endoderm cells in the tail of the Ascidian larva has been supposed to represent a rudimentary intestine homologous with the straight intestine of Amphioxus, the larval tail being on this view equivalent to the post-branchial portion of the trunk in Amphioxus. This view, however, is probably not correct, although there is something to be said in favour of it. The probability is that the tail of the Ascidian larva or tadpole, as it is often called, is an organ which has been specially elaborated in the course of its evolution for the particular benefit of the Ascidians, since (exclusive of the pelagic forms) it is their sole organ of locomotion, and hence of transportation from place to place; this only being possible during the larval period.

As a rule, the larval phase of an Ascidian's existence is a remarkably brief one, and there is on this account all the more need for an effective propelling organ, which will enable the larva to arrive at a suitable resting-place.

In Amphioxus, as described above, locomotion is effected by serpentine movements of the whole trunk in virtue of its muscle-segments, and there is therefore no need for a tail in addition; but there is, nevertheless, a short post-anal extension of the body, which alone can be regarded as the homologue of the tail of the Ascidian larva. In the latter (*e.g.* Ciona, Phallusia, etc.) the muscles are entirely confined to the tail, none being formed in the body proper, until after the resorption of its caudal appendage.

On the view which I am endeavouring to make clear, it follows that the tail of the Tunicate tadpole is of the same nature as that of the Amphibian tadpole, and, in fact, of the craniate Vertebrates generally, and, as has just been said, is only represented by the short post-anal section of the trunk in Amphioxus.

The solid cord of endoderm in the tail is not, therefore, a rudiment of a primitive intestine, but it is analogous to, even if not, as first suggested by BALFOUR, homologous with, the so-called *post-anal gut* which occurs in the embryos of the higher Vertebrates, and bears a similar relation to the formation of the tail that the endoderm-cord in the Ascidian embryo does.

Thus in the typical Ascidian embryo the elongation of the trunk (body proper) does not take place to any considerable extent during the embryonic or even larval period, but only after the metamorphosis.

With the formation of the tail the enteric cavity becomes confined as a closed sac to the anterior portion of the embryo. It is bounded dorsally by the nerve-tube, which is somewhat dilated in this region, and in front, at the sides and below, it is in close contiguity with the ectoderm.

Formation of the Adhesive Papillæ.

At a much later stage than that represented in Fig. 101, the ectoderm bounding the convex anterior extremity of the body becomes raised up into three prominences, whose relations to one another are those of the corners of a triangle. They are due to the ectodermic cells at the respective points assuming a high columnar shape. They become eventually raised very much above the adjoining surface of the ectoderm, and become the *adhesive papillæ* or *fixing glands* of the larva. The cells composing them acquire the power of secreting a viscid substance, by which the larva can fix itself to any favourable surface (Fig. 102).

Cerebral Vesicle and its Sense-organs.

We have spoken above of the dilated anterior portion of the nerve-tube. This is the part of the central nervous system which undergoes the most striking subsequent changes. By a gradual widening of its cavity, accompanied by a local thinning out of its wall, this portion of the neural tube lying in front of the notochord becomes transformed into a spacious sub-spherical vesicle, known as the *cerebral vesicle* (Fig. 102).

While the anterior portion of the neural tube is enlarging to form the cerebral vesicle, granules of black pigment are deposited by certain cells in the dorsal wall of the vesicle. The granules are at first scattered about in the interior of the cells. The most anterior of the cells containing the pigment is at first distinguished from the others solely on account of the fact that the pigment-granules which it contains are somewhat larger than those in the succeeding cells. (Cf. Fig. 103.)

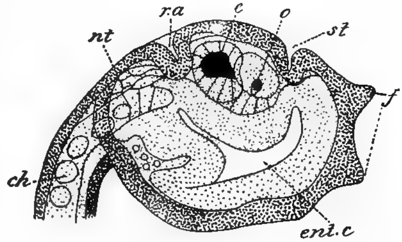

Fig. 102. — Embryo of *Ascidia mentula* shortly before hatching; from the right side. (After WILLEY.)
ch. Notochord, undergoing vacuolisation. *e.* Eye. *ent.c.* Enteric cavity. *f.* Adhesive papillæ. *nt.* Anterior portion of nerve-tube (spinal cord). *o.* Otocyst, lying on the floor of the cerebral vesicle and projecting up freely into its cavity. *r.a.* Right atrial involution. *st.* Stomodœum.

Later on, however, the first pigmented cell is seen to separate itself from the others, and it becomes gradually transferred by a differential growth of the wall of the vesicle down the right wall to its final position in the ventral wall of the vesicle (Figs. 102, 103). This cell is the *otocyst*, and the pigment-granules become consolidated together to form the *otolith.* The latter is apparently extruded from the cell (otocyst) in which it was originally formed, and the latter assumes a cup-shape, in the hollow of which the otolith lies. The two structures together form the so-called auditory organ, whose function may be not so much of an auditory nature as that of an equilibrating apparatus.

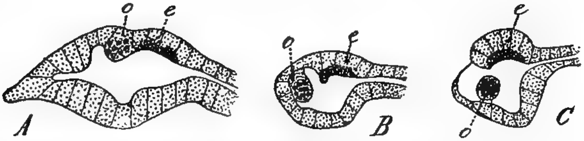

Fig. 103. — Optical sections through cerebral vesicle of embryos of *Ascidia mentula*, to show mode of origin of eye and otocyst. (After WILLEY.)
e. Eye. *o.* Otocyst.

The other pigment-cells of the dorsal wall of the cerebral vesicle collect themselves together and form a slight protuberance in the right dorso-lateral corner of the vesicle, while the pigment-granules, which were at first scattered about in the interior of the cells, become concentrated at their converging extremities towards the cavity of the vesicle. And in this way is formed the single *eye* of the Ascidian tadpole; the original pigment-producing cells constitute the *retina*, which retains its primitive position as part of the epithelial wall of the brain.*

Subsequently two or three cells from the adjoining wall of the vesicle take up a position, one above the other, in front of the mass of pigment and, having previously, by an alteration in the character of their protoplasmic contents, acquired a high refractive index, constitute the *lens* of the eye, which projects obliquely downwards into the cavity of the vesicle. (Cf. Fig. 105 *A*.)

The cerebral vesicle of the Ascidian tadpole is the undoubted homologue of the corresponding, but less pronounced, structure in Amphioxus. It differs from the latter in lying wholly in front of the anterior extremity of the notochord, in possessing a more highly organised eye, provided with a cellular lens, and in the presence of an otocyst, which, as we have seen, is evolved from the same group of cells which gave rise to the eye.

The eye of the Tunicate tadpole agrees fundamentally with the type of eye peculiar to the Vertebrates, in that the retina is derived from the wall of the brain. On this

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* The fact that the lens of the Tunicate eye as well as the retina and the otocyst arise by differentiation of one and the same epithelial layer of the primitive cerebral vesicle, has recently been described by SALENSKY for the larva of Distaplia, magnilarva. (W. SALENSKY. *Morphologische Studien an Tunicaten: I. Ueber das Nervensystem der Larven u. Embryonen von Distaplia magnilarva.* Morph. Jahrb. XX. 1893. pp. 48–74.)

account it is called a *myelonic eye.* In the typical Invertebrate eye, on the contrary, the retinal cells are differentiated from the external ectoderm.

Comparison of Tunicate Eye with the Pineal Eye.

The Tunicate eye, however, differs essentially from the paired eyes of the craniate Vertebrates in that the lens, as well as the retina, is derived from the wall of the brain. The lens of the lateral eye of the Vertebrates is derived by an invagination of the external ectoderm, which meets and fits in with the retinal cup at the end of the optic vesicle.

It is, therefore, an extremely interesting fact which was pointed out by BALDWIN SPENCER, that the Tunicate eye agrees, in respect of the origin of its lens, with the *parietal* or *pineal* eye of the Lacertilia, in which the lens is likewise derived from cells which form part of the wall of the cerebral outgrowth which gives rise to the pineal body.

The pineal body is another of those remarkable rudimentary structures whose constant presence in all groups of Vertebrates forms such an eminently characteristic feature of their organisation. It develops as a hollow median outgrowth from the dorsal wall of the brain (thalamencephalon), the distal extremity of which dilates into a vesicle and becomes separated from the proximal portion.*

For a long time the pineal body was a persistent enigma

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* According to the most recent work on the subject the distal vesicle becomes entirely constricted off from the primary epiphysial (pineal) outgrowth of the brain, and the parietal nerve does not represent the primitive connexion of the pineal eye with the roof of the brain, but it arises quite independently of the proximal portion of the epiphysis.

See A. KLINCKOWSTRÖM, *Beiträge zur Kenntniss des Parietalauges.* Zoologische Jahrbücher (Anat. Abth.), VII. 1893. pp. 249–280.

and the subject of much speculation, one of the most celebrated hypotheses with regard to its significance being that of Descartes, who regarded it as the seat of the soul.

More recently it has been shown to represent a rudimentary, unpaired eye. Although in most cases, curiously enough, it exhibits in existing forms no trace of an eye-structure, it has been shown by de Graaf and Spencer that, as a matter of fact, in many lizards the distal vesicle does actually become converted into an eye which, though of a rudimentary character, is possessed of a retina, pigment, and lens. In these forms the pineal body pierces the roof of the cranium, occasioning the parietal foramen, which is so characteristic of the Lacertilian skull, and the pineal eye lies outside the cranium immediately below the skin, through which it can be distinguished in external view by the presence of a modified scale placed above it.

In the animals below the lizards in the scale of organisation (Amphibians and Fishes), as well as in those above them, the distal vesicle of the pineal body apparently does not become so far differentiated as to be recognised as an actual eye, except in the case of the Cyclostome fishes, where, as shown by Beard, it presents the three essential elements of an eye; namely, retina, pigment, and lens, lying, however, inside the cartilaginous cranium.

The facts in our possession would seem to indicate that the remote ancestors of the Vertebrates possessed a median, unpaired, myelonic eye, which was subsequently replaced in function by the evolution of the paired eyes. It would, however, be premature either to assert this or to express it as a definite opinion, especially since, in referring to the evolution of the paired eyes of Vertebrates, we are bordering on ground upon which I have no immediate intention of treading. The pineal eye may not have been primitively so much an organ of vision as a light-perceiving organ, as is no doubt the case with the eye of the Tunicate tadpole.

We may at least conclude that there can be no doubt that the Tunicate eye is the functional homologue of the pineal eye of the higher Vertebrates, as Spencer suggested.

Stomodæal and Atrial Involutions.

By the time that the cerebral vesicle of the Ascidian embryo with its contained sense-organs (eye and otocyst) is approaching the completion of its full development, no less than three ectodermic invaginations occur in the body of the embryo. One of these is situated immediately in front of and in contact with the anterior wall of the cerebral vesicle, the blind end of the involution pressing against the subjacent endoderm. This is the *stomodæum*, and its formation is preliminary to the perforation of the mouth which takes place later, and places the stomodœum in open communication with the portion of the enteric cavity which will become the branchial sac (Fig. 102). It should be emphatically noted that the stomodœal invagination occurs in the dorsal middle line immediately adjacent to the anterior extremity of the central nervous system.

The other two ectodermic invaginations occur symmetrically, one to the right and the other to the left of the dorsal middle line, behind the region of the cerebral vesicle, and constitute the pair of *atrial involutions*, which, by their subsequent growth and modification, give rise to the atrial or peribranchial cavity. We see, therefore, that the epithelium which forms the lining membrane of this cavity is, as in Amphioxus, derived from the external ectoderm.

For some considerable time after the metamorphosis the young Ascidian possesses two separate atrial cavities, right and left, each opening to the exterior by its own atrial aperture. Eventually the two cavities extend round the branchial sac dorsally, so that their walls come into contact in the dorsal middle line, and finally the dividing line breaks down, and they become continuous one with another dorsally, remaining separated ventrally, as described above.

At the same time that the two atrial cavities grow towards one another, their external apertures become involved in the same process of growth, and, moving together, finally fuse in the dorsal middle line, and so form the single atrial or cloacal aperture of the adult.*

Beyond agreeing in its ectodermal origin, there might appear to be not much in common between the mode of development of the atrial cavity in the Ascidians and in Amphioxus.

No morphologist would recognise a fundamental difference in the fact that the right and left halves of the atrial cavity in Amphioxus arise by a single median involution of the ectoderm, instead of from a pair of involutions, and that they are from the first continuous with one another instead of becoming so secondarily (Fig. 104).

In like manner, the fact that the two halves of the atrial cavity are continuous with one another ventrally in Amphioxus and dorsally in the Ascidians, is easily brought into correlation with the other differences in the organisation of the two types, which have been described above, and is no bar to our regarding the atrial cavity of the one as being homologous with that of the other.

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* The time at which the atrial cavities fuse together varies very much in different genera. In *Molgula manhattensis*, for instance, whose stigmata develop on a similar plan to those of Ciona (see below), there is a single atrial aperture at the moment of the metamorphosis.

One feature in connexion with the formation of the atrial cavity, in which the Ascidians stand in marked contrast to Amphioxus, does, however, require a special explanation.

Whereas in Amphioxus the atrial involution has the form of a *longitudinal groove*, in the Ascidians it occurs on each side, as a local inpushing of the ectoderm with a minute circular orifice of invagination.[2]

The fact has already been stated above that the elongation of the body proper of an Ascidian embryo or larva does not, in the main, take place until after the metamorphosis.

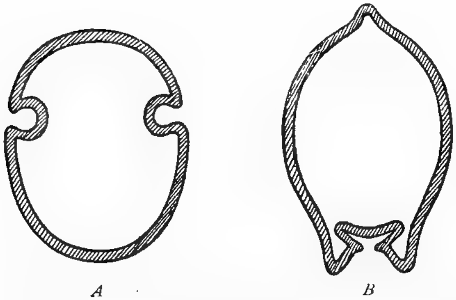

Fig. 104. — Diagrammatic transverse sections, to illustrate the mode of formation of the atrium in (*A*) an Ascidian and (*B*) Amphioxus. (After WILLEY.)

The atrial involutions occur at a time when the tail is rapidly increasing its length; the body proper, on the contrary, remaining stationary so far as increase in size is concerned, and retaining at this stage approximately the dimensions which it possessed when the tail first began to grow out. Moreover, they occur *before* the appearance of any gill-clefts in the wall of the branchial sac, so that in the Ascidians the gill-slits never open directly to the exterior.

In Amphioxus, on the other hand, there is no such delay in the elongation of the body of the embryo, but it goes on continuously till the full complement of myotomes has been formed. The post-anal portion of the body, which we suppose to be the homologue of the tail of the Ascidian tadpole, does not appear until a somewhat late period in the development. There is very little of it present in the larva with three gill-slits (Fig. 73).

The reason of this, as explained above, is that the post-anal section of the trunk is of only minor functional significance in Amphioxus, but is all-important to the Ascidian larva, and consequently, as is the case with many other structures of great functional importance in the various groups of the animal kingdom, it exhibits a *precocious* development.

Not only, therefore, has the elongation of the body of Amphioxus already taken place before the occurrence of the atrial involution, but the primary gill-slits have also broken through the wall of the pharynx, and open freely to the exterior before the atrium begins to be closed in.

In Amphioxus, then, the atrial involution has been drawn out into the form of a longitudinal groove because it occurs subsequently to the elongation of the body and the perforation of the gill-slits.

In the Ascidian embryo the (paired) atrial involution has the form of a simple pit with a circular margin, because it arises before the elongation of the body proper of the embryo and before the perforation of the gill-clefts, so that no influence has been at work to draw it out into the form of a groove.

We see, therefore, that a great many of the differences between the Ascidian tadpole and the larva of Amphioxus can be explained sufficiently to allow of their being brought into genetic relation with one another, by considering the relative time at which corresponding developmental processes take place in the two cases.

The following table will help to make this matter clearer.

ORDER OF OCCURRENCE.	ASCIDIAN.	AMPHIOXUS.
1.	Gastrulation.	Gastrulation.
2.	Oval embryo with medullary tube, neurenteric canal, notochord, and mesoblast. (Last two commencing.)	Oval embryo with medullary tube, neurenteric canal, notochord, and mesoblast. (Last two commencing.)
3.	Outgrowth of tail.	Commencing elongation of body of embryo, and escape from vitelline membrane.
4.	Continued growth of tail.	Continued elongation of embryo.
5.	Formation of stomodœum and atrial involutions.	Formation of mouth, and commencing perforation of gill-clefts.
6.	Escape from vitelline membrane.	Continued formation of gill-clefts and outgrowth of tail (*i.e.* post-anal section of trunk).
7.	Commencing perforation of gill-clefts.	Formation of longitudinal atrial involution.
8.	Metamorphosis and commencing elongation of body proper.	Metamorphosis.

Of course the above table has no concern with the actual time (hours and days) from the commencement of the development at which such and such an event occurs. The type of Ascidian referred to in the above description is a simple Ascidian like *Ciona* or *Phallusia.*

The above table also shows how the development of the Ascidian and of Amphioxus moves along parallel lines up to a certain point, and then at the time of the outgrowth of the tail in the embryo of the former and the hatching of the embryo of the latter, divergences set in.

It has long been recognised that the development of an Ascidian is much abbreviated in comparison with that of Amphioxus, since in the former it neither comes to the formation of a ciliated embryo nor to the production of archenteric pouches for the mesoderm. One of the chief evidences, however, of abbreviation in the Ascidian development is the precocious formation of the larval tail.

Formation of Alimentary Canal and Hatching of Larva.

When the enteric cavity of the Ascidian embryo begins to grow in length so as to give rise to the stomach and intestine, which it does shortly after the appearance of the atrial involutions, there is only one resource open to it on account of the limited space in which it lies, and that is to double round upon itself. This it accordingly does. As the growth progresses, the posterior dorsal angle of the enteric cavity bends sharply downwards on the right side, and then upwards and slightly forwards on the left side, ending at first blindly in the vicinity of the left atrial sac. In this way the four divisions of the alimentary canal become established; namely, pharynx or branchial sac, œsophagus, stomach, and intestine. (Cf. Fig. 105.)

By the time these changes have taken place, the embryonic development is at an end, and the larva is ready to hatch. By spasmodic jerkings of its tail, the larva finally succeeds in bursting the egg-follicle or vitelline membrane in which it has been hitherto enclosed, and so escapes into the open sea.

Clavelina and Ciona.

While the development of most forms of Tunicata is reducible to a common type, yet the details vary within very wide limits in different genera. The tendency here, as elsewhere, is to abbreviate the development by omitting certain ontogenetic processes, and so arriving at the desired end, as it were, by a short cut.

One of the most impressive instances of such an abbreviated development, and one which can be demonstrated with the utmost certainty, is afforded by the genus *Clavelina*, in contrasting it with the closely allied genus *Ciona.*

Clavelina (see Fig. 96) is an Ascidian, provided at its base with creeping processes or stolons containing a lumen continuous with the body-cavity, by which it adheres to rocks and weeds. Buds are formed from the stolon, which grow up into new individuals precisely like the parent form which developed from the egg, and so a colony is produced.

Ciona also has similar basal processes of the test, containing prolongations of the original body-cavity, but no buds are produced.

In Clavelina, the embryonic development, up to the time of the hatching of the larva, takes place inside the peribranchial chamber of the parent, which becomes converted into a kind of *brood-pouch.*

In Ciona, the eggs are extruded into the water, where they are fertilised by the simultaneous extrusion of spermatozoa from the same individual. Finally, in Clavelina the egg is much larger and contains more food-yolk than that of Ciona.

We see, therefore, that in these two genera the egg is at the outset subjected to different sets of conditions, both internally and externally.

METAMORPHOSIS OF CIONA INTESTINALIS.

Three stages in the metamorphosis of the larva of *Ciona intestinalis* are shown in Fig. 105. First, there is the free-swimming larva, which, after a pelagic existence of one or perhaps two days' duration, is on the point of fixing itself to a foreign object by means of the sticky secretion of its three adhering papillæ.

This larva possesses features which we have not yet considered. Let us give our attention in the first place to the tail.

Vacuolisation of the Notochord.

The vacuolisation of the notochordal tissue, which was described above for Amphioxus, has already proceeded to such an extent that there is no longer any trace of cellular structure in the centre of the notochord. It is entirely filled with a perfectly colourless substance, probably of gelatinous consistency, while the nuclei have been displaced entirely from the centre and can be seen to lie closely pressed against the dorsal and ventral sides of the sheathing membrane of the notochord (Fig. 105 *A*).

There is one respect in which the above vacuolisation of the cells of the notochord differs considerably from the corresponding process in Amphioxus and the higher Vertebrates.

Whereas in the latter forms the vacuoles appear inside the individual cells, — in other words, are *intracellular*, — in the Ascidian tadpole they occur between the cells, and are therefore *intercellular*. This was first made out by Kowalevsky, and can readily be observed. (Cf. Fig. 102.) The intercellular spaces separate the cells which were previously fitted accurately together, end to end, and, gradually increasing in size, they eventually flow together and so constitute a continuous space, while the cells with their nuclei become thrust aside.

Assuming that the vacuoles contain a more or less fluid substance secreted by the protoplasm of the cells, the above difference in the vacuolisation of the notochordal tissue in Amphioxus and the Ascidian larva would resolve itself into saying that the secretion was retained inside the cells in the one case, and deposited outside them in the other.

Mesenchyme and Body-cavity.

The endoderm cells of the tail, which formed at first a solid cord below the notochord, have now become converted into loose corpuscles, which have mostly floated out of the tail into the hinder portion of the body-cavity, and have become indistinguishable from the mesoderm-cells. The latter are beginning to lose their compact disposition in the form of the two mesodermic bands, especially in the hinder region, and to be scattered about in the body-cavity.

The body-cavity of the young Ascidian is not unreservedly homologous with that of Amphioxus, on account of this remarkable behaviour of the mesoderm. The cavity does not arise in the midst of the mesoderm by a splitting apart of its component cells, but it is simply produced by a separation of the endoderm from the ectoderm, the two layers being at first in contact at the sides and below; in fact, everywhere, except where the dorsal nerve-tube intervenes.

In the cavity thus produced between ectoderm and endoderm the mesodermic bands at first lie freely, and then their component cells break away from their compact association and float about the cavity in the form of scattered corpuscles, known collectively as *mesenchyme.*

This mesenchyme later gives origin to the musculature of the body proper of the Ascidian, and also to the definitive blood-corpuscles, genital organs, and renal vesicles.* All these structures are differentiated from the loose mesenchyme cells, all of which at first course round about the body of the young Ascidian like blood, being kept in motion by the beating of the heart.

In the stage shown in Fig. 105 *A* the mesodermic bands are still fairly compact in front, having extended themselves anteriorly at the sides of the enteron by interstitial growth.

Præoral Body-cavity and Præoral Lobe.

When the larva first hatches, the endoderm and ectoderm are in contact with one another at the anterior extremity of the body, just as they are in the earlier stages. (Cf. Fig. 102.) Soon, however, the ectoderm, with the adhering papillæ, springs away from the endoderm at this point, leaving a space into which the two lateral mesodermic bands force their way.

In this way a special anterior portion of the body-cavity, præoral and præenteric, is produced, and is at first completely filled by a compact mass of rounded cells derived from the mesodermic bands.

The end of the body of the larva at which the adhering papillæ are placed of course corresponds to the tip of the snout in Amphioxus.

Just as Amphioxus burrows into the sand with its snout, so the Ascidian larva fixes itself to the surface of a rock or weed by its snout. The anterior or præoral portion of the body-cavity, of which we have just traced the origin, is, and subsequently becomes in a still more pronounced way, the *cavity of the snout*, or *præoral lobe.*

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* The pericardium arises ventrally from the endodermic wall of the branchial sac, and the heart is formed by an infolding of the dorsal wall of the pericardium.

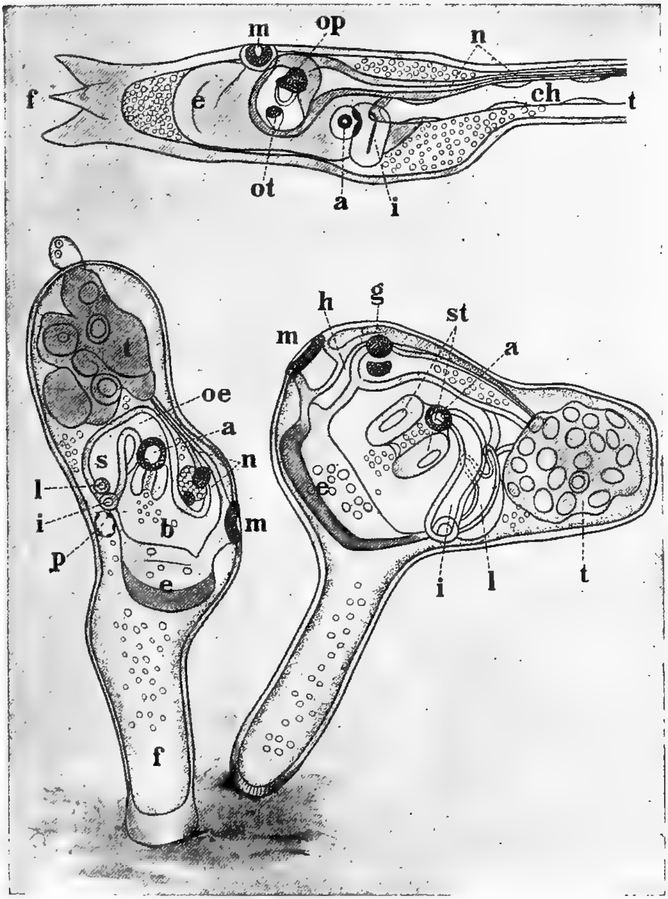

Fig. 105. — Metamorphosis of *Ciona intestinalis;* above is represented the anterior portion of the free-swimming larva from the left side; on the left, the larva, shortly after fixation, from the right side; and on the right, the stage at which the change of axis commences, from the left side. (After WILLEY.)

a. Atrial aperture. *b.* Branchial sac. *ch.* Notochord. *e.* Endostyle. *f.* Organ of fixation. *g.* Ganglion. *h.* Neuropore (having reopened into branchial sac). *i.* Intestine. *l.* Pyloric gland. *m.* Mouth. *n.* Nerve-tube. *oe.* Œsophagus. *op.* Eye. *ot.* Otocyst. *p.* Pericardium. *s.* Stomach. *st.* Stigmata. *t.* Tail.

Body-cavity of an Ascidian and Cœlom of Amphioxus.

We must now endeavour to show how the body-cavity of the Ascidian can be brought into genetic relationship with the cœlom of Amphioxus. The question of the absence of metamerism in connexion with the origin of mesoblast in the Ascidians need not detain us, since it is so obviously correlated with their mode of life. It may safely be asserted that the Ascidian mesoderm, as a whole, is homologous with that of Amphioxus as a whole, but in the details of its origin and fate it is widely different.

If we figure to ourselves the cœlomic epithelium of Amphioxus losing its character as a membrane and breaking up into its constituent cells, which would then lie loosely in the body-cavity, we should have essentially the same condition of things as in the Ascidians. There are numerous precedents in the animal kingdom for such a disintegration of an epithelial membrane.

A most perfect instance of it has been described by Dr. R. von Erlanger* in connexion with the origin of the mesoderm in the fresh-water snail, *Paludina vivipara.* Here the mesoderm appears at first in the form of a median bilobed archenteric pouch of relatively large dimensions. Soon, however, the cells forming the wall of the pouch begin to assume irregular shapes, and so disturb the contour of the epithelium, and eventually they break apart entirely and fill every nook and corner of the available space with a loose *mesenchyme.* Similar out-wanderings of cells from an epithelial wall, though not often of such a complete character as the instance above cited, are by no means infrequent.

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* *Zur Entwicklung der Paludina vivipara.* Parts I. and II. Morphologisches Jahrbuch, XVII. 1891.

A striking example is afforded by the body-cavity of the worm-like *Balanoglossus*, of which we shall speak later.

Here, according to BATESON, the cells lining the cavity are continually budding off daughter-cells, which fall into the cavity, and eventually almost entirely fill it up with *mesenchymatous tissue.* In this case, therefore, mesenchyme and an epithelial wall coexist.

Similarly, the *epithelial sclerotome* of Amphioxus is represented by a *mesenchymatous sclerotome* in the higher Vertebrates. It is not necessary to multiply instances, but many others could be adduced.

If, now, this disintegration of *parietal* and *visceral* layers of the mesoderm, which we have imagined above to take place in the ontogeny of an animal like Amphioxus, be supposed to be thrown back in the development, or, in other words, abbreviated to such an extent that the preliminary formation of a continuous cœlomic epithelium no longer takes place, we should have precisely those conditions which we actually find in existing Ascidians.

As in the cases above quoted for purposes of illustration, so in the Ascidians the *mesenchymatous* condition undoubtedly originated ancestrally from what we may call an epithelial condition.

In the Ascidians we may conclude, therefore, that while ontogenetically the mesenchymatous condition is to all intents and purposes primary, from a phylogenetic point of view it is pre-eminently secondary or cenogenetic.

Having made the reservations implied in the above statements, we may confidently assert that as a whole the body-cavity of the Ascidians is homologous with the cœlom of Amphioxus, and we may define the former as a cœlom in which the cells, instead of associating together to form a lining membrane round the cavity, remain independent of one another and scattered about inside the cavity.

Fixation of the Ascidian Larva.

When the larva first fixes itself to some available surface, the tail remains for a time stretched straight out and almost motionless, giving perhaps an occasional twitch. Soon the tail is observed to become shorter and to finally disappear, having been drawn within the body proper of the young Ascidian. The entire tail, with the whole of the notochord, musculature, and caudal portion of nerve-tube, becomes thus retracted and invaginated into the posterior region of the body-cavity, where it forms a coiled amorphous mass, which goes through a gradual series of histolytic changes, and is finally absorbed by being dissolved in the fluid of the body-cavity (Fig. 105 *B*).

By the time the tail has been completely drawn up into the body, the organ of fixation or snout, as we have called it above, becomes drawn out into a long probosciform structure in a line with the long axis of the body. Its cavity is no longer completely filled with mesoderm-cells as it was at first (Fig. 105 *A*), but it has become so voluminous that its contained cells are loosely scattered about (Fig. 105 *B*). In the concluding chapter we shall endeavour to show, what has been already implied, namely, that the organ of fixation is seen to the best possible advantage from a morphological point of view in the species now under consideration, viz. *Ciona intestinalis*, and that it is homologous with the præoral lobe (snout) of Amphioxus, including under that term both the præoral body-cavity and the præoral pit, and further that it is homologous with the proboscis of Balanoglossus.

At the stage shown in Fig. 105 *A*, the lumen of the alimentary canal is extremely reduced, and in many places, as in the region of the endostyle, *e*, its opposite walls are in actual apposition, so that the lumen at these points is almost obliterated.

This temporary reduction of the lumen of the alimentary canal is due to the narrow space into which it has to be compressed, combined above all with the relatively enormous size of the cerebral vesicle, which exercises a great pressure on the subjacent dorsal wall of the branchial sac. It may be added that the larva of Ciona does not take in food independently until after fixation.

Reopening of Neuropore; Degeneration of Cerebral Vesicle; Formation of Definitive Ganglion.

One of the most obvious features of the metamorphosis is the rapid expansion undergone by the enteric and body cavities and the no less rapid degeneration of the cerebral vesicle. This expansion, by relieving the crowded character of the various parts, facilitates greatly the study of the changes which take place in the internal organisation.

The neuropore, which we have described above as having closed up at an early period, now reopens again and places the neural tube — that is to say, as much of it as remains after the atrophy of the tail — in open communication with the base of the buccal tube (Fig. 105 *B*, *n*).

The spacious cavity of the cerebral vesicle has vanished, and its walls have undergone disintegration, and, except for a portion of the dorsal wall which becomes converted into another channel, are now represented by a mass of histolytic residua filling the original cavity of the vesicle and lying below the anterior portion of the nerve-tube.

This remnant of the cerebral vesicle of the larva with its sense-organs becomes eventually absorbed, and the eye and otolith may often be found floating about the body-cavity with the ordinary mesenchyme-cells, and occasionally they can be seen actually passing through the heart.

The anterior portion of the nerve-tube itself, which now opens into the base of the buccal tube or stomodœum,* is derived from a portion of the dorsal wall of the original cerebral vesicle which was constricted off from the latter in the form of a narrow tube slightly to the left of the mid-dorsal line (Fig. 105 *B*, *n*).

Subsequently the cells forming the dorsal wall of this portion of the nerve-tube proliferate and form a solid thickening which becomes the definitive ganglion of the adult (Figs. 105 *C*, 106, and 107, *g*).

The lumen of the nerve-tube behind the region of the definitive ganglion finally becomes obliterated by the mutual approximation of its constituent cells, and that portion of the primitive nerve-tube which in the larva lay between the cerebral vesicle and the root of the tail is thus represented in the adult by a solid "*cordon ganglionnaire viscéral*" (van Beneden and Julin) which starts from the posterior end of the adult cerebral ganglion, and, proceeding along the dorsal side of the pharynx above the dorsal lamina, becomes lost among the viscera. (Cf. Figs. 96, 105, and 107.)

Below and in front of the definitive ganglion, which finally becomes quite separate from the dorsal wall of the neural tube, the lumen of the latter persists and becomes

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* According to renewed observations on Ciona, I find that the neuropore reopens into the buccal tube precisely in the line of junction of the stomodœum with the wall of the branchial sac, so that its upper margin is continuous with the (ectodermic) stomodœal epithelium, and its lower margin with the (endodermic) branchial epithelium. (See below, V.)

by subsequent extension the lumen of the subneural gland and its duct.

Thus the anterior portion of the primitive neural tube, having become constricted off from the cerebral vesicle of the larva, and having given rise by proliferation from its dorsal wall to the definitive ganglion, becomes bodily converted into that structure which we shall call, in agreement with JULIN, the *hypophysis.*

The opening of the latter into the base of the buccal tube becomes the *dorsal tubercle* of the adult. Finally, at a much later stage, the glandular portion of the hypophysis arises by proliferation of spongy tissue from the ventral wall of that portion of the *neuro-hypophysial* tube which lies immediately below the ganglion.

A section through the cerebral vesicle of a larva of *Distaplia,* a colony-building Ascidian, showing the hypophysis in process of being constricted off from the vesicle, is given in Fig. 106. In this genus the condition of things generally is very different from what obtains in Ciona, but it is introduced to show the essential similarity in the mode of origin of the hypophysis in this form, as observed by Dr. JOHAN HJORT.

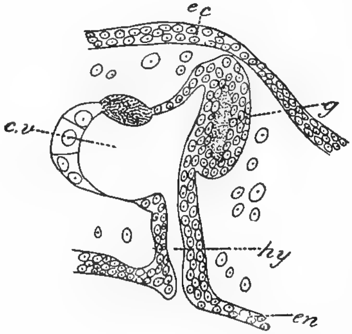

Fig. 106. — Frontal section through cerebral vesicle of a larva of *Distaplia magnilarva,* to show the origin of the ganglion and hypophysis. (After HJORT; combination of two figures.)

In the larva of Distaplia, the hypophysis opens into the branchial sac behind the stomodœum.

c.v. Cerebral vesicle. *ec.* Ectoderm. *en.* Endoderm. *g.* Ganglion. *hy.* Hypophysis (neuro-hypophysial tube).

In *Distaplia,* as is also the case to a less extent in *Clavelina,* the ganglion begins to develop from the wall of the neuro-hypophysial tube while the latter is still in connexion with, and therefore before the atrophy of, the cerebral vesicle, thus indicating a hastening in the development as compared with *Ciona.*

The convexity caused in the dorsal wall of the branchial sac by the pressure of the cerebral vesicle persists as the anterior portion of the dorsal lamina, and in many or most simple Ascidians becomes grooved, forming the *epibranchial groove* of JULIN (Fig. 97). At present it is merely a ridge, the *epibranchial ridge.*

In Fig. 105 *C* the proximal (oral) end of the endostyle, *e*, is seen to be connected with the epibranchial ridge by the *peripharyngeal band*, which we have already described in the adult. It apparently arises *in situ* by simple specialisation of the cells forming the epithelial wall of the pharynx at this point.

Primary Topographical Relations and Change of Axis.

It must be especially noted that the long axis of the young Ciona for some time after fixation is identical with that of the tailed larva, and therefore the primary topographical relations of the various parts are maintained at the stage shown in Fig. 105 *B*, and we can accordingly make use of this stage in which different structures are much clearer than in the free-swimming larva for the purpose of describing the primary topography, which is of the utmost importance when it is desired to institute a comparison with Amphioxus.

Since, as we have seen, the details of the embryogenetic processes differ in many respects widely from what occurs in Amphioxus, we are inevitably compelled to rely to a very large extent on topographical relations in order to estimate the homology of this or that structure in the

Ascidians and in Amphioxus. Fortunately there is one structure as to whose complete homology, in the Urochorda (Tunicata), on the one hand, and the Cephalochorda, on the other, no one entertains a doubt, and that is the *endostyle.* We thus have in the endostyle a firm basis upon which to ground our deductions.

In the larva and in the young Ascidian before the primary long axis has been disturbed in the way which we shall shortly describe, the endostyle is the most anterior endodermic structure in the body, and lies dorso-ventrally at right angles to the long axis of the body (Fig. 105 *A* and *B*, *e*).

As described above in the larvæ of Amphioxus, particularly in the younger larvæ (see Figs. 64 and 73), the endostyle, though lying asymmetrically on the right side, being involved in the general asymmetry of the larva, is quite anterior in position, in front of all the gill-slits and partly in front of, though also partly opposite, the mouth (on account of its asymmetry), and almost at right angles (see especially Fig. 64) to the long axis of the body. As there is only a short stretch of simple endoderm in front of the endostyle in the larva of Amphioxus, we may describe it as the most anterior differentiated endodermic structure in the larva, thus corresponding with remarkable precision to the condition described above in the larval and newly fixed Ascidian.

In the middle of the wall of the branchial sac in Fig. 105 *B* are seen, somewhat in front of and below the atrial aperture, *a*, of this side, two lens-shaped structures whose slightly concave sides face each other. These are the borders of the two first-formed primary branchial stigmata or gill-clefts. Their actual openings into the atrial chamber are at present so small that they can hardly be seen in surface-view, but they are situated at the inner or concave sides of the two thickenings. On either side of the latter can be seen the ordinary cavity of the pharynx proceeding towards the œsophagus.

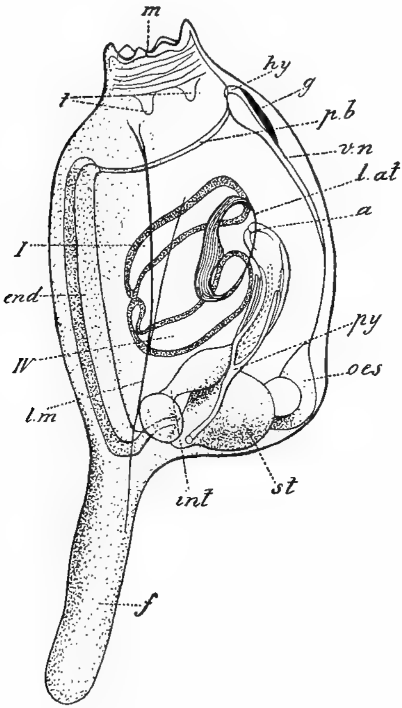

Fig. 107. — Young *Ciona intestinalis* after the completion of the change of axis; from the left side. (After Willey.)

I, IV. Primary stigmata. *a.* Anus, situated immediately below the left atrial aperture. *end.* Endostyle. *f.* Organ of fixation. *g.* Ganglion. *hy.* Hypophysis. *int.* Intestine. *l.at.* Left atrial aperture. *l.m.* Longitudinal muscle. *m.* Mouth. *oes.* Œsophagus. *p.b.* Peripharyngeal band. *py.* Pyloric gland. *st.* Stomach. *t.* Coronary tentacles. *v.n.* Visceral nerve (cordon ganglionnaire viscéral).

At a later stage the openings of the two first-formed stigmata become distinctly visible (Fig. 105 *C*). Meanwhile a change of axis is taking place in the body of the young Ascidian.

During the extraordinary change of axis which we are about to describe the prosbosciform præoral lobe (snout, organ of fixation) remains stationary, and the rest of the body actually rotates through an angle of 90 degrees, using the organ of fixation as a pivot about which it turns. In Fig. 105 *C* the rotation which takes place very gradually is only half performed; while in Fig. 107 it is complete. The method of growth by which this rotation takes place is of a very singular character, and it is difficult to define it in precise terms.

In this way then the endostyle (and branchial sac generally) comes to be placed at right angles to its primary position.

Since in Amphioxus the endostyle altered its primary axis by a process of independent growth while the long axis of the pharynx was constant throughout the development, we find that here again, as in so many previous instances, the details by which similar end-results are arrived at are widely dissimilar.

This complete change of axis by which the præoral lobe (organ of fixation) becomes placed at the posterior extremity of the body can only be regarded as a cenogenetic feature.*

It is therefore chiefly to the primary relations which the various structures bear to one another, before the change of axis, that we must turn for purposes of comparison. If we do this, we find that the following sequence of organs obtains as well in the larva of Amphioxus as in the newly fixed larva of Ciona; namely: 1, præoral lobe; 2, endostyle; 3, mouth; 4, gill-clefts.

Formation of Additional Branchial Stigmata.

After the change of axis of the body, the long axes of the stigmata lie transversely. In their further growth they go on elongating in the same (transverse) direction, and after they have attained a certain size their ventral ends—that is to say, the ends nearest the endostyle—bend round towards each other, and from each of the two first-

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* It goes without saying that the primary long axis of the Ascidian larva is homologous with the long axis of Amphioxus.

formed stigmata a minute portion becomes gradually constricted or nipped off. Thus between and cut off from the two original stigmata, there come to lie two intermediate stigmata of much smaller size. (Cf. Fig. 107.)

In this way, then, in Ciona, we arrive at the stage with four branchial stigmata on each side of the pharynx. For convenience we shall refer to these by the Roman numerals, I., II., III., and IV. It is a remarkable fact that II. and III. do not arise by new perforations, but are cut off from I. and IV. respectively.

On account of the close relations which the two first-formed stigmata, I. and IV., bear to one another during the production of the intermediate stigmata, their ventral extremities coming into contact and apparently sometimes fusing together so that II. and III. might almost be described as a joint production of I. and IV. rather than as entirely independent offshoots, one is forced to the conclusion that the two first-formed stigmata themselves, though they actually appear simultaneously as separate perforations, in reality represent the two halves of a single primitive gill-slit divided into two by a tongue-bar. If, moreover, we examine the exact origin of these two stigmata (I. and IV.) by means of transverse and horizontal sections, we may become convinced that such is indeed the case; namely, that they represent the two halves of a primitive gill-slit which, on account of the precocious formation of the tongue-bar between them, become perforated separately.

For the formation of any two or more consecutive gill-slits, we usually expect to find separate endodermic pockets or pouches of greater or less depth growing out towards the ectoderm. (Cf. Figs. 72 and 92.)

We ought to find something analogous to this in Ciona if the two first-formed stigmata had the value of independent gill-slits.

Instead, however, of anything approaching to two endodermic outgrowths, we find at the base of the atrial involution a single endodermic ingrowth making its appearance (Fig. 108).

The angles made by this ingrowth with the neighbouring wall of the branchial sac remain in contact with the floor of the atrium, then fuse with it, and finally become perforated (Fig. 108). This is the way in which the stigmata, I. and IV., arise, and it is difficult, if not impossible, to interpret the above-mentioned endodermic ingrowth otherwise than as a *precocious tongue-bar.*

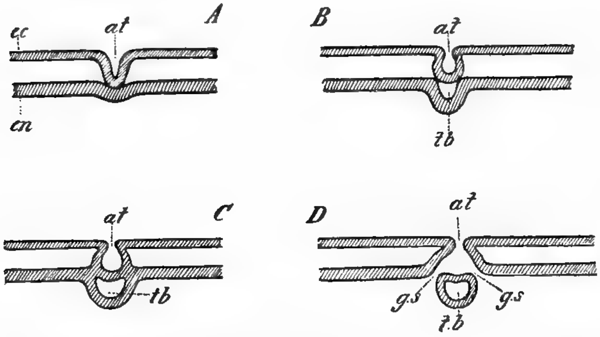

Fig. 108. — Diagrams illustrating the mode of origin of the two first-formed branchial stigmata in Ciona. (After WILLEY.)

at. Atrial involution. *ec.* Ectoderm. *en.* Endoderm. *g.s.* Stigmata. *t.b.* Tongue-bar.

Even in Amphioxus it was seen how the tongue-bars of the secondary slits arose relatively much earlier than those of the primary slits. If they arose still a trifle earlier, we should have the two halves of each slit becoming separately perforated, just as it happens in Ciona. In a species of Balanoglossus an analogous precocious formation of tongue-bars, before the perforation of the slits, has been described by Professor T. H. Morgan.

From what has been said above, we conclude that the first four pairs of primary branchial stigmata of Ciona (and this probably applies equally to many species of Phallusia) represent and are derivatives of one pair of primitive, ancestral gill-slits.

After a comparatively long interval, during which the intermediate stigmata, II. and III., increase in length transversely, two more stigmata, V. and VI., arise at intervals, one after the other, by separate perforations behind those already formed (Fig. 109).

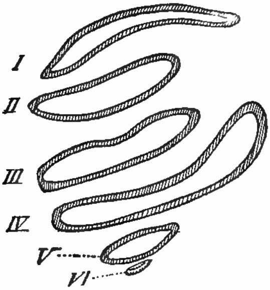

Fig. 109. — Primary branchial stigmata of the right side of a young Ciona. (After Willey.)

On account of the independent origin of V. and VI., it might be supposed that they would have the morphological value of distinct gill-slits, and that we had before us three pairs of ancestral gill-slits represented by six pairs of primary branchial stigmata. For this interpretation to hold good, we should expect to find that in other forms in which six primary branchial stigmata were produced, their origin was either the same or reducible to the same type as that of the branchial stigmata of Ciona.

This, however, is not the case, since I have found that in *Molgula manhattensis*,* a simple Ascidian which occurs in great numbers at New Bedford, Mass., the six primary stigmata, corresponding precisely to those in

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* My observations on the development of *Molgula manhattensis* were made at the Marine Biological Laboratory, at Woods Holl, Mass., in the summer of 1893.

Ciona, have a somewhat different mode of origin. The two first-formed stigmata (= I. and IV. in Ciona) appear simultaneously as in Ciona. Then after growing to a certain size, they curve round at their ventral ends, not in opposite directions so as to meet each other as they do in Ciona, but in the same direction (Fig. 110). The recurved ends then become constricted off from the parent stigmata. Later on, a fifth gill-opening arises behind the first four stigmata by independent perforation, and after attaining a certain size, it, in its turn, curves round at its ventral end, and eventually the sixth stigmatic opening is constricted off from the fifth.

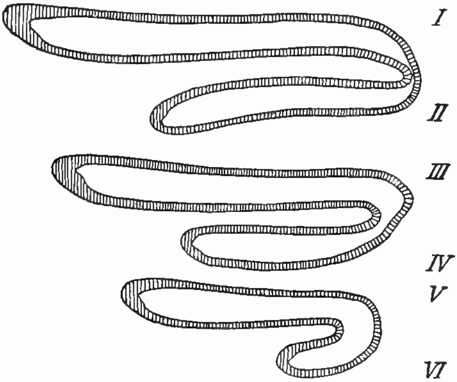

Fig. 110. — Diagram illustrating the mode of origin of the six primary branchial stigmata of *Molgula manhattensis.* The numbers are placed at the ventral ends of the slits. The figure is a combination of several hitherto unpublished drawings of different stages in the development. *I*, *III*, and *V* arose by separate perforation.

Since the first six primary stigmata have such different origins in two different species, it is obvious that in attempting to make a comparison with Amphioxus we can only use the two first-formed stigmata, because they agree in the above-mentioned species, and in many others in arising simultaneously, and in representing, in all probability, the two halves of a primitive gill-slit, cut in two by a tongue-bar.

The stigmata which are added to these must, therefore, be regarded as secondary modifications, hardly comparable to the successive formation of new gill-slits in Amphioxus.

In the Ascidians, therefore, we can only detect the representatives of one pair of primitive gill-slits, and there is every reason for supposing them to be homologous with the first pair of gill-slits in Amphioxus as defined above.

The six primary stigmata of each side give rise, by repeated subdivision, to the innumerable stigmata of the adult, both in Ciona and Molgula. The following description, however, applies more particularly to Ciona.

In the first place, the primary stigmata grow to a surprising transverse length, and then commence to divide into two equal portions by small tongue-like projections, which grow across the aperture indifferently from the anterior or posterior walls of the respective stigmata, and, fusing with the opposite wall, divide the transversely elongated slit into two completely separated halves. Then each of the latter divides again in the same manner, and so the process of subdivision of existing stigmata goes on. In this way six transverse rows of stigmata arise. These may be distinguished as secondary stigmata, since they arise by division from the primary.

Gradually, by a peculiar process of growth, the long axes of the secondary stigmata change their direction, and instead of lying transversely they become directed antero-posteriorly. This is their definitive position, and the stigmata now go on rapidly dividing again, and the number of transverse rows of stigmata is in this way doubled, trebled, quadrupled, etc., and we thus arrive at the adult condition. Out of the multitude of stigmata which are present in the adult Ciona only four arise by independent perforation; namely, the primary stigmata I. and IV. (which we regard as the two halves of a primitively single slit) and V. and VI.

First Appearance of Musculature.

By the time the change of axis of the entire body of the young Ciona has been effected the musculature characteristic of the adult begins to put in an appearance. In Fig. 107 circular sphincter muscles are present round the buccal and atrial apertures. The latter are still paired, but are carried by differential growth dorsalwards at a later stage, and finally coalesce together in the dorsal middle line to produce the single atrial aperture of the adult.

One strand of the longitudinal muscles of the later muscular mantle is likewise to be seen in Fig. 107. It tends to branch dichotomously. Posteriorly it is inserted on the inner surface of the organ of fixation near the point where it joins on to the body. Later new muscle-bands arise similar to the first, and become distributed over the body-wall in a spreading fan-like fashion, but posteriorly they are all inserted in the same region of the organ of fixation.

Alimentary Canal and Pyloric Gland.

The course of the alimentary canal can be gathered so plainly from the accompanying figures (Figs. 105 and 107) that it hardly needs a verbal description. From the posterior dorsal corner of the branchial sac the œsophagus leads into the wide stomach, and from the latter, again, the intestine, which often possesses a strangulated appearance, doubles up obliquely forwards to the left atrial chamber, into which it opens by the anus (Fig. 107).

In the angle made by the outgoing intestine with the stomach, a blind diverticulum arises. It is at first a simple cœcum, but soon begins to branch (Fig. 105 *C*), and finally forms an arborescent growth embracing the intestine (Fig. 107). This is the so-called *pyloric gland,* and it is probably homologous with the *hepatic cæcum* of Amphioxus.

Appendicularia.

It is generally agreed among those who have a voice in the matter, that most of the pelagic Ascidians (Salpa, Doliolum, Pyrosoma) are highly modified forms, specially adapted to a pelagic life, one of the results of which is that their reproduction is marked by a complicated alternation of generations.

It would, therefore, not assist us in our comparison with Amphioxus to describe these types.

There is, however, one family of pelagic Ascidians, the *Appendiculariæ,* with respect to which there are two widely different opinions.

The Appendicularиæ are pelagic, free-swimming Ascidians, whose adult condition is so far similar to the

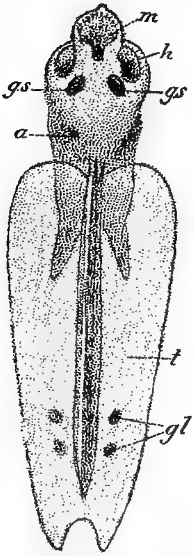

Fig. 111. — *Appendicularia* (*Fritillaria*) *furcata*, from the ventral surface. (After Lankester.)

a. Anus. *gl.* Unicellular glands. *g.s.* Gill-slits. *h.* Dorsal hood-like fold of integument. *m.* Mouth. *t.* Tail.

larval condition of the fixed Ascidians, that they retain the tail as their organ of locomotion throughout life (Fig. 111).

The tail is inserted in the middle of the ventral surface of the body proper, and is obviously a mere appendage of the latter.

The mouth is terminal or sub-terminal. There is a single pair of branchial stigmata, which open into a pair of tubular atrial cavities, whose separate external apertures are seen in front, on the ventral surface behind the mouth.

The alimentary canal is U-shaped, and the anus opens on the ventral surface to the right of the middle line, sometimes behind and sometimes (according to the species) in front of the stigmata (Figs. 111, 112). The endostyle is always quite anterior in position, and sometimes, as in Fig. 112, removed by a considerable interval from the stigmata.

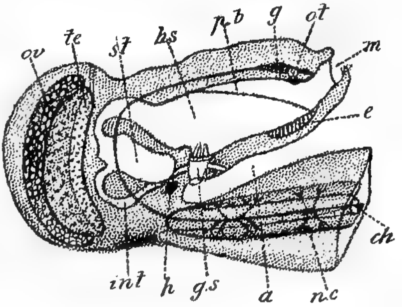

Fig. 112. — Diagram of the organisation of a species of Appendicularia, from the right side. (After Herdman.)

a. Anus; the index line was accidentally drawn about ⅛ of an inch in front of the anus. *b.s.* Branchial sac. *ch.* Notochord. *e.* Endostyle. *g.* Ganglion, from which the nerve-cord proceeds backwards to the tail, passing to the right of the alimentary canal. *g.s.* Gill-slit. *h.* Heart. *int.* Intestine. *m.* Mouth. *n.c.* Nerve-cord, with ganglionic enlargements in the tail. *ot.* Otocyst; beneath which the hypophysis opens into the branchial sac. *ov.* Ovary. *p.b.* Peripharyngeal band. *st.* Stomach. *te.* Testis.

In the posterior extremity of the body are placed the gonads, male and female, in close proximity to one another, the testis in front and the ovary behind. The heart, as described by Lankester, is a unique example of a functional organ reduced to the lowest possible level of histological structure. It consists simply of two cells placed opposite one another and connected together by contractile protoplasmic threads, which keep up a pulsating motion.

The tail is, as might be expected, more elaborately organised than that of the Ascidian larva. The dorsal nerve-cord is solid, and proceeds backwards from the ganglion, passing to the *right* of the alimentary canal until it reaches the tail, along which it is continued, lying to the *left* of the notochord; it possesses ganglionic enlargements at intervals in the tail, from which nerves pass out.

The caudal musculature also shows somewhat doubtful traces of being segmented in correspondence with the ganglionic swellings of the nerve-cord.

In connexion with the cerebral ganglion there is a sense-organ in the form of an otocyst, with an enclosed otolith, and below this a ciliated pit opens into the anterior region of the branchial sac, corresponding to the hypophysis, or sub-neural organ, of the fixed Ascidians.

According to one view, Appendicularia is the living representative of the free-swimming ancestor of the Ascidians.

According to the other view, it is less primitive than the fixed Ascidians, and was derived from the latter by the gradual increase, from generation to generation, of the duration of the pelagic existence of the larvæ, until they ceased to metamorphose, and so retained the larval structure throughout life, becoming at the same time sexually mature.[3]

These two views are, of course, antagonistic, and the former of them is held by a number of well-known authorities. As we are ignorant of the development of Appendicularia, it is impossible to decide definitely between them.

With the facts which are at our disposal, however, the second view — namely, that the Appendicularię represent Ascidian larvæ which have become secondarily adapted to a pelagic life, and have acquired the faculty of attaining sexual maturity — would be more in harmony with what we know of the relation of Amphioxus to the Ascidians. And it would seem that this affinity can be better demonstrated through the comparison of Amphioxus, both adult and larva, with a fixed Ascidian like Ciona than with Appendicularia.[3]

On the latter view, therefore, the so-called metamerism of the tail of Appendicularia, on which so much stress has been laid, would be simply a secondary elaboration of the tail for the purpose of serving as a permanent locomotor organ.

The dorsal nerve-cord of Appendicularia was regarded by FOL as a simple peripheral nerve. We have described above how a portion of the primitive nerve-tube in Ciona and other Ascidians becomes reduced to a solid nerve.

It would be of the greatest interest to discover the mode of origin of this nerve-cord in Appendicularia.

Abbreviated Ontogeny of Clavelina.

In order to demonstrate clearly the relatively primitive character of the development of Ciona it is sufficient to enumerate a few facts drawn from the development of Clavelina as described by Dr. OSWALD SEELIGER. As mentioned above, Clavelina is a near relative of Ciona, and in the adult condition resembles it very closely in many respects.

The development of Clavelina was formerly regarded as being of a primitive character, but is in reality, more especially in the later stages, abbreviated and hastened to a remarkable extent.

Like Ciona it possesses in the adult numerous transverse rows of stigmata. Each opening, however, arises by an independent perforation, so that all those preliminary ontogenetic processes which precede the establishment of the transverse rows of stigmata in Ciona are dropped out of the development of Clavelina.*

In Clavelina, again, the change of axis of the body proper occurs in the unhatched larva; so does the fusion of the two atrial apertures to form the dorsal cloacal siphon. The longitudinal muscles of the body proper commence to appear in the free-swimming larva, while the caudal muscles are enjoying their highest functional activity. The vacuolisation of the notochord does not proceed so far as in Ciona, since the cells are never actually removed from the centre of the notochord, but remain as thin discs stretching across the latter, so that the vacuolar spaces do not become continuous.

The behaviour of the organ of fixation in the larva of Clavelina is such that it could hardly be recognised as a præoral lobe except in the light of Ciona.

NOTES.

1. (p. 183.) The test or cellulose mantle of the Ascidians contains great numbers of cells of various kinds. These were formerly supposed to be derived from the subjacent ectoderm of the body-wall. KOWALEVSKY has recently shown, however, that the cells of the outer (cellulose) mantle of the Ascidians are derived from wandering mesenchyme-cells which wander from the body-cavity through the ectoderm (either *between* the ectodermic cells or actually passing *through* the individual cells) into the mantle.

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* A mode of formation of the branchial stigmata, intermediate between that of Clavelina and Ciona or Molgula, has been described by GARSTANG for Botryllus. In this genus, the primary branchial stigmata all arise by independent perforations, and then later become divided up into the transverse rows of stigmata. (W. GARSTANG. *On the development of the stigmata in Ascidians.* Proc. Roy. Soc., Vol. LI. 1892.)

2. (p. 211.) In *Clavelina* the atrial involutions do not merely arise as minute circular invaginations of the ectoderm, but at first they appear as short, though quite distinct, longitudinal grooves. Compare also the remarkable longitudinal atrial tubes of *Pyrosoma*.

3. (p. 238.) There is another possible way of interpreting the structure and systematic position of Appendicularia which may perhaps be nearer the truth than either of the views mentioned in the text. It is not absolutely necessary to suppose that the ancestors of Appendicularia were fixed Ascidians; but both Appendicularia and the fixed Ascidians may have descended from a common free-swimming stock, and have undergone certain modifications in common, such as loss of true vascular system and cœlom. Then, while the Ascidians proper became adapted to a sessile existence, Appendicularia may be supposed to have gone to the opposite extreme, and have become adapted to an absolutely pelagic existence. In becoming adapted to such a purely pelagic or oceanic environment as that of Appendicularia, it is eminently conceivable that an animal would have to undergo as radical a modification of structure as it would in becoming adapted to a sessile existence. (Compare *Salpa*, *Doliolum*, etc.)

V.

THE PROTOCHORDATA IN THEIR RELATION TO THE PROBLEM OF VERTEBRATE DESCENT.

> "*Den Schlüssel richtigen Verständnisses gibt nicht das Hineinpressen neuer Thatsachen in eine alte Schablone, sondern das Aufsuchen des genetischen Zusammenhangs der Erscheinungen.*" — WEISMANN.

BALANOGLOSSUS.

External Features.

Of the free-living protochordates, the lowest type of organisation is undoubtedly presented by the *Enteropneusta* (Hemichorda), the group to which *Balanoglossus* belongs.

Balanoglossus is a remarkable worm-like creature which lives buried in the sand or mud of the sea-shore. By means of numerous unicellular integumentary glands which are distributed over the surface of the body, it secretes a mucous substance to which particles of sand adhere, and so makes for itself tubes of sand in which it lives at about the level of the low tide-mark. It possesses such a characteristic external form and odour (like iodoform) as to render it peculiarly easy of recognition.

In front there is a long and extremely sensitive *proboscis* which is capable of great contraction and extension, and is, in the living animal, of a brilliant yellow or orange colour. Behind the proboscis follows a well-marked *collar-region*, consisting externally of a collar-like expansion of the integument, with free anterior and posterior margins overlapping the base of the proboscis in front and the anterior portion of the *gill-slits* behind.

In the ventral middle line, at the base of the proboscis and concealed by the collar, is situated the mouth (Fig. 113). Following behind the collar is the region of the trunk or body proper, which, in the adult of some species, reaches a relatively enormous length, even extending to two or three feet. The ectodermal covering of the body consists in general of ciliated cells, among which are scattered unicellular mucous glands ; the cilia, however, appear to be more prominent on the proboscis than elsewhere.

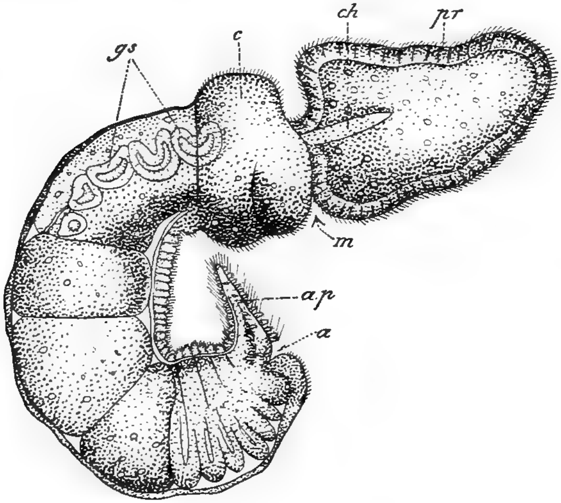

Fig. 113. — Larva of *Balanoglossus Kowalevskii*, with five pairs of gill-slits; from the right side. (After BATESON.)

a. Anus. *a.p.* Temporary pedicle of attachment. *c.* Collar. *ch.* Notochord. *g.s.* Gill-slits. *m.* Mouth. *pr.* Proboscis.

In the region of the trunk, which immediately follows upon the collar region, there are a great number of paired openings on the dorsal side of the body, placing the anterior portion of the digestive tract in communication with the outer world. These are the *gill-slits*, and they are arranged strictly in consecutive or metameric pairs to the number of upwards of fifty in the adult. In their structure, and more especially in the possession of tongue-bars, they bear a remarkable resemblance to the gill-slits of Amphioxus. This is particularly striking in young individuals. As the adult form is approached in the development, the bulk of the gill-slits sinks below the surface, only opening at the latter by small slit-like pores, and thus their true character is obscured in a superficial view.

Projecting into the interior of the proboscis is a rod-like structure which arises as an outgrowth from the alimentary canal dorsal to the mouth. The lumen of this endodermic diverticulum becomes narrowed down and, in fact, partially obliterated, while the cells constituting its walls give rise to a spongy vacuolar tissue which strongly resembles the notochordal tissue of Amphioxus and the higher Vertebrates. On account of its dorsal position above the mouth, its endodermic origin, and the *vacuolisation* of its cells, this structure was identified by BATESON in 1885 as the *notochord.*

Nervous System and Gonads.

The nervous system of Balanoglossus presents many features of the utmost interest and suggestiveness. It consists essentially of an ectodermal network of nerve-fibres forming the inner layer of the skin (ectoderm) all over the body. In this primitive nervous sheath, which envelops the whole body, there are certain definite local thickenings. Two of these thickenings occur respectively along the whole length of the dorsal and ventral middle lines in the trunk-region, thus producing the dorsal and ventral median longitudinal nerve-cords. In the region of the collar the dorsal nerve-cord becomes entirely separated from the ectoderm, and this portion of it contains, at least in young individuals, a central canal which, from its origin and relations, was shown by Bateson, and more recently by Morgan, to be homologous with the central canal of the vertebrate spinal cord. Anteriorly the dorsal nerve-cord becomes continuous with a specially dense tract of the general nerve-plexus at the inner posterior surface of the proboscis (Fig. 114). This proboscidian plexus thins out somewhat towards the anterior extremity, but nevertheless forms a complete nerve-sheath for the proboscis and indicates the sensitive character of the latter (Fig. 115).

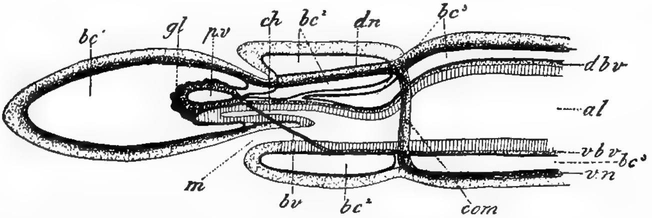

Fig. 114. — Diagram of the organisation of Balanoglossus, from the left side. (From a drawing kindly lent by Professor T. H. Morgan.)

al. Alimentary canal. bc^1. Cœlom of proboscis (anterior or præoral body-cavity). bc^2. Cœlom of collar. bc^3. Cœlom of trunk. *b.v.* Blood-vessel, proceeding from the so-called heart (which lies at base of proboscis above the notochord) to the ventral blood-vessel. *ch.* Notochord. *com.* Commissure, between dorsal and ventral nerve-cords. *dn.* Dorsal nerve-cord, separated from the integument in the collar-region. *d.b.v.* Dorsal blood-vessel. *gl.* Proboscis-gland; modified cœlomic epithelium surrounding heart and front end of notochord. *m.* Mouth. *p.v.* Pulsating vesicle, lying inside the "heart." *v.b.v.* Ventral blood-vessel. *v.n.* Ventral nerve-cord.

The ventral nerve-cord does not extend into the region of the collar, but from the point where the collar joins on to the trunk the ventral cord is connected with the dorsal nerve-cord by a commissure-like thickening of the integumentary plexus, which passes in the skin on each side round the hinder end of the collar-region (Fig. 114).

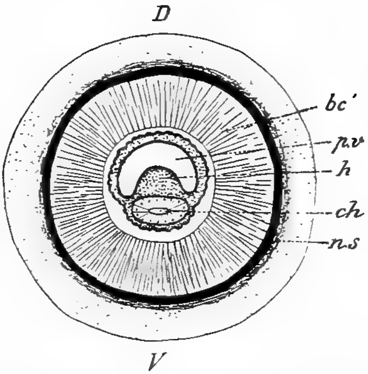

Fig. 115.—Diagrammatic transverse section through hinder region of proboscis of Balanoglossus. (From a drawing kindly lent by Professor T. H. MORGAN.)

D. Dorsal. *V.* Ventral. *bc^1.* Proboscis-cavity, almost filled up by mesenchymatous and muscular tissue,* proliferated from the original cœlomic epithelial layer (indicated by the black line below the ectoderm). *p.v.* Pulsating vesicle. *h.* Heart. *ch.* Notochord. *n.s.* Integumentary nerve-plexus.

The genital organs, testes or ovaries, according to the sex of the individual, occur as a paired metameric series of pouch-like bodies or gonadic sacs which extend backwards far beyond the region of the gill-slits. The gonadic sacs are suspended in the body-cavity by solid cords attached to the dorsal integument, which become perforated in the spawning season to admit of the expulsion of the reproductive elements.

Metamerism.

Although there is no muscular metamerism in Balanoglossus, yet we have seen that other organs (gill-slits and gonads) are arranged metamerically. And in point of fact, among those Invertebrates which are not included under the phylum of the Articulata, if there is one peculiarity of organisation more sporadic in its occurrence than another, it is metamerism. It may affect the most different organs of the body either collectively or individually, and nothing is more patent than the fact that the metameric repetition of parts has arisen independently over and over again in different groups of animals.[1]

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* This tissue is not represented in Figs. 114 and 116, although it is present throughout the body-cavity.

Far from assuming as a self-evident fact that the extreme metamerism of the Annelids and Arthropods is genetically identical with that of the Vertebrates, we have every reason to suppose that it has been elaborated entirely independently in the two cases, and that the apparent similarity is due, as already intimated, to a *parallel evolution.*

Body-cavities; Proboscis-pore; Collar-pores.

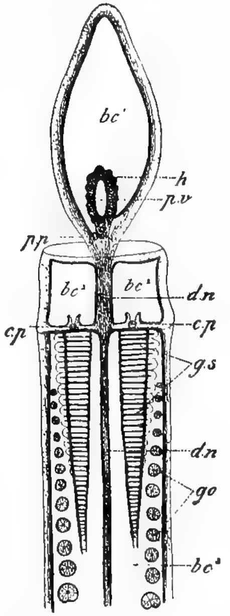

Fig. 116. — Diagram of the organisation of Balanoglossus, from the dorsal side. (From a drawing kindly lent by Professor T. H. Morgan.)

c.p. Collar-pores. *go.* Gonads. *g.s.* Gill-slits; the dark lines converging behind indicate the superficial portions of the gill-slits; below the surface are seen the free ends of the tongue-bars. *pp.* Proboscis-pore. Other letters as above.

Corresponding to the three regions into which the body of Balanoglossus is divided, — namely, proboscis, collar, and trunk, — the body-cavity is divided up into three systems of cavities. These are (*a*) the anterior body-cavity or cavity of the proboscis, (β) a pair of collar-cavities, and (γ) a pair of body-cavities which form the unsegmented cœlom of the trunk (Figs. 114, 115).

These cavities arise essentially as pouches from the archenteron (Fig. 117), although their actual development differs considerably in different species (Morgan).

The proboscis-cavity is placed in communication with the exterior by an opening through the posterior wall of the proboscis known as the *proboscis-pore.* In *B. Kowalevskii* this pore lies asymmetrically to the left of the dorsal middle line (Fig. 115), while in *B. Kupfferi* a corresponding opening occurs to the right of the middle line, so that in this species there are two proboscis-pores constituting a symmetrical pair.

The left proboscis-pore of Balanoglossus is obviously to be compared with the præoral pit of Amphioxus.

The collar-cavities also open to the exterior by pores, one on each side underneath the dorsal posterior free fold of the collar, and on a level with the opening of the first gill-slit. These are the funnel-shaped *collar-pores.* Spengel states that water is taken in through the collar-pores into the cavity of the collar in order to swell the latter up, so that it may serve as an accessory organ of locomotion in so far as an alternate inflation and collapse of the collar would assist the animal in its slow burrowings in the sand.

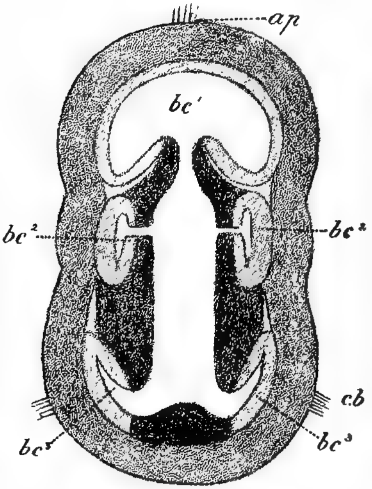

Fig. 117. — Diagrammatic horizontal section through an embryo of Balanoglossus (type of the direct development), to show the origin of the body-cavities as archenteric pouches. (After Bateson.)

ap. Tuft of cilia at the apical pole (indication of an apical plate). bc^1. Proboscis-cavity. bc^2. Collar-cavities. cb^3. Trunk-cavities. *cb.* Circular band of cilia.

Alimentary Canal.

The mouth cannot be closed, as there is no sphincter muscle, and accordingly, as the animal progresses through the sand, it swallows a large quantity of the latter in which food-particles (unicellular organisms, etc.) may also be involved. As the sand passes through the intestine, it becomes enveloped in the mucous secretion of the intestinal epithelium, and is ejected through the anus in a cord of slime.

The alimentary canal is a straight tube between mouth and anus. In its hinder portion it is usually sacculated, *i.e.* provided with paired lateral saccular dilatations comparable to the so-called *intestinal cæca* of the Nemertine worms. (See below.) In the region of the pharynx the lumen of the alimentary canal is incompletely divided by lateral constrictions into two portions, an upper or *branchial* portion carrying the gill-slits, and a lower or *digestive* portion (Fig. 118). The latter was compared by GEGENBAUR* to the endostyle of the Ascidians, but it is probable that this comparison, although a very natural and useful one at the time at which it was made, will not hold good, since there is

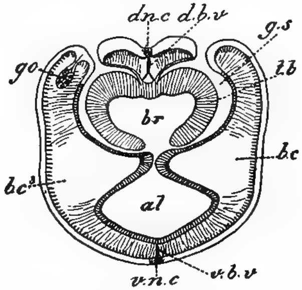

Fig. 118.—Transverse section through the gill-region of Balanoglossus. (After SPENGEL.)

al. Digestive portion of gut. *br.* Branchial portion of gut. *bc*³. Third body-cavity (trunk cœlom); this is also nearly obliterated in the adult by the proliferation of mesenchyme or "parenchyme" from its walls. *d.n.c.* Dorsal nerve-cord. *d.b.v.* Dorsal blood-vessel. *go.* Gonad. *g.s.* Gill-slit. *t.b.* Tongue-bar. *v.b.v.* Ventral blood-vessel. *v.n.c.* Ventral nerve-cord.

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* CARL GEGENBAUR, *Elements of Comparative Anatomy.* Translated by F. Jeffrey Bell. London, 1878.

nothing in the structure or development of this part of the alimentary tract in Balanoglossus which will bear comparison with the endostyle.* As indicated in the larvæ of Amphioxus and the Ascidians, it would seem that the endostyle first became evolved or differentiated at the anterior end of the pharynx, *in front of* the gill-slits, in correlation with the dorsal position of the mouth.

Development; the Tornaria Larva.

The development of *Balanoglossus Kowalevskii* as made known to us by the admirable work of Bateson is what is known as a strictly *direct development;* that is to say, the embryonic, larval, and adult stages follow one another by gradual transitions concomitantly with the simple progressive growth of the individual and without any striking *metamorphosis.* In other species of Balanoglossus the larval form is remarkably different from the adult, and becomes transformed into the latter by a very distinct metamorphosis. The extraordinary larval form here referred to was discovered in 1848 by Johannes Müller, who named it *Tornaria*, and regarded it, as did his successors Krohn, Alexander Agassiz, and Fritz Müller, as the larva of an Echinoderm (Starfish).

It was not until 1869 that its true character as the larva

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* A ciliated tract in the floor of the œsophagus of a Tornaria from the Pacific has recently been compared to the endostyle by W. E. Ritter. (*On a New Balanoglossus Larva from the Coast of California and its Possession of an Endostyle.* Zool. Anz. XVII. 1894. pp. 24–30.)

The comparison is at present somewhat doubtful. More recently Garstang has suggested that the endostyle is derived from the adoral ciliated band of the Echinoderm larva. (See Fig. 119.) The suggestion is an interesting one, but Garstang's idea of the relations of the præoral lobe is very different to the one here set forth. (Walter Garstang, *Preliminary Note on a New Theory of the Phylogeny of the Chordata.* Zool. Anz. XVII. pp. 122–125.)

of a species of Balanoglossus was demonstrated by Elias Metschnikoff. Shortly afterwards, Metschnikoff's discovery was confirmed and amplified by Alexander Agassiz.

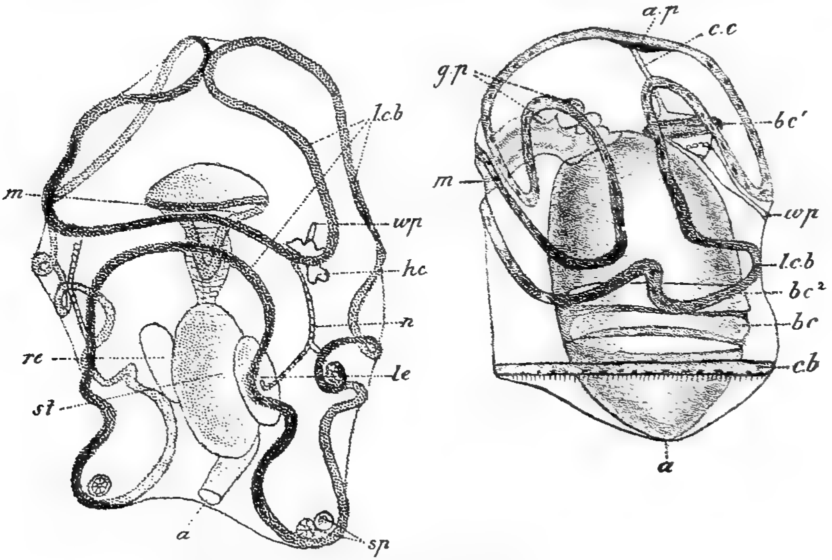
The superficial likeness between Tornaria and such Echinoderm larvæ as Bipinnaria or Auricularia is astonishing, and a renewed study of the detailed organisation of Tornaria, recently made by Morgan, appears to have established the fact, originally insisted upon by Metschnikoff, that this resemblance can only be accounted for on the ground of genetic affinity.

In Figs. 119 and 120 two types of larvæ, Tornaria and Auricularia, are shown side by side; and although unfortunately they are not figured from exactly the same aspect, yet it is obvious at a glance that, in spite of certain differences which will be enumerated below, they both belong to the same category of larval forms.

A highly characteristic feature of these larvæ is the remarkable ectodermal ciliated band which constitutes a perfectly symmetrical but somewhat complicated undulating seam round the body. The larvæ are strictly pelagic, and swim about in the open sea by means of their cilia; but the latter, instead of being distributed evenly over the whole surface of the body, are concentrated in the region of the ciliated bands which are composed of thickened ectoderm.

In Tornaria there are two ciliated bands, viz.: 1) the above-mentioned undulating seam which is usually known as the *circumoral* or *longitudinal* ciliated band, and 2) a *postoral* circular ciliated band. Only the former is present in Auricularia, and the absence of the circular band in this form constitutes one of the chief differences between the two larvæ.

From a morphological point of view a more striking resemblance between the two larvæ than that furnished by the longitudinal ciliated bands exists in connexion with the anterior body-cavity or *enterocœl.* In the Echinoderm larva this cavity arises as a median pouch of the archenteron, and there is every reason to suppose that it has a similar origin in Tornaria, although this point has not yet



Figs. 119 and 120.—Auricularia, larva of Synapta (after SEMON); and Tornaria, larva of Balanoglossus. (After MORGAN.)

a. Anus. *a.p.* Apical plate. bc^1. Anterior body-cavity, communicating with exterior by the water-pore. bc^2, bc^3. Second and third body-cavities of Tornaria. *c.b.* Circular ciliated band of Tornaria. *c.c.* Contractile cord between apical plate and anterior body-cavity of Tornaria. *g.p.* Gill-pouches. *h.c.* Hydrocœl of Auricularia (anterior body-cavity). *l.c.b.* Longitudinal (circumoral) ciliated band. *l.e.* Left enterocœl (body-cavity). *m.* Mouth. *n.* Lateral (paired) nerve-band of Auricularia. *r.e.* Right enterocœl. *sp.* Calcareous spicules. *st.* Stomach. *wp.* Water-pore.

N.B.—In Auricularia, the margin of the mouth is surrounded by a ciliated band discovered by SEMON, and known as the *adoral ciliated band.* The posterior, V-shaped portion of this band lies inside on the ventral floor of the larval œsophagus.

been determined. The primary anterior enterocœl in the Echinoderm larva is not quite the same as the corresponding cavity in Tornaria, since it contains also the elements of the general body-cavity. Apart from slight differences, the collar-cavities and general body-cavities arise essentially in the same way in Tornaria as they do in the case of the direct developing larva of Balanoglossus (see above).*

In the Echinoderm larva, however, the paired body-cavities do not arise as independent archenteric pouches, but they become constricted off from the anterior enterocœl. Making allowance for these deviations in the origin of the body-cavities, — deviations which are by no means fundamental, since in both cases the body-cavities are ultimately reducible to archenteric pouches, — it is an extremely striking fact that both in Tornaria and Auricularia the anterior enterocœl acquires an opening to the exterior on the dorsal surface to the left of the middle line. This opening is called the *water-pore*, since it forms the outlet (possibly both outlet and inlet) of the water-vascular system of the Echinoderm. In Tornaria it persists after the metamorphosis as the *proboscis-pore*, which has been described above.

The Larva of Asterias vulgaris; Water-pores and Præoral Lobe.

In view of what was said above as to the occurrence of paired proboscis-pores in *B. Kupfferi*, it is interesting to note that sometimes there are two water-pores, a right and a left, in Echinoderm larvæ. This has been observed by

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* As to the origin of the body-cavities in different species of Balanoglossus, MORGAN summarises his observations as follows: "They may arise as enteric diverticula, as endodermal proliferations, or even arise from mesenchymatous beginnings." (See MORGAN. No. 125 bibliog.)

Brooks and G. W. Field in the larvæ of a common starfish, *Asterias vulgaris.* In this case the primary enterocœl becomes constricted off from the archenteron in the form of two equal pouches. The right and left enterocœlic sacs then take up a symmetrical position on each side of the larval œsophagus, and each sac next opens to the exterior by a *water-pore.* The pore in connexion with the right sac (Fig. 121) is, however, of a transitory, rudimentary character, and soon closes up, while the left pore persists as the definitive water-pore. As in Tornaria, so here, the cavity of the larval body generally, and of the præoral region (*præoral lobe*) in particular, is the primary body-cavity or blastocœl, and contains scattered mesenchyme-cells. At a later stage in the larva of Asterias the right and left enterocœlic sacs, having increased greatly in length, meet one another in the region of the præoral lobe and fuse together, thus putting their two cavities into communication across the median line. The median portion of the enterocœl thus produced extends up into the præoral lobe, and so the primary blastocœlic cavity of the latter is replaced by a secondary ingrowth of the enterocœl (Fig. 122).

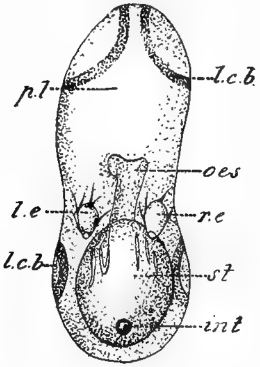

Fig. 121. — Young larva of *Asterias vulgaris*, from the dorsal side. (After G. W. Field.)

p.l. Præoral lobe. *l.c.b.* Circumoral (longitudinal) ciliated band. *oes.* Œsophagus. *r.e.* and *l.e.* Right and left enterocœlic sacs, each opening by a "water-pore" to the exterior. *st.* Stomach. *int.* Aperture, leading from stomach into intestine.

Similarly with the metamorphosis of Tornaria, the anterior enterocœl, which is at first of very inconsiderable extent (Fig. 120), increases greatly in size, and assumes its definite position and proportions as the cavity of the præoral lobe (*i.e.* proboscis), thus replacing the original blastocœlic space, while the water-pore remains as the proboscis-pore.

As described in the previous chapter, the cavity of the præoral lobe (fixing stolon) of the Ascidian tadpole is of the nature of a blastocœl or primary body-cavity, containing loose mesenchyme-cells, and it is therefore of great importance to note that whether the cavity of the præoral lobe is a *blastocœl* or an *enterocœl*, the morphological value of the structure itself remains the same.

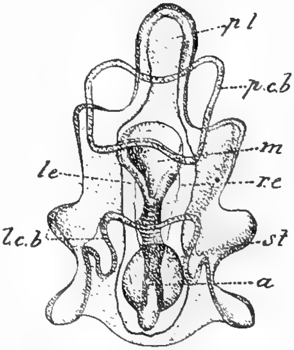

Fig. 122. — Older larva (Bipinnaria) of *Asterias vulgaris*, from the ventral side. (After G. W. FIELD.)

By a fusion of the two præoral loops of the ciliated band across the apex of the præoral lobe, followed by a separation in the transverse direction, the originally single circumoral band (cf. Figs. 119 and 121) has become divided into two bands, a præoral ciliated band *p.c.b.* and a postoral longitudinal ciliated band *l.c.b.* The posterior transverse portion of the præoral ciliated band has undergone a fusion with the front end of the originally distinct adoral band (cf. Fig. 119). *p.l.* Præoral lobe, into which the enterocœl has extended. *m.* Mouth. *r.e.* and *l.e.* Right and left enterocœlic cavities. *st.* Stomach. *a.* Anus.

Apical Plate of Tornaria.

At the anterior end of the body, or, in other words, at the apex of the præoral lobe, in Tornaria, there is an ectodermic thickening in which nerve-cells and nerve-fibres and a pair of simple eyes have become differentiated. This is the so-called *apical plate*, and it constitutes the central nervous system of the larva. It can be recognised for some time after the metamorphosis at the tip of the proboscis, but eventually disappears completely. A similar apical plate occurs in a great number of Invertebrate larvæ, and is especially characteristic of the free-swimming larvæ (Trochophores, or Trochospheres) of Annelids and Molluscs. We shall return to this later.

In Tornaria a single contractile cord passes from the apical plate to the anterior enterocœl.

There is no apical plate in Auricularia, nor in most of the other Echinoderm larvæ; but there is reason to suppose that it has been secondarily lost, since a transitory ectodermal thickening at the apical pole can frequently be observed in the course of their development; and, moreover, in what is probably the most primitive Echinoderm larva known (viz. the larva of the Crinoid, *Antedon*), there is a well-developed apical plate.

Metamorphosis of Tornaria.

The metamorphosis of Tornaria, as originally described by Alexander Agassiz, takes place with relative suddenness. According to the more recent account of the metamorphosis given by MORGAN, a marked diminution in size occurs; the internal organs are drawn together in such a way that the larval œsophagus, with the gill-pouches (see Fig. 120), is drawn backwards into the body, and the anterior enterocœl, as already described, is carried forwards into the præoral lobe. The longitudinal (circumoral) ciliated band, which was the first to develop, is also the first to disappear, while the posterior circular band persists to a somewhat later stage.

The Nemertines.

It is thus evident that Balanoglossus, especially through its Tornaria larva, shows undoubted marks of affinity to the Echinoderms. It will next be shown that there are certain features in the adult anatomy which apparently indicate a distinct genetic relationship to another group of the Invertebrates; namely, the *Nemertine* worms.

The Nemertines are elongated, flattened, or cylindrical worms, with a smooth *ciliated* skin and no external segmentation, occurring, as a rule, in a closely similar habitat to that of Balanoglossus, buried in the sand or mud of the sea-shore.

Like Balanoglossus, they also possess unicellular integumentary glands, by means of which they secrete a mucous substance, to which frequently sand-grains adhere, thus producing a tube of sand round the body. Some of them reach an enormous length, and one at least must be measured in yards (*Lineus longissimus* exceeding three yards in length).

The chief anatomical features which offer material for direct comparison between the Nemertines and Balanoglossus relate to the ectoderm, proboscis, nervous system, mesenchymatous tissue, the reproductive organs, and the alimentary canal.

As for the ectoderm, considered apart from the nervous system, it need only be repeated that in both cases it is composed of ciliated cells and scattered mucous glands.

The proboscis of the Nemertines is one of the most characteristic organs of this group of animals. It is not permanently protruded, and does not serve as an organ of locomotion, as in Balanoglossus, but is usually carried about entirely withdrawn within the body of the animal, from which it can be shot out with great force and rapidity when the occasion demands it. During the process of extrusion it is turned completely inside out, and conversely, during the process of *introversion*, the retraction takes place from the tip backwards by the in-rolling of its walls. According to the graphic description of HUBRECHT, it is retracted "in the same way as the tip of a glove finger would be if it were pulled backwards by a thread situated in the axis and attached to the tip."

When at rest within the body the proboscis lies freely within a hollow cylinder, the wall of which is thick and muscular, and constitutes the *proboscis-sheath* (Fig. 123).

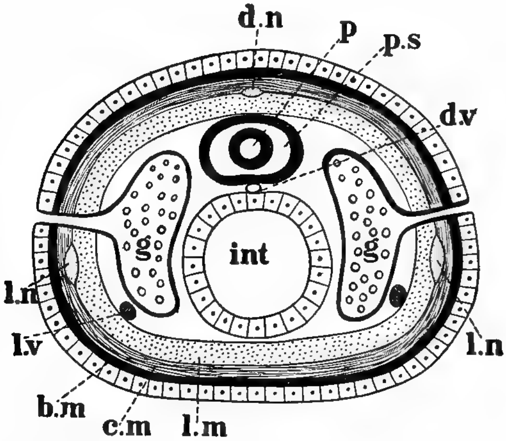

Fig. 123. — Diagrammatic transverse section through the middle of the body of a Nemertine. (After LANG, *Text-book of Comp. Anat.*)

b.m. Basement-membrane. *c.m.* Circular muscles. *d.n.* Dorsal or "medullary" nerve. *d.v.* Dorsal blood-vessel. *g.* Gonads. *int.* Intestine. *l.m.* Longitudinal muscles. *l.n.* Lateral nerves. *l.v.* Lateral blood-vessel. *p.* Proboscis. *p.s.* Proboscis-sheath.

Sometimes beneath the ectodermal epithelium of the Nemertine proboscis there is a continuous sheath of nerve-fibres, comparable to the nervous plexus in the proboscis of Balanoglossus.

Partly, therefore, on account of its structure, and partly on account of its topographical relations when extruded, we are led to suppose that a certain homology exists between the retractile proboscis of the Nemertines and the non-retractile proboscis of Balanoglossus (BATESON).

In the most primitive Nemertines the nervous system consists essentially of a somewhat complicated pair of cerebral ganglia and a diffuse nerve-plexus, with nerve-cords lying at the base of the ectoderm.* As the cerebral ganglia probably belong to the same category as the cerebral ganglia of all other typical Invertebrates, and are not represented in Balanoglossus, we can afford to neglect them at present. Confining our attention to the ectodermal nerve-plexus, we find occurring in it, along definite lines, local thickenings, after the same principle, but not all on the same lines, as was described above for Balanoglossus. Directly comparable with the dorsal longitudinal nerve-cord of Balanoglossus, there is a similar thickening or concentration of the integumentary nerve-plexus in some of the Nemertines, in the dorsal middle line (*Carinina, Cephalothrix*). Hubrecht, who discovered this, calls it the *medullary nerve.* There is, however, no corresponding ventral nerve-cord in the Nemertines, but, instead of this, there is a pair of lateral thickenings, constituting the well-known *lateral nerves* of the Nemertines (Fig. 124).

It is usually supposed that the lateral nerves of the Nemertines are homologous with the two halves of the ventral nerve-cord in the Annelids. In the Annelids the primitive lateral nerves (which are so typical of the Platyhelminths, or flat-worms) have approached one another in the mid-ventral line, and have often undergone intimate fusion together. In some cases, however, they are separated from one another by a wide interval (Sabellaria, etc.).

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* HUBRECHT compared the lobes of the cerebral ganglia of a Nemertine to the cranial ganglia of the Vertebrates, the lateral nerves to the Rami laterales vagi, and the proboscis-sheath to the notochord.

In the Annelids, in contrast to the Nemertines, the ganglion-cells are not distributed uniformly along the whole length of the nerve-cord, but are collected together to form definite ganglionic swellings.

It is, therefore, very significant that in the Nemertines we have a median dorsal "medullary" nerve, in addition to the elements which constitute the ventral nerve-cord of the Annelids.

In many Nemertines the dorsal and lateral nerve-cords do not continue to lie in the ectoderm throughout life, but sink deeper into the body, and so come to be separated from the ectoderm, first by the basement membrane, and then by one or more muscular layers of the body-wall. In the Hoplonemertea (those in which the proboscis is armed with stylets) the medullary nerve is absent. In all cases, however, the longitudinal nerve-cords remain connected with one another by a more or less plexiform arrangement of nerve-fibres; although sometimes a more definite connexion, by means of metameric ring-nerves, has been observed by HUBRECHT (Fig. 124).

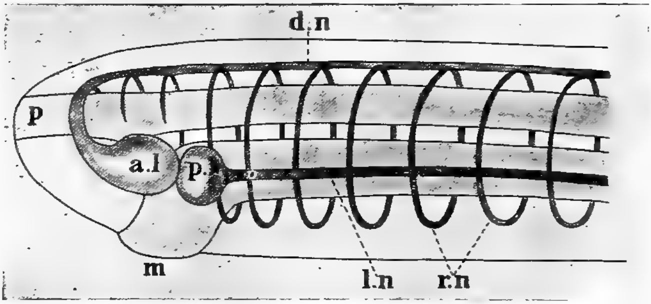

Fig. 124. — Diagrammatic view of anterior portion of a Nemertine, from the left side. (After HUBRECHT, from LANG.)

a.l. Anterior lobe of brain. *p.l.* Posterior lobe of brain. *p.* Opening of proboscis. *m.* Mouth. *d.n.* Dorsal nerve. *l.n.* Lateral nerve. *r.n.* Ring-nerves.

There is no true cœlom in the Nemertines, and the space between the alimentary canal and body-wall is occupied by a gelatinous mesenchyme, containing muscular and connective tissue elements. In Balanoglossus the cavity of the cœlom becomes largely obliterated in the adult, by the proliferation of cells from the epithelium of its walls, thus filling up the cavities with a more or less solid parenchymatous tissue.

Like Balanoglossus, the Nemertines have a straight alimentary canal, provided with paired lateral outgrowths or *intestinal cœca*, and a terminal anus.

The gonadic sacs of the Nemertines offer a striking resemblance to those of Balanoglossus. They occur as a metameric series of paired sacs, which alternate with the above-mentioned intestinal cœca, and communicate with the exterior by short tubes, which are at first solid, as in Balanoglossus, subsequently becoming hollowed out and opening above the lateral cords (Fig. 124).

Finally it should be pointed out that, while excretory organs, in the form of a well-developed single pair of elongated nephridia, provided with numerous internal "end-sacs," are present in the Nemertines, nothing of the kind has yet been detected in Balanoglossus.

CEPHALODISCUS AND RHABDOPLEURA.

It is interesting to note that there are some remarkable animals which stand in a similar relation to Balanoglossus that the Ascidians do to Amphioxus. While Balanoglossus is free-living, does not produce buds, and has a straight alimentary canal, these creatures, of which only two genera are at present known, *Cephalodiscus* and *Rhabdopleura*, lead a sessile existence, produce buds, and have a U-shaped alimentary canal. Both are deep-sea forms, Cephalodiscus having been dredged during the Challenger Expedition, from the Straits of Magellan, at a depth of 245 fathoms; while Rhabdopleura was first dredged independently, off the Shetland Islands, at 90 fathoms, by the Rev. Canon Norman, and off the Lofoten Islands, at 200 fathoms, by Professor G. O. Sars (1866–68). Rhabdopleura is the name given by Allman (1869), who published a short account of it; and it has since been described by Sars, Lankester, and G. H. Fowler.

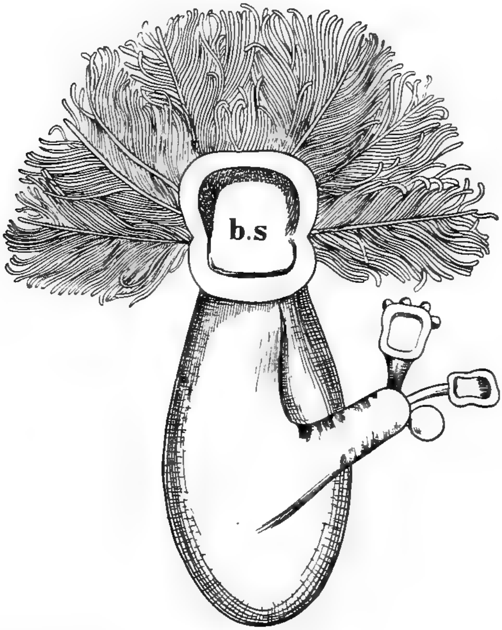

Fig. 125. — *Cephalodiscus dodecalophus*, from the ventral side. (After M'Intosh.)

Actual length of polypide from extremity of branchial plumes to the tip of the pedicle is about 2 mm.

b.s. Buccal shield; the shading on its surface indicates pigment-markings. At the tip of the pedicle, buds are produced.

The account which we possess of Cephalodiscus forms one of the Challenger Reports, and was written by Professor W. C. M'Intosh, who made out the main features of its anatomy. It was further treated, from a morphological standpoint, by Sidney F. Harmer, who pointed out its remarkably close affinity to Balanoglossus.

The most important morphological features in the anatomy of Cephalodiscus are shown in Figs. 125–127. The individuals live in colonies, in a "house" or *cœnœcium*, which consists of a ramifying and anastomosing system of tubes, the walls of which are composed of a semi-transparent, gelatinous material, whose outer surface is covered with spinous projections. The walls of the cœnœcium are furthermore perforated by numerous apertures, which allow of the ingress and egress of water.

The adult members of a colony have no organic connexion between themselves, but each one is independent and free to wander about the tunnels of the cœnœcium. Although Cephalodiscus has not been studied in the living condition, there is every reason to suppose that it moves about in its tube by means of the large *buccal shield* (Fig. 125) overhanging the mouth, by which it can attach itself to the inner surface of the tube, and then help itself along by the curious *pedicle* which occurs ventrally near the hinder end. It thus seems probable that this pedicle can be used as a sucker, but its chief function lies in the production of buds which grow out from it, and eventually become detached. Bateson has described a somewhat similar sucker at the hinder end of the body in young individuals of Balanoglossus (Fig. 113).

Behind and above the buccal shield there is a row of twelve tentacles or branchial plumes, each possessing a central stem or shaft which carries numerous lateral pinnæ. An important function of these plumes is to produce currents of water by the action of their cilia, which vibrate in such a direction that the water with food-particles is led into the mouth. The superfluous water is led out from the proximal portion of the alimentary canal by a single pair of *gill-slits* which are not visible in surface view, since they are overhung by a fold of the integument known as the *post-oral lamella* or *operculum*, corresponding to the posterior free fold of the collar in Balanoglossus (Fig. 126).

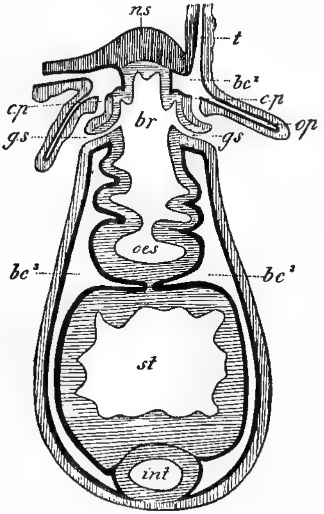

Fig. 126. — Longitudinal frontal (right and left) section through an adult Cephalodiscus. (After HARMER.)

*bc*². Second portion of body-cavity (collar-cœlom). *bc*³. Third portion of body-cavity (trunk cœlom). *br.* Pharynx. *c.p.* Collar-pores. *g.s.* Gill-slits. *int.* Intestine. *n.s.* Nervous system. *op.* Operculum. *oes.* Œsophagus. *st.* Stomach. *t.* Base of tentacle.

In its internal organisation, if due allowance be made for its U-shaped alimentary canal, Cephalodiscus greatly resembles Balanoglossus (Figs. 126, 127). The buccal shield of the former is obviously the equivalent of the proboscis of the latter, and the cavity which it contains corresponds to the proboscis-cavity. Moreover, the proboscis-cavity in Cephalodiscus (*i.e.* the cavity of the buccal shield) communicates with the exterior by *two proboscis-pores* placed right and left of the dorsal middle line.

Following behind the buccal shield is the *collar-region*, from which the branchial plumes arise dorsally, while laterally and ventrally it is produced into a free fold to form the above-mentioned operculum. The collar-region contains a section of the cœlom which is precisely homologous with the collar-cavities of Balanoglossus. As in the latter form, it communicates with the exterior by a pair of *collar-pores* which open at the level of the gill-slits.

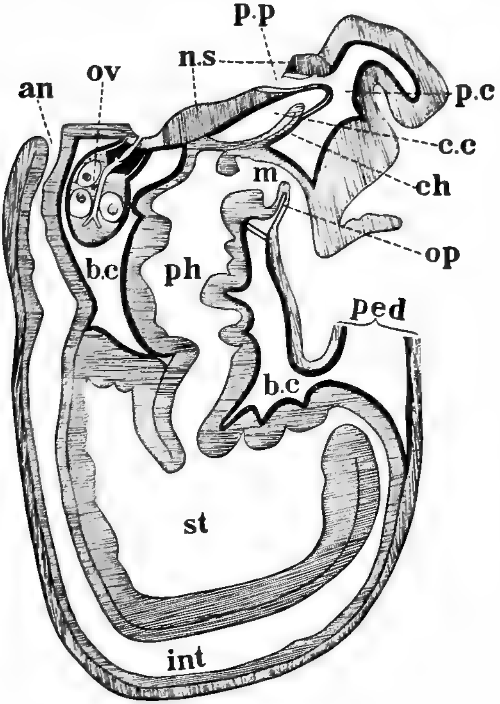

Fig. 127. — Longitudinal sagittal section through an adult Cephalodiscus. (After HARMER.)

The section is supposed to be taken sufficiently to one side of the middle line to allow of the representation of one of the ovaries and one of the proboscis-pores.

a. Anus. *b.c.* Trunk-cœlom. *c.c.* Collar-cœlom. *ch.* Notochord. *int.* Intestine. *m.* Mouth. *n.s.* Nervous system. *op.* Postoral lamella (operculum). *ov.* Ovary; the oviduct is deeply pigmented. *p.c.* Præoral cœlom (cavity of buccal shield). *ph.* Pharynx. *p.p.* Proboscis-pore. *ped.* Base of pedicle. *st.* Stomach.

The collar-cœlom is continued posteriorly into the operculum, and anteriorly into the twelve tentacular appendages.

Finally, behind the collar comes the region of the body containing the viscera, which are surrounded by the third section of the cœlom.

Only the female reproductive organs have been observed up to the present time in Cephalodiscus. They occur as a pair of gonadic sacs, opening to the exterior on each side of the dorsal middle line between the anus and the central nervous system. The latter is very simple, being represented merely by a dorsal thickening of the ectoderm, with nerve-fibres in the region of the collar and posterior portion of proboscis.

Finally, a short notochordal diverticulum projects into the base of the buccal shield as in Balanoglossus.

Rhabdopleura differs considerably from Cephalodiscus in many respects, but, nevertheless, has some fundamental characteristics in common with it. In Rhabdopleura the individuals of a colony are not independent, but are connected with each other by a common cord or *caulus*, which represents the remains of the contractile stalks of the polyps. As the growth of the colony proceeds, the distal portions of the stalks (*i.e.* the portions farthest away from the animals) become shrunken and hard. The buds arise from the soft portions of the caulus, and never become detached as they do in the case of Cephalodiscus. There is only a single pair of tentacular plumes in Rhabdopleura.

FOWLER has recently shown that in Rhabdopleura the cœlom, whose existence was first established by LANKESTER, exhibits the same subdivisions as have been mentioned above for Cephalodiscus; namely, (1) the cavity of the large buccal shield, (2) the collar-cavity opening to the exterior by a pair of dorsally placed collar-pores, and (3) the body-cavity proper surrounding the alimentary canal. According to Fowler, who has recently described them in Rhabdopleura, the nervous system and notochord have essentially similar relations to those which obtain in Cephalodiscus, but there are no proboscis-pores and no gill-slits.

THE PRÆORAL LOBE OF ECHINODERM LARVÆ.

In the previous pages a good deal of stress has been laid on the existence of a præoral lobe in the various types considered. We have recognised it in the snout of Amphioxus (præoral cœlom + præoral pit), in the proboscis of Balanoglossus, the fixing organ of the Ascidian tadpole, and in the buccal shield of Cephalodiscus and Rhabdopleura.

From a morphological standpoint the præoral lobe is probably one of the most important, as it is certainly one of the oldest, structures of the body of bilateral animals, and it becomes, therefore, a matter of the first moment to be able to trace the modifications which it has undergone along the different lines of evolution which have culminated in the existing types of animal life. The subject is a very large one, and can only be treated here in its broadest outlines.

It is now very generally admitted by zoölogists that the Echinoderms (star-fishes, sea-urchins, etc.) owe the *radial* symmetry, which is one of the most obvious characteristics of their organisation, to their having been derived from *bilaterally* symmetrical ancestors, which became adapted to a fixed or sessile existence. If this view is correct, and there is good reason for supposing that it is, it follows that the majority of living Echinoderms have secondarily lost their sessile mode of existence, and have again become free-living, retaining, however, their radial symmetry. At the present time the fixed habit of life is only retained by the members of one of the subdivisions of the Echinoderm class; namely, the *Crinoidea.*

Most genera of Crinoids (*Rhizocrinus*, *Pentacrinus*, etc.) remain fixed by a long, jointed stalk throughout life; but the well-known "feather-star," *Antedon rosacea*, is only fixed during a certain period of its larval development. At the close of the period of fixation the body of the animal, or, as it is called, the *calyx*, breaks away from the stalk by which it was attached to the rocks, and so begins to lead a free existence, being capable of swimming vigorously by the flapping of its arms.

Although the existing Crinoids have become extensively modified along their particular line of evolution, yet there is reason to believe that they represent the more immediate descendants of the primæval form which exchanged its primitively free life and bilateral symmetry for a sessile existence and radial symmetry. This view is strengthened by the character of the free-swimming larva of Antedon. This larva does not possess, in any extravagant degree, those fantastic structures which are so characteristic of other Echinoderm larvæ, such as the provisional ciliated processes or arms of the "Pluteus" (larva of sea-urchins), or the undulating ciliated bands of Auricularia.

On the contrary, the larva of Antedon is a simple barrel-shaped organism, with regular ciliated bands passing around it (Fig. 128).

Perhaps the structure which, above all, stamps the free-swimming larva of Antedon as having, from a phylogenetic point of view, a more primitive type of organisation than that of other Echinoderm larvæ, is the well-developed *apical plate* at its anterior extremity. We may express this in other words by saying that the larva of Antedon possesses a central nervous system at the apex of its præoral lobe. That the præoral lobe in this larva is not sharply marked off from the rest of the body is a detail of no morphological significance.

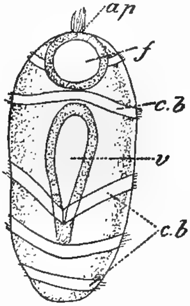

Fig. 128.—Free-swimming larva of *Antedon rosacea*, from the ventral side. (After SEELIGER.)

a.p. Apical pole. *c.b.* Ciliated bands. *f.* Fixing disc. *v.* Vestibulum (so-called larval mouth, although at this stage simply an ectodermic groove).

The apical nervous system of the Antedon larva was discovered in 1888 by H. BURY, and has been more clearly brought out and emphasised in a recent work by Dr. OSWALD SEELIGER. At the point which is marked externally by the anterior tuft of long cilia in Fig. 129 there is a slight groove in the ectoderm below which nerve-fibres and ganglion-cells can be identified. Seeliger further describes a pair of longitudinal nerves running from the nervous area of the apex along the ventro-lateral margins of the body.

As already indicated, the *apical plate* is, as a general rule, conspicuous by its absence in the typical Echinoderm larva. In the free-swimming larva of Antedon, however, it is emphatically present, although destined to become entirely aborted after the fixation of the larva.

In most Invertebrate larvæ in which an apical plate is present (*e.g.* the Trochophore-larva of Annelids and Molluscs) it becomes, during the metamorphosis, involved in other ectodermic thickenings of the præoral lobe, which collectively give rise to the cerebral or supracœsophageal ganglion. The apical plate may thus be defined as a primitive central nervous system at the apex of the præoral lobe, being the forerunner and formative centre of the cerebral ganglion of the Invertebrates.

Although, with the exception of the Crinoids, there is no apical plate in the typical Echinoderm larva, yet, as noted above, in many cases a curious transitory lengthening of the ectodermic cells at the apical pole has been, and can be without great difficulty, observed in larvæ of star-fishes and sea-urchins. This alone would seem to indicate the former existence of a central nervous system at the apex of the præoral lobe in the bilateral ancestor of the Echinoderms.

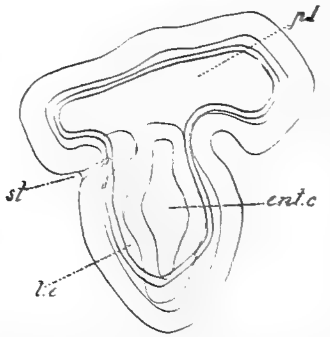

Fig. 129.—Larva of *Asterina gibbosa*, viewed as a transparent object from the left side. (After LUDWIG.)

ent.c. Enteric cavity. *l.e.* Left enterocœl, communicating with the right enterocœl through *p.l*, the præoral lobe. *st.* Stomodœum.

The way in which the primary blastocœlic cavity of the præoral lobe can be replaced by a dilatation of the enterocœl has been described above, both for Tornaria and for the larva of *Asterias vulgaris* (Figs. 121–122). In some cases, as in *Asterina gibbosa*, the præoral lobe is occupied by the enterocœl from the very beginning. In the "Pluteus" larva of the Echinids (sea-urchins) the præoral lobe is much reduced; but in other Echinoderms, as in the singular larva of *Asterina gibbosa*, and in the so-called Brachiolaria-larva of the Asterids (star-fishes) in general, it is very prominent, and serves as an effective locomoton (*creeping*) organ.

The very interesting observation has recently been made by MacBride, that the larva of *Asterina gibbosa* actually undergoes temporary fixation at the beginning of the metamorphosis, the fixation being effected by the præoral lobe in a manner strikingly similar to that of the larvæ of *Antedon* and of *Ciona*.

In the larva of Antedon the adhering disc, by which the larva eventually fixes itself to some foreign surface, is placed near the front end of the præoral lobe immediately below the apical plate.

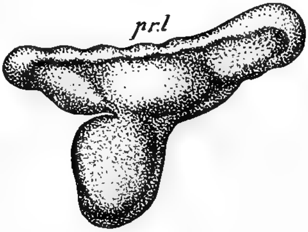

Fig. 130. — Larva of *Asterina gibbosa*, viewed as an opaque object from the left side. (After Ludwig.)
pr.l. Præoral lobe.

The central nervous system of the adult Echinoderm arises in entire independence of the actual or suppressed apical nervous system of the larva, and not at all from the ectoderm of the præoral lobe.

We have thus seen how within the limits of a single group (viz. the Echinoderms) the præoral lobe can become completely emancipated from the central nervous system; and we have further recognised the fact that whether the cavity of the præoral lobe is a derivative of the primary or secondary body-cavity, whether it contains loose mesenchyme or is lined by an endothelium, the morphological value of the præoral lobe itself remains the same.

THE PRÆORAL LOBE OF THE PROTOCHORDATES.

It is probable that the misunderstandings and disagreements which are of such frequent occurrence among morphologists with regard to the comparison of the types of central nervous system presented respectively by the

Vertebrates and the Invertebrates, are largely due to the failure to detect some general principle of evolution to which that archaic structure, the præoral lobe, has been subjected.

Nevertheless, there are many indications which point irresistibly to the conclusion, which I have recently brought forward, that the prime factor which must be recognised in the evolution of the præoral lobe, from the relations which it presents in the Invertebrates to those which it holds in the Protochordates and Vertebrates, is its *emancipation from the central nervous system.*

In the great groups of the Annelids, Molluscs, and Arthropods, the præoral lobe (prostomium, procephalic lobe) is essentially the seat of the brain or cerebral ganglion. The latter, through its representative, the *apical plate,* is the main and often the sole element of the central nervous system in the Trochophore-larva of Annelids and Molluscs.*

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* In speaking of the apical plate as the forerunner or formative centre of the cerebral ganglion, it must not be assumed that these are not distinct structures. The apical plate is essentially median and unpaired, while the cerebral ganglion is paired. They can both, however, be included under the general term, *apical nervous system,* since they arise from the ectoderm of the præoral lobe. On the other hand, the cerebral ganglion may arise independently of an apical plate; as, for instance, in *Lumbricus,* where there is no apical plate, or in the *Nemertines,* where the apical plate is discarded together with other larval structures (Pilidium). Again, as in Lumbricus and many other cases, the cerebral ganglion, after having separated from the ectoderm of the præoral lobe, may recede backwards for a considerable distance, so as not to lie in the præoral lobe in the adult. It is possible that the position of the cerebral ganglia of Nemertines may be accounted for by some such phylogenetic recession from the præoral lobe.

If necessary, it might be said that the præoral lobe can acquire emancipation from the central nervous system by a simple recession of the cerebral ganglion. In the case of the Protochordates, however, on the view here advocated, the præoral lobe has acquired emancipation from the central nervous system, not by the mere recession, but by the complete disappearance of the Invertebrate cerebral ganglion.

At a later stage of development the longitudinal nerve-cord (confining the description to the Annelids for the sake of simplicity) arises *independently* of the cerebral ganglion, from a pair of longitudinal thickenings of the ectoderm near the mid-ventral line, becoming secondarily connected with the cerebral ganglion by the circumœsophageal nerve-collar or commissure.

As already indicated, it seems probable, as was suggested by Balfour and Gegenbaur, that the ventral nerve-cord of the Annelids is to be regarded as having arisen phylogenetically by the mutual approximation of two such lateral cords as occur in the Nemertines, and like the latter may be supposed to have originated by a concentration on the ventral side of the body of that primitively continuous sub-epidermic nerve-plexus which is such a characteristic feature of the Nemertines. From a consideration of the adult nervous system in the Echinoderms, Nemertines, Enteropneusta (Balanoglossus), Annelids, and Molluscs, it is evident that such a concentration of nervous tissue has from first to last occurred along very different lines.

Speaking in broad terms, it may be said that the only portion of the Invertebrate nervous system which, in its prime essence, is invariable and universal (due allowance being made for exceptional cases) is the cerebral ganglion or its forerunner, the apical plate, the seat of which lies in the præoral lobe.[2]

Under these circumstances it will suffice to confine our attention to the præoral lobe, in the belief that if an understanding can be arrived at with regard to that important structure, one of the chief difficulties in the way of a just conception of the relations existing between Vertebrates and Invertebrates will have been overcome.

Returning now to Balanoglossus, we have to remark that in the Tornaria larva the central nervous system is represented entirely by the apical plate of the præoral lobe, the situation of the apical plate corresponding to the anterior tip of the proboscis of the adult. Unlike the Annelids, however, the apical plate of Tornaria does not become replaced after the manner of the Invertebrates by the development of a cerebral ganglion arising like it from the ectoderm of the præoral lobe and with it as a formative centre. On the contrary, it completely disappears after the metamorphosis, having become replaced physiologically by the development of the medullary tube in true Vertebrate fashion from the dorsal ectoderm of the collar-region behind the præoral lobe.*

In the Ascidian larva, however, and in Amphioxus, the characteristic Invertebrate apical nervous system no longer appears in any stage of development, its physiological function having been once for all assumed by the medullary tube (cerebral vesicle + spinal cord) which lies *par excellence* behind the præoral lobe (Fig. 131).

Anterior and Posterior Neurenteric Canals, and the Position of the Mouth in the Protochordates.

After the postoral medullary tube had led indirectly to the complete obliteration of the præoral apical nervous system, and had attained to such a degree of development as we find, for instance, in the Ascidian tadpole, the central canal of the cerebro-spinal nervous system appears to have acquired remarkable relations with the alimentary canal. At both ends of the body connecting ducts be-

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* For a detailed account of the formation of the medullary tube in the collar-region of Balanoglossus see MORGAN (Bibliography, Nos. 124 and 125).

came established between the nervous and digestive systems, known respectively as the *anterior* and *posterior neurenteric* canals.

The posterior neurenteric canal is only of transitory occurrence in all existing Vertebrates, and leads from the

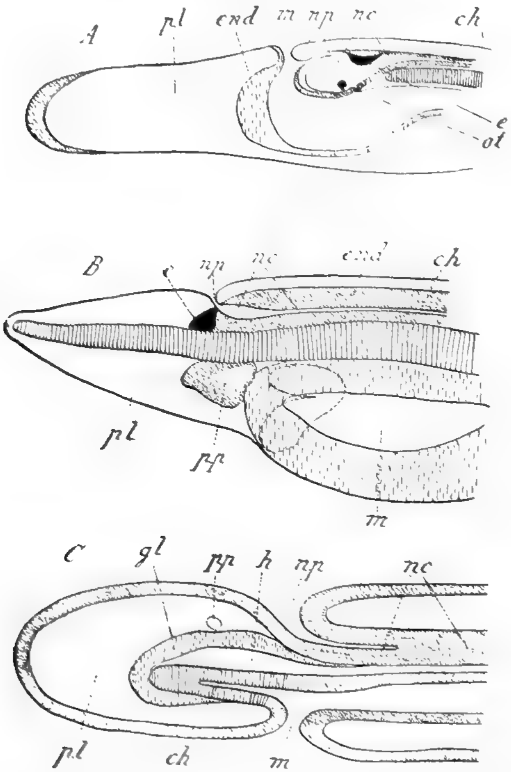

Fig. 131.—Diagrammatic representations of the anterior region of the body in (*A*) an Ascidian larva, (*B*) larva of Amphioxus, and (*C*) Balanoglossus. (After Willey.)

The figure of Balanoglossus was compiled from Bateson's figures; the proboscis-pore is indicated rather too far forwards.

p.l. Præoral lobe (fixing organ, snout, proboscis). *cnd.* Endostyle. *p.p.* Præoral pit or proboscis-pore. *m.* Mouth. *np.* Neuropore. *nc.* Medullary tube. *ch.* Notochord. *e.* Eye. *ot.* Otocyst. *gl.* and *h.* Proboscis-gland and proboscis-heart of Balanoglossus neural tube into the extreme posterior end of the alimentary canal; in fact, into that portion of it which, in the embryos of the higher forms, is known as the post-anal gut. The anterior neurenteric canal, in its most primitive condition, opens into the base of the buccal tube (Fig. 131).

On this account we find in the Ascidian tadpole that the mouth is no longer ventral, as it is in Balanoglossus, but is placed dorsally, immediately in front of the anterior extremity of the medullary tube. This intimate relation between the mouth and the central nervous system gives a reason for the contrast between the dorsal position of the mouth in the Ascidian tadpole and its ventral position in Balanoglossus.

In Amphioxus we have seen that the mouth has been forced aside from its more primitive dorsal position by the forward extension of the notochord to the tip of the

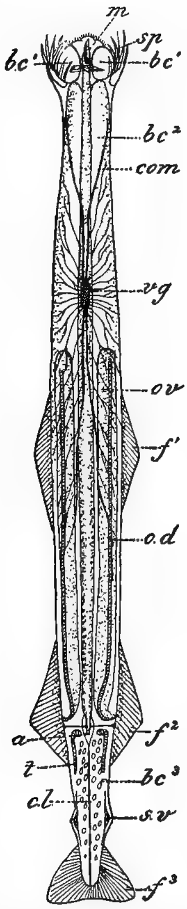

Fig. 132. — *Sagitta hexaptera* from the ventral surface; nearly three times natural size. (After O. HERTWIG.)

a. Anus. *bc*¹. Head-cavities. *bc*². Trunk-cœlom. *bc*³. Caudal cœlom. *c.l.* Caudal septum. *com.* Commissure, from the cerebral ganglion to the single ventral ganglion. *f*¹, *f*², *f*³. Fins. *m.* Mouth. *o.d.* Oviduct. *ov.* Ovary. *sp.* Prehensile bristles. *s.v.* Seminal vesicle. *t.* Testis. *v.g.* Ventral ganglion.

præoral lobe. The origin of the main cavity of the præoral lobe in Amphioxus from the right of a symmetrical pair of head-cavities (anterior intestinal diverticula of Hatschek) has been described in a previous chapter. In Balanoglossus there is no such complete division of the præoral body-cavity, but it is throughout a single space, its right and left halves being confluent. If we now compare the condition of things in the embryo of Amphioxus, where we have a symmetrical pair of head-cavities, with that of some other form which, in the adult condition, possesses a distinct pair of such cavities, it may assist us in imagining how the mouth could have assumed such opposite relations as have been mentioned above.

But first it may be pointed out that in *Appendicularia*, where, as it would appear, in correlation with the secondary acquirement of a purely pelagic habit of life (although this point of view is not shared by such authorities as Herdman, Seeliger, and Brooks), the præoral lobe has been reduced to a minimum, or to zero, the mouth has thereby come to lie in a terminal, or sub-terminal, position, with a slight tendency towards the dorsal side.*

In the curious pelagic worm, *Sagitta*, we meet with another instance of an animal in which the præoral lobe, in the ordinary sense of the term, is reduced to a minimum, and the mouth has therefore a sub-terminal position, with a ventral inclination (Fig. 132). But although there is no distinct præoral lobe in Sagitta, there is, nevertheless, a *pair of head-cavities*, which are directly comparable, if not perfectly homologous, with the above-mentioned

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* Whatever the truth may be as to the precise systematic position and phylogenetic value of Appendicularia, one thing, to my mind, remains absolutely certain, namely, that it has descended from a form which possessed a præoral lobe, and that it has secondarily lost that structure.

head-cavities of Amphioxus, although they have a somewhat different origin.

It should not be forgotten that Sagitta occupies a very isolated position in the zoölogical system, being placed in a group by itself, the *Chætognatha*, and that therefore the peculiarities of its organisation cannot be taken as representing any definite intermediate stage in the phylogeny of other forms, yet, from a general standpoint, the conditions which it presents in its life-history are highly instructive.

The head-cavities of Sagitta arise by constriction from the anterior extremities of the single pair of archenteric pouches which give rise to the cœlom of the adult. They remain distinct and separate on either side of the head throughout life. If, now, we imagine them to grow forward and fuse together in front of the mouth, in a similar manner to that described above for the enterocœlic pouches of Asterias, we should have a præoral body-cavity of a similar character to that of Balanoglossus.

Now, the ultimate position of the mouth under these new conditions would depend upon circumstances affecting the whole organisation of the animal.

In an animal whose grade of organisation was on an approximate level with that of Sagitta the mouth would undoubtedly remain on the ventral side of the body. But in an animal whose organisation had reached the stage of evolution represented by that unknown ancestor of Amphioxus (most nearly represented at the present time by the Ascidian tadpole), whose notochord did not extend beyond the anterior limit of the neural tube, the mouth would pass to the dorsal side of the body to come into connexion with the neural canal.

THE PRÆORAL LOBE IN THE CRANIATE VERTEBRATES.

After what has been said above, in this and the preceding chapters, the question as to how the præoral lobe is represented in the craniate Vertebrates need not detain us long.

Since, as shown above, the nervous element of the præoral lobe (apical plate and cerebral ganglion) is entirely lacking in the Vertebrates, we can only expect to find the mesodermal element represented in the head-cavities of the higher forms.

In consequence of the great development of the brain, even in the lowest craniate Vertebrates, as compared with Amphioxus, and in consequence too of the cranial flexure, the head-cavities have been made to assume a more subordinate position, and no longer take part in the formation of a prominent lobe in front of the body. This is a perfect illustration of "le principe du balancement des organes" of Geoffroy Saint-Hilaire, the præoral lobe decreasing as the brain increases. A comparison between Figs. 70, 72, 117, and 135 will show at once that the præoral head-cavities of Amphioxus and Balanoglossus are the homologues of the *præmandibular head-cavities* of the craniate Vertebrates.

These cavities lie at first below the mid-brain, and later their walls give rise to most of the eye-muscles. In Figs. 91 and 135 the median portion of the præmandibular cavities can be seen still in the form of an anterior pocket of the endoderm, and it may be noticed how far it is removed from the anterior extremity of the body to which it extends in Amphioxus, etc. In the craniate Vertebrates the brain extends forwards, and the head-cavities remain behind. This is, as we should expect, the exact reverse to what obtains in Amphioxus.

In connexion with the evolution of the præoral lobe, we thus have an excellent example of repeated change of function.

We may conclude, therefore, that the præoral lobe, which, in the *Invertebrates*, is above all the bearer of the cerebral ganglion, and in the *Protochordates* is released from this function and becomes in part a locomotor (Balanoglossus, Cephalodiscus) fixing (Ascidian) and burrowing (Amphioxus) organ, is represented in the craniate Vertebrates by the *præmandibular head-cavities*, whose walls give rise to most of the eye-muscles.

THE MOUTH OF THE CRANIATE VERTEBRATES.

In consequence of the increase in the size of the brain, its forward extension and its cranial flexure, together with the relative reduction of the head-cavities, it is obvious that the mouth has been carried round from its primitively dorsal position to its final position on the ventral side of the head in the craniate Vertebrates. (Cf. Fig. 91.) This would have been all that need be said about the mouth were it not for the fact that the view, originally started by Dohrn, that the Vertebrate mouth was a new formation resulting from the fusion of two gill-slits, has received such wide support and still in a measure holds its own.

Since the Annelid mouth perforates the central nervous system in passing through the circumœsophageal nerve-collar, it was necessary to frame a theory which would get over the difficulty that nothing of the kind occurs in the Vertebrates. Accordingly Dohrn supposed that the old Annelid mouth had become aborted, and was replaced by a new mouth derived from a fusion across the mid-ventral line of a pair of gill-clefts. Dohrn was a trifle uncertain as to the rudiment of the old mouth, but Beard was more certain on this point, and thought he had established the fact that the hypophysis cerebri represented the remains of the old Annelid mouth.

Dohrn certainly succeeded in bringing forward some apparently good evidence in support of his theory of the gill-slit origin of the mouth. This evidence was derived from the study of the development of the mouth in Teleostean or bony fishes.

In many Teleosteans the mouth has at first an apparently double origin, in that two separate ectodermal ingrowths occur which fuse with the endoderm, instead of the median stomodœal involution which is so characteristic of other Vertebrates. This double origin of the mouth is particularly well shown in the embryos of the remarkable toad-fish, *Batrachus tau*, as observed by Miss Cornelia Clapp at the Marine Biological Laboratory of Woods Holl, Mass., in 1889 (Fig. 133). In this case the mouth-cavity is seen to be divided into two halves by a median septum.

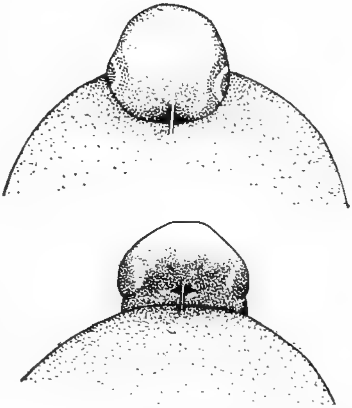

Fig. 133. — Two frontal views of an embryo of *Batrachus tau*, to show the double nature of the stomodœum. (From hitherto unpublished drawings kindly lent by Miss C. M. Clapp.)

The embryo is lying upon the yolk, and the septum which divides the stomodœum passes from the upper lip to the surface of the blastoderm which covers the yolk. The lower figure is a drawing of the same embryo as the upper, a few hours later. Above the stomodœum are seen the small nasal pits (rudiments of the external nares), and at the sides of the head are the rudiments of the eyes.

Subsequently the septum becomes absorbed, and the two halves of the mouth coalesce. In view of the previous existence of the gill-slit theory of the mouth, some such theory being a necessary accessory to the Annelid-theory, it is not surprising that this undoubted double origin of the mouth in Teleosteans should be regarded as a striking confirmation of Dohrn's hypothesis. And yet, occurring as it does only in the Teleosteans, whose development is admittedly in many respects highly modified, the interpretation which Dohrn and his followers have placed upon this observation must always have been open to doubt. The simplest explanation of the double origin of the Teleostean mouth is that, owing to certain conditions (possibly mechanical) of development, the two angles of the mouth develop before the median portion. This is the conclusion which H. B. POLLARD has also reached in his recent studies on the development of the head in the Teleostean fish, *Gobius capito.*

According to the standpoint I have adopted in the foregoing pages, there is no *a priori* reason for doubting that the Vertebrate mouth is completely homologous with the Protochordate mouth; and that the latter in its turn is the direct descendant of the typical Invertebrate mouth.

Again, the anatomy and development of the Protochordates and of the Cyclostomi (Ammocœtes) show no indication whatever of a discontinuity in the evolution of the most highly elaborated mouth of the gnathostomous or jawed Vertebrates.

We conclude, therefore, that the ventral mouth of the craniate Vertebrates is the homologue of the primordial dorsal mouth as we find it in the Protochordates, and that its direction of evolution has been, as was so ably maintained by BALFOUR, from the cyclostomous to the gnathostomous condition.

SIGNIFICANCE OF THE HYPOPHYSIS CEREBRI.

The pituitary body, or hypophysis, belongs to the series of ductless "glands" (pineal body, thyroid gland, thymus, etc.) which are such a characteristic feature of the vertebrate organisation. It arises as an ectodermal involution from the roof of the stomodœum, directed towards the base of the primary fore-brain, from which the infundibulum grows out.

The pituitary involution becomes in most forms nipped off from the stomodœum, and then lies as a closed sac in contiguity with the infundibulum. Later on it produces a system of branches, the lumina of which tend to disappear; and in some forms (*e.g.* Mammalia) it undergoes actual fusion with the infundibulum.

The very constant relation of the hypophysis to the infundibulum in the craniate Vertebrates (see Fig. 134) naturally led to the supposition that there must originally have been a functional connexion between the two structures of a similar nature to that which exists between the olfactory pit and neuropore in Amphioxus. Recent researches, however, have rendered it probable that such a supposition is erroneous. Von Kupffer has discovered the homologue of the lobus olfactorius of Amphioxus in the craniate Vertebrates, and has shown that it occurs at a point far removed from the infundibular region.

Until recently it was also very generally thought that the infundibulum represented the anterior end of the brain, which had become bent downwards and backwards by the cranial flexure. Kupffer, however, has brought forward weighty reasons for doubting this view. According to him, the infundibulum is essentially a downgrowth or evagination from the floor of the brain, occurring behind the anterior terminal extremity of the brain.

It follows that the morphological anterior extremity of the craniate brain coincides with the median *lobus olfactorius impar*, which also represents the point of last connexion of the medullary tube with the superjacent ectoderm. The lobus olfactorius impar lies in the anterior vertical wall, which forms the boundary of the primary fore-brain in front, known as the *lamina terminalis*. RABL-RÜCKHARD has also observed the median olfactory lobe in the Selachian embryo (Fig. 134), and it has since been found by BURCKHARDT in other forms.

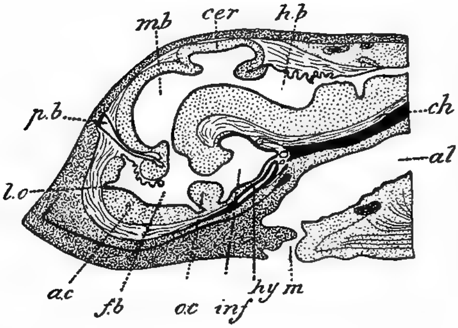

Fig. 134. — Sagittal section through the head of an embryo of *Acanthias*. (After RABL-RÜCKHARD.)

a.c. Position of anterior commissure. *al.* Alimentary canal. *cer.* Cerebellum. *ch.* Notochord; the black shading below the notochord indicates the aorta. *f.b.* Fore-brain. *h.b.* Hind-brain. *hy.* Hypophysis, already shut off from the stomodœum and lying as a closed sac at the base of *inf*, the infundibulum. *l.o.* Lobus olfactorius. *m.* Mouth. *m.b.* Mid-brain. *o.c.* Optic chiasma. *p.b.* Pineal body (epiphysis).

It can thus hardly be doubted that the median rudimentary olfactory lobe of the embryos of the higher Vertebrates is homologous with the lobus olfactorius of Amphioxus (Fig. 51), and, like the latter, represents the remains of the neuropore. In Amphioxus, however, the olfactory lobe abuts against the olfactory pit, and, in fact, in young individuals opens into it by the neuropore (Fig. 45).

On the view which I have urged above, that the olfactory pit of Amphioxus is homologous with the hypophysis cerebri of the craniate Vertebrates, it must be assumed that in the latter forms, the neuropore having ceased to be in any way a functional organ, the hypophysis, which has likewise become (morphologically) a vestigial structure, has been mechanically separated from the neuropore, with which it was primitively in functional connexion. It must be supposed that this separation of the hypophysis from the neuropore has been effected by the more rapid downward growth of the ectoderm (from which the hypophysis arises) than of the wall of the brain, so that the hypophysis has been carried farther round to the lower side of the head than the neuropore (Fig. 135). The reason for this unequal growth of the external body-wall and of the cerebral wall may, perhaps, be sought for in the great and independent increase in the cubical contents of the brain.[3]

We thus arrive at the conclusion that the present relation of the hypophysis to the infundibulum in the craniates, however intimate it may be in some cases, is, nevertheless, incidental and secondary.

That this conclusion is not so strained as might appear at first sight is clearly shown by the fact that the infundibulum is not the only structure with which the hypophysis enters into close relations.

In the exceptional cases of Myxine and Bdellostoma, for instance, the distal end of the hypophysis has nothing to do with the infundibulum, but actually opens into the pharynx. In these hag-fishes, as also in the lamprey (where there is no internal opening of the hypophysis into the pharynx), the external opening of the hypophysis does not close up, as in the higher forms, but persists throughout life, becoming carried round to the top of the head during the embryonic development by differential growth of neighbouring parts, as has been actually observed in Petromyzon.

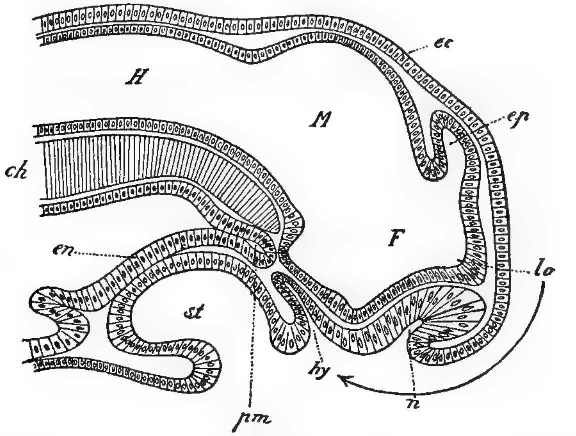

Fig. 135. — Median sagittal section through the head of young Ammocœtes. (After KUPFFER.)

The arrow indicates the extent to which the hypophysis has been (hypothetically) removed from the neighbourhood of the neuropore (lobus olfactorius impar).

ch. Notochord. *ec.* Ectoderm. *en.* Endoderm. *ep.* Epiphysis. *hy.* Hypophysial involution. *l.o.* Lobus olfactorius impar. *n.* Nasal involution. *pm.* Median portion of præmandibular cavity. *st.* Stomodœum. *F.M.H.* Primary fore-, mid-, and hind-brain.

In other cases, as, for example, in the embryo of the rabbit, it has been observed that the hypophysis actually undergoes a temporary fusion with the front end of the notochord; and in all cases the distal end of the hypophysis grows inwards as much towards the notochord as towards the infundibulum, so that for the embryonic stages of the craniate Vertebrates it might be said that the relations of the hypophysis to the front end of the notochord are as constant as its relations to the infundibulum. So close is the apparent relation of the hypophysis to the notochord that at least one zoölogist, HUBRECHT, has suggested that there was originally a functional connexion between the two structures.

Again, in the embryo of *Acipenser*, the sturgeon, as shown by KUPFFER, the distal end of the hypophysis undergoes temporary fusion with the subjacent wall of the alimentary cavity. In spite of the extremely modified character of the embryo of Acipenser (the embryo being flattened out like a disc over the yolk), Kupffer regards this fusion of the hypophysis with the endoderm as being of great morphological significance.

On the contrary, for the reasons mentioned above, I would regard all these fusions of the hypophysis in the craniate Vertebrates, whether with the infundibulum, notochord, or endoderm, as being of an entirely incidental character, often due, perhaps, to a tendency of such contiguous embryonic tissues to fuse together.

I therefore suggest that : *The hypophysis arose in connexion with a functional neuropore ; when the neuropore ceased to be functional, there was no longer any bond of union between its inner portion, which opened into the cerebral cavity, and its outer portion, which opened into the buccal cavity ; and these two portions became separated by differential growth of the cerebral and body-walls* (cf. Fig. 135).

The Ascidian Hypophysis.

The development of the hypophysis in a typical Ascidian, its constriction from the wall of the cerebral vesicle in the form of a tube, and its opening into the buccal cavity, or branchial sac, have been described above. The most serious objection which has been raised against the comparison of the hypophysis of the Ascidians with that of the craniate Vertebrates is, that in the former the hypophysis opens, not at an ectodermal surface into the stomodœum, but at an endodermal surface (behind the stomodœum) into the branchial sac. This is undoubtedly the case in some Ascidians, *e.g.* *Distaplia*, and probably also in *Clavelina*, etc. In *Ciona*, however, as I can state after renewed study of the question, it apparently opens at first into the buccal cavity precisely in the line of junction between the stomodœum and the branchial sac, so that its upper margin is continuous with the stomodœal epithelium, while its lower margin is continuous with the epithelium of the branchial sac.

It is probable that too much stress has been laid on the question whether the hypophysis of the Ascidians opens at an endodermic or at an ectodermic surface, and that thus the attention has been diverted from the essential fact that the hypophysis opens into the buccal tube at the entrance to the branchial sac. In the case of the Ascidians, therefore, I should also regard the fusion of the hypophysis, whether with the ectoderm of the stomodœum or with the endoderm of the branchial sac, as being in itself non-essential, while the actual opening of the hypophysis (itself derived by constriction from the nerve-tube) into the buccal cavity, apart from the question of an ectodermal or endodermal surface, is the essential point.

CONCLUSION.

From the facts that have been recorded and the considerations that have been urged in these pages, it would follow that one of the chief factors in the evolution of the Vertebrates has been the concentration of the central nervous system along the dorsal side of the body (in contrast to the position of the longitudinal nerve-cord of Annelids, etc., along the ventral or *locomotor* surface), and its conversion into a hollow tube. If it be admitted that the hypophysis became evolved in connexion with a functional neuropore, it is obviously a structure which has arisen within the limits of the Vertebrate phylum, and can, therefore, have no representative in the typical Invertebrate organisation. It has been suggested by ADAM SEDGWICK and VAN WIJHE that the original function of the central canal of the spinal cord was to promote the respiration (oxygenation) of the tissue of the central nervous system, water entering by the neuropore, and passing out through the posterior neurenteric canal.

It is not so easy to form a conception as to the prime origin of the other two cardinal characteristics of a Vertebrate (Chordate); namely, gill-slits and notochord.

As to the origin of gill-slits, it has been suggested independently by HARMER and BROOKS, that they arose at first not so much to perform the direct function of respiration, as to carry away the bulk of the water which constantly entered the mouth with the food, so as to avoid the necessity and discomfort of the never-ceasing flow of water through the entire length of the alimentary canal. In Cephalodiscus, for example, the luxuriant branchial plumes must be sufficient for the respiration of the minute animal, while the usefulness of the pair of gill-slits, in allowing the surplus water to pass out of the pharynx, is evident.

The notochord is more difficult to explain, and the fact of its occurrence in the proboscis of Balanoglossus and in the tail of the Ascidian tadpole is very puzzling. The mode of its occurrence in Balanoglossus is undoubtedly divergent, and not in the direct line of Vertebrate descent. It is possible that the notochord has not arisen through a process of elaborate change of function from a pre-existing structure, but simply as a solidification of the endoderm which was continued into the caudal or post-anal extension of the body to form the axial support for a locomotor tail; while the subsequent extension of the notochord into the præ-anal region of the body is not difficult to understand. The general capacity of the endoderm for producing skeletal tissue is already present in some of the Medusæ and Hydroid polyps whose tentacles are stiffened by a solid endodermal axis.

From a purely morphological point of view it now seems as though the præoral lobe and in a lesser degree, perhaps, the hypophysis, would materially assist in furnishing the key to a correct appreciation of the relationship between the craniate Vertebrates, the Protochordates, and the Invertebrates.

As we have indicated above, in the formulation of the Annelid-theory[4] no allowance has been made for the principle of *parallelism* in evolution; but it is impossible to doubt that this is a very potent factor which should always be borne in mind in estimating the genetic affinity between widely different groups of animals. The closer the superficial resemblance between an Annelid and a Vertebrate (in the possession of somites, segmental organs, etc.) is shown to be, the more perfect appears the parallelism in their evolution and the more remote their genetic affinity.

For the present we may conclude that the proximate ancestor of the Vertebrates was a free-swimming animal intermediate in organisation between an Ascidian tadpole and Amphioxus, possessing the dorsal mouth, hypophysis, and restricted notochord of the former; and the myotomes, cœlomic epithelium, and straight alimentary canal of the latter. The ultimate or primordial ancestor of the Vertebrates would, on the contrary, be a worm-like animal whose organisation was approximately on a level with that of the bilateral ancestors of the Echinoderms.

NOTES.

1. (p. 246.) For the discussion of the phenomena of metamerism and the enumeration of examples of independent metameric repetition of parts, consult the following: LANG, ARNOLD. *Der Bau von Gunda Segmentata und die Verwandtschaft der Plathelminthen mit Cœlenteraten und Hirudineen.* Mitth. Zool. Stat. Neapel, Bd. III. 1882. p. 187 *et seq.* SEDGWICK, ADAM. *On the Origin of Metameric Segmentation, and Some Other Morphological Questions.* Quarterly Jour. Micro. Sc. XXIV. 1884. pp. 43–82. BATESON, WILLIAM. *The Ancestry of the Chordata.* Quarterly Jour. Micro. Sc. XXVI. 1886. pp. 535–571. CALDWELL, H. *Blastopore, Mesoderm, and Metameric Segmentation.* Quarterly Jour. Micro. Sc. XXV. 1885. pp. 15–28. HUBRECHT, A. A. W. *Report on the Nemertea collected by H. M. S. Challenger, 1873–76.* Chall. Rept. Zoöl. XIX. 1886. (Also, HUBRECHT. *The Relation of the Nemertea to the Vertebrata.* Quarterly Jour. Micro. Sc. XXVII. 1887. pp. 605–644.) VAN BENEDEN, ÉDOUARD. *Recherches sur le Développement des Arachnactis. Contribution à la Morphologie des Cérianthides.* Archives de Biologie, XI. 1891. pp. 115–146. Also consult the recent great work of BATESON, *Materials for the Study of Variation.* London, 1894.

2. (p. 273.) On the subject of the præoral lobe and the apical nervous system of Invertebrates, see the following: BALFOUR, F. M. Comparative Embryology. 1881. Vol. II. Chap. 12. *Observations on the Ancestral Form of the Chordata.* BEARD, J. *The Old Mouth and the New, A Study in Vertebrate Morphology.* Anat. Anz. III. 1888. pp. 15–24. WILSON, E. B. *The Embryology of the Earthworm.* Jour. Morph. III. 1889. pp. 387–462. HATSCHEK, B. *Lehrbuch der Zoologie.* 3d Lieferung. Jena, 1891. WILLEY, A. *On the Evolution of the Præoral Lobe.* Anat. Anz. IX. 1894. pp. 329–332.

3. (p. 285.) From what has been said in the text, it is obvious that the hypophysis of the craniate Vertebrates, in becoming separated from the neuropore, has retained (at least in the embryo) its primitive relations with the buccal cavity, and, like the latter, has been made to assume its present position in consequence of the forward growth of the brain and the ensuing cranial flexure. In Amphioxus, the hypophysis (*i.e.* olfactory pit) arises as an ectodermic involution immediately over the neuropore, but still independent of the latter. In other words, the neuropore exists in Amphioxus for a considerable length of time before the hypophysis forms; and this is in accordance with what we should expect from the analogy of the craniate Vertebrates. In the Ascidians, however, the conditions are somewhat different, and there is at first no such obvious differentiation between neuropore and hypophysis. For the simple Ascidians (*e.g.* Ciona) it must at present remain doubtful whether the increase in size of the hypophysis takes place entirely by interstitial growth, or whether there is any ingrowth from the wall of the buccal tube at the lips of the aperture (dorsal tubercle) of the hypophysis. In any case there are not wanting indications in the Ascidians of a distinction, and even separation, between the distal portion of the hypophysis, which at first opens into the cerebral vesicle, and the proximal portion, which opens into the buccal cavity. In the adult, the proximal portion of the hypophysis has the form of a simple duct, opening by the so-called dorsal tubercle into the buccal cavity, while the subneural gland arises as a proliferation from the ventral wall of the distal portion. In *Phallusia mammillata*, as was discovered by JULIN (*Archives de Biologie*, II. 1881. pp. 211–232), num-

bers of secondary tubules grow out from the principal duct of the hypophysis, and acquire ciliated funnel-like openings into the peribranchial chamber; subsequently HERDMAN (*Proc. Roy. Soc. Edinburgh*, XII. 1882–84. p. 145) found that in this form the dorsal tubercle, or opening of the hypophysis into the buccal cavity, is sometimes absent. In *Ciona intestinalis* I have found in young individuals an obliteration of the lumen of the hypophysis between the proximal and the distal portions. In other cases, as in *Appendicularia*, the glandular portion of the hypophysis may be reduced or absent.

On the subject of the Ascidian hypophysis, the following papers should also be consulted: SHELDON, LILIAN. *Note on the Ciliated Pit of Ascidians and its Relation to the Nerve-ganglion and So-called Hypophysial Gland.* Quarterly Jour. Micro. Sc. XXVIII. 1888. pp. 131–148. HJORT, JOHAN. *Ueber den Entwicklungscyclus der Zusammengesetzten Ascidien.* Mitth. Zool. Stat. Neapel, X. 1893. pp. 584–617. METCALF, MAYNARD M. *The Eyes and Subneural Gland of Salpa.* Baltimore, 1893. (Published as Part IV. of Professor Brooks's Monograph of the Genus Salpa.)

4. (p. 290.) The most complete presentation of the Annelids-theory is contained in the classical *Monographie der Capitelliden des Golfes von Neapel*, by Dr. HUGO EISIG. It is needless to add that this monograph will command the gratitude and admiration of zoölogists to the end of time.

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2 DOHRN, ANTON. *Der Ursprung der Wirbelthiere und das Princip des Functionswechsels*. Leipzig, 1875.

3 HAECKEL, ERNST. *Anthropogenie oder Entwickelungsgeschichte des Menschen*. Leipzig, 1874; 4th Edit., 1891.

4 LANKESTER, E. RAY. Article "*Vertebrata*." Encycl. Brit., 9th Edit. Republished in "Zoölogical Articles," London, 1891.

5 PERRIER, EDMOND. *La Philosophie Zoologique avant Darwin*, 2d Edit. Paris, 1886.

6 SEMPER, CARL. *Die Verwandtschaftsbeziehungen der gegliederten Thiere*. Parts I. to III. Würzburg, 1875–76.

I. AND II.

ANATOMY OF AMPHIOXUS.*

7 ANDREWS, E. A. *The Bahama Amphioxus* (preliminary account). Johns Hopkins University Circulars, Vol. XII. p. 104. June, 1893.

8 ANDREWS, E. A. *An Undescribed Acraniate: Asymmetron lucayanum*. Studies from the Biol. Lab. Johns Hopkins University, Vol. V. No. 4. 1893. pp. 213–247. Plates XIII.–XIV.

Contains bibliography of systematic and faunistic works on Amphioxus.

9 ANTIPA, GR. *Ueber die Beziehungen der Thymus zu den sogenannten Kiemenspaltenorganen bei Selachiern*. Anat. Anz. VII. 1892. pp. 690–692. One figure in text.

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* This bibliography does not by any means include all that has been written on the anatomy of Amphioxus. Some of the older and shorter works, as well as some of those relating to special points of histological detail, have been omitted, as they are fully dealt with in many of the memoirs here cited.

10 Balfour, F. M. *A Preliminary Account of the Development of the Elasmobranch Fishes.* Quarterly Jour. Micro. Sc. XIV. N. S. 1874. pp. 323–364. Plates 13–15.

Paper in which Balfour first published his discovery of the segmental origin of excretory tubules. This was made out also in the same year by Semper and Schultz. (Vide infra, *Schultz.*)

11 Balfour, F. M. *On the Origin and History of the Urinogenital Organs of Vertebrates.* Jour. of Anat. and Physiol. X. 1875. pp. 17–48. Eight figures in text. Amplification of his previous work, with bibliography up to date.

12 Balfour, F. M. *The Development of Elasmobranch Fishes. Development of the Trunk.* Jour. of Anat. and Physiol. XI. 1876. pp. 128–172. Plates 5 and 6. First account of origin of paired limbs from continuous epiblastic thickenings.

13 Balfour, F. M. *A Monograph on the Development of Elasmobranch Fishes.* London, 1878.

14 Beddard, Frank Evers. *On the Occurrence of Numerous Nephridia in the Same Segment in Certain Earthworms, and on the Relationship between the Excretory System in the Annelida and in the Platyhelminths.* Quarterly Jour. Micro. Sc. XXVIII. N. S. 1888. pp. 397–411. Plates 30–31. Contains discovery of nephridial network in Perichæta.

15 Benham, W. Blaxland. *The Structure of the Pharyngeal Bars of Amphioxus.* Quarterly Jour. Micro. Sc. XXXV. N. S. 1893. pp. 97–118. Plates 6–7.

16 Bourne, Alfred Gibbs. *Contributions to the Anatomy of the Hirudinea.* Quarterly Jour. Micro. Sc. XXIV. N. S. 1884. pp. 419–506. Plates 24–34.

Contains discovery of nephridial network in Pontobdella.

17 Boveri, Theodor. *Ueber die Niere des Amphioxus.* Münchener Medicin. Wochenschrift. No. 26. 1890. Sep. Abd. pp. 1–13. Two figures in text. (Preliminary note.)

18 Boveri, Theodor. *Die Nierencanälchen des Amphioxus. Ein Beitrag zur Phylogenie des Urogenitalsystems der Wirbelthiere.* Zoolog. Jahrbücher. Abth. für Morphol. V. 1892. pp. 429–510. Taf. 31–34 and five figures in text.

19 Costa. O. Gabriele. *Cenni zoologici ossia descrizione sommaria delle specie nuove di animali discoperti in diverse contrade del regno nell' anno* 1834. Napoli, 1834. See also *Fauna del regno di Napoli.* 1839–50.

20 Cuénot, L. *Etudes sur le sang et les glandes lymphatiques dans la série animale.* Archives de zool. expérimentale, XIX. 1891. Amphioxus. pp. 55–56.

Notes absence of blood-corpuscles in Amphioxus. Those described by previous authors must therefore require another explanation.

21 Dohrn, Anton. *Studien zur Urgeschichte des Wirbelthierkörpers. IV. Section* 5. *Entstehung und Bedeutung der Thymus der Selachier.* Mitth. Zool. Stat. Neapel. V. 1884. pp. 141–151. Taf. 8. Figs. 1 and 2.

22 Eisig, Hugo. *Die Segmentalorgane der Capitelliden.* Mitth. Zool. Stat. Neapel. I. 1879. pp. 93–118. Taf. IV.

Discovery of numerous nephridia in single segments and anastomoses between successive nephridia.

23 Emery, Carlo. *Le specie del genere Fierasfer nel Golfo di Napoli.* 2d Monograph in the "Fauna und Flora des Golfes von Neapel." Leipzig, 1880.

24 Emery, Carlo. *Zur Morphologie der Kopfniere der Teleostier.* Biologisches Centralblatt, I. 1881. pp. 527–529. See also Zoologischer Anzeiger, VIII. 1885. pp. 742–744.

25 Fusari, Romeo. *Beitrag zum Studium des peripherischen Nervensystems von Amphioxus lanceolatus.* Internationale Monatsschrift für Anatomie und Physiologie, VI. 1889. pp. 120–140. Taf. VII.–VIII.

26 Goodsir, John. *On the Anatomy of Amphioxus lanceolatus.* Transactions of the Royal Society of Edinburgh, Vol. XV. Part I. 1841. pp. 241–263.

27 Grenacher, H. *Beiträge zur nähern Kenntniss der Musculatur der Cyclostomen und Leptocardier.* (*Leptocardia* proposed by Haeckel as a classificatory name on account of the simple tubular "heart" of Amphioxus.) Zeitschr. für Wiss. Zoologie, XVII. 1867. pp. 577–597. Taf. XXXVI. First isolation of muscle-plates of Amphioxus.

28 Günther, Albert. *Synopsis of Genus Branchiostoma.* In Report on Zoöl. Collections of H. M. S. Alert. 1881–82. pp. 31–33. London, 1884.

29 Hatschek, Berthold. *Die Metamerie des Amphioxus und des Ammocœtes.* Verh. Anat. Gesellschaft, 6th Versammlung. Wien, 1892. pp. 137–161. Eleven figures in text.

29 *bis.* Hatschek, Berthold. *Zur Metamerie der Wirbelthiere.* Anat. Anz. VII. Dec. 1892. pp. 89–91.

30 Huxley, T. H. *Preliminary Note upon the Brain and Skull of Amphioxus lanceolatus.* Proceedings of the Royal Society, XXIII. 1874. pp. 127–132.

Points out that in Myxine and Ammocœtes a velum is present separating the buccal (stomodœal) from the branchial cavity.

The resemblance of the buccal cavity and tentacles (cirri) of Ammocœtes to the corresponding parts in Amphioxus is so close that there can hardly be any doubt the two are homologous. The anterior end of the nerve-tube of Amphioxus corresponds to the *lamina terminalis* of the craniate Vertebrates.

31 Huxley, T. H. *On the Classification of the Animal Kingdom.* Journal of the Linnæan Society (London), XII. 1876. pp. 199–226. (Read 3d Dec., 1874.)

Section on "*epicœl,*" p. 216 *et seq.* Atrial cavity of Amphioxus and Ascidians is an epicœl like the opercular cavity of the Amphibian tadpole.

32 Kölliker, Albert. *Ueber das Geruchsorgan von Amphioxus.* Müller's Archiv für Anat. Physiol., etc. 1843. pp. 32–35. Taf. II. Fig. 5.

Discovery of olfactory pit and first description of the spermatozoa of Amphioxus.

33 Köppen, Max. *Beiträge zur vergleichenden Anatomie des Centralnervensystems der Wirbelthiere. Zur Anatomie des Eidechsengehirns.* Morphologische Arbeiten (Schwalbe), I. 1892. pp. 496–515. Taf. 22–24.

Contains discovery of giant-fibres in caudal portion of spinal cord of *Lacerta viridis.*

34 Kohl, K. *Einige Bemerkungen über Sinnesorgane des Amphioxus lanceolatus.* Zool. Anz. 1890. pp. 182–185.

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35 Krukenberg, C. Fr. W. *Zur Kenntnis des chemischen Baues von Amphioxus lanceolatus und der Cephalopoden.* Zool. Anz. 1881. pp. 64–66. See also Hoppe-Seyler's reply. pp. 185–187. Compare also Cuénot (supra).

36 Kupffer, Carl von. *Studien zur vergleichende Entwicklungsgeschichte des Kopfes der Kranioten, I. Die Entwicklung des Kopfes von Acipenser sturio an Medianschnitten untersucht.* 95 pp. 8°. 9 Tafeln. München und Leipzig, 1893.

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37 Langerhans, Paul. *Zur Anatomie des Amphioxus lanceolatus.* Archiv für mikroskopische Anatomie, XII. 1876. pp. 290–348. Taf. XII.–XV.

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38 Lankester, E. Ray. *On Some New Points in the Structure of Amphioxus and their Bearing on the Morphology of Vertebrata.* Quarterly Jour. Micro. Sc. XV. N. S. 1875. pp. 257–267.

39 LANKESTER, E. RAY. *Contributions to the Knowledge of Amphioxus lanceolatus, Yarrell.* Ib., Vol. XXIX. 1889. pp. 365–408. Five plates.

40 LWOFF, BASILIUS. *Über den Zusammenhang von Markrohr und Chorda beim Amphioxus und ähnliche Verhältnisse bei Anneliden.* Zeitschrift fur wiss. Zoologie. Bd. 65. 1893. pp. 299–308. Taf. XVII.

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41 MAYER, PAUL. *Über die Entwicklung des Herzens und der grossen Gefässstämme bei den Selachiern.* Mitth. Zool. Stat. Neapel. VII. 1887. pp. 338–370. Taf. 11–12.

42 MEYER, EDUARD. *Studien über den Körperbau der Anneliden.* Mitth. Zool. Stat. Neapel. VII. 1887. pp. 592–741. Taf. 22–27.

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43 MÜLLER, WILHELM. *Ueber die Stammesentwicklung des Sehorgans der Wirbelthiere.* 76 pp. Five plates. 4°. Leipzig, 1874.

44 MÜLLER, WILHELM. *Ueber das Urogenitalsystem des Amphioxus und der Cyclostomen.* Jenaische Zeitschr. für Naturwissenschaft, Bd. II. (neue Folge). 1875. Sep. Abdruck. pp. 1–38. Two plates.

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45 MÜLLER, JOHANNES. *Über den Bau und die Lebenserscheinungen des Branchiostoma lubricum Costa, Amphioxus lanceolatus, Yarrell.* Berlin, 1844. 4°. 40 pp. Five plates.

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46 NANSEN, FRIDTJOF. *The Structure and Combination of the Histological Elements of the Central Nervous System.* Bergens Museums Aarsberetning for 1886. Bergen, 1887.

47 Owsjannikow, Philip. *Ueber das Centralnervensystem des Amphioxus lanceolatus.* Bulletin de l'Acad. imp. des Sciences de St. Pétersbourg, Tome XII. 1868. pp. 287–302, with one plate. Also in Mélanges Biologiques, T. VI. pp. 427–450.

Introduced a method of maceration by which he was able to shake out the central nervous system and thus isolate it from the body. In this way he was able to correct the erroneous descriptions of *de Quatrefages* and others (who stated that there were ganglionic enlargements in the spinal cord), and to discover the alternate arrangement of the spinal nerves.

48 Platt, Julia B. *Fibres connecting the Central Nervous System and Chorda in Amphioxus.* Anat. Anz. VII. 1892. pp. 282–284. Three figures in text.

49 Pollard, E. C. *A New Sporozoön in Amphioxus.* Quarterly Jour. Micro. Sc. XXXIV. N. S. 1893. pp. 311–316. Plate XXIX.

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49 *bis.* Pouchet, Georges. *On the Laminar Tissue of Amphioxus.* Quarterly Jour. Micro. Sc. XX. N. S. pp. 421–430. Plate XXIX.

50 de Quatrefages, Armand. *Mémoire sur le système nerveux et sur l'histologie du Branchiostome ou Amphioxus.* Annales des sciences nat. Zoologie. 3d series. IV. 1845. pp. 197–248. Plates 10–13.

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52 *bis.* Retzius, Gustav. *Das hintere Ende des Rückenmarks und sein Verhalten zur Chorda dorsalis bei Amphioxus lanceolatus.* Verh. Biol. Vereins. (Biologiska Föreningens Förhandlingar.) Stockholm. Bd. IV. pp. 10–15. 9 figs. 1891.

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belthiere. In Denkschriften der Math.-Naturwiss. Classe der kais. Akad. der Wissenschaften. Bd. XLV. Wien, 1882. 64 pp. 4°. Six plates.

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55 ROLPH, W. *Untersuchungen über den Bau des Amphioxus lanceolatus.* Morphologisches Jahrbuch, II. 1876. pp. 87–164. Taf. V.–VII.; also figures in text.

56 RÜCKERT, JOHANNES. *Entwickelung der Excretionsorgane.* Ergebnisse der Anatomie und Entwicklungsgeschichte (Merkel und Bonnet), I. 1891. pp. 606–695. Includes an extensive bibliography.

57 SCHNEIDER, ANTON. *Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere. I. Amphioxus lanceolatus.* pp. 3–31. Taf. XIV.–XVI. 4°. Berlin, 1879.

58 SCHULTZ, ALEXANDER. *Zur Entwickelungsgeschichte des Selachiereies.* Archiv. für Mikr. Anat. XI. 1875. pp. 569–580. Taf. 34.

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61 SPENGEL, J. W. *Benham's Kritik meiner Angaben über die Kiemen des Amphioxus.* Anat. Anz. VIII. 1893. pp. 762–765.

62 STIEDA, LUDWIG. *Studien über den Amphioxus lanceolatus.* Mém. de l'Acad. Impériale des Sciences de St. Pétersbourg, 7th series, Vol. XIX. No. 7. 70 pp. Four plates. 1873.

Contains some good observations on the central nervous system. First to show that the split-like structure above central canal did not correspond to the posterior fissure of the vertebrate spinal cord, but was a portion of the original central canal itself, the lumen of which had been partially obliterated by approximation of its walls. First identification of ventral (motor) roots of spinal nerves in Amphioxus.

63 Thacher, James K. *Median and Paired Fins; a Contribution to the History of Vertebrate Limbs.* Transactions Connecticut Academy, III. No. 7. 1877. pp. 281–310. Plates 49–60.

64 Weiss, F. Ernest. *Excretory Tubules in Amphioxus lanceolatus.* Quarterly Jour. of Micro. Sc. XXXI. N. S. 1890. pp. 489–497. Plates 34–35.

65 van Wijhe, J. W. *Ueber Amphioxus.* Anat. Anz. VIII. 1893. pp. 152–172.

66 van Wijhe, J. W. *Die Kopfregion der Cranioten beim Amphioxus, nebst Bemerkungen über die Wirbeltheorie des Schädels.* Anat. Anz. IV. 1889. pp. 558–566.

67 van Wijhe, J. W. *Ueber die Mesodermsegmente des Rumpfes und die Entwicklung des Excretionssystems bei Selachiern.* Archiv. f. Mikr. Anat. XXXIII. 1889. pp. 461–516. Taf. 30–32.

68 Willey, Arthur. *Report on a Collection of Amphioxus, made by Professor A. C. Haddon, in Torres Straits,* 1888–89. Quarterly Jour. Micro. Sc. XXXV. N. S. January, 1894. pp. 361–371. One figure in text.

Branchiostoma cultellum. Peters.

III.

DEVELOPMENT OF AMPHIOXUS.

69 Ayers, Howard. *Bdellostoma Dombeyi, Lac. A Study from the Hopkins Marine Laboratory.* Biological Lectures, Marine Biological Laboratory, Woods Holl. 1893. No. VII. Boston, 1894.

69 *bis*. Bert, Paul. *On the Anatomy and Physiology of Amphioxus.* Annals and Mag. of Nat. Hist., 3d Series. Vol. XX. 1867. pp. 302–304. (Translated from Comptes Rendus. Aug. 26th, 1867. pp. 364–367.)

Breeding season of Amphioxus at Arcachon is from March to May. Was the first to observe the ejection of the sperm through the atriopore. Calls attention to remarkable lack of regenerative power in Amphioxus. Individuals cut in two will live for several days, but will not regenerate. "If the extremity of the body of an Amphioxus be cut off, the wound does not cicatrize; on the contrary, the tissues become gradually disintegrated. I have seen animals, with only the tail mutilated, become gradually eaten away up to the middle of the branchial region, and live thus without any intestines, without abdominal walls, and without branchiæ for several days." These observations of Paul Bert are capable of easy confirmation, and should be borne in mind in view of the extraordinary regenerative power which Wilson discovered in the segmentation stages of the embryo.

70 Boveri, Theodor. *Über die Bildungsstätte der Geschlechtsdrüsen und die Entstehung der Genitalkammern beim Amphioxus.* Anat. Anz. VII. 1892. pp. 170–81. Twelve figures.

71 Dohrn, Anton. *Studien zur Urgeschichte des Wirbelthierkörpers. III. Die Entstehung und Bedeutung der Hypophysis bei Petromyzon Planeri.* Mitth. Zool. Stat. Neapel. IV. 1882.

72 Dohrn, Anton. Studien, VIII. *Die Thyreoidea bei Petromyzon, Amphioxus und Tunicaten.* Ib. VI. 1885.

Dohrn lays unnecessary stress upon the fact that often in transverse section, especially in the anterior region of the pharynx, the endostyle of Amphioxus projects up into the cavity of the pharynx in the form of a convex lens-shaped ridge. This is merely due to the muscular contraction of the pharynx, which almost invariably takes place when Amphioxus is placed in a killing reagent. It is, therefore, not an anatomical feature of any significance.

73 Dohrn, Anton. Studien, XII. *Thyreoidea und Hypobranchialrinne, Spritzlochsack und Pseudobranchialrinne bei Fischen, Ammocœtes und Tunikaten.* Ib. VII. 1887.

74 Dohrn, Anton. Studien, XIII. *Über Nerven und Gefässe bei Ammocœtes und Petromyzon Planeri.* Ib. VIII. 1888.

75 Froriep, August. *Entwickelungsgeschichte des Kopfes.* Ergebnisse der Anat. und Entwickelungsgesch (Merkel und Bonnet), I. 1891. pp. 561–605. Eleven figures.

Includes an extensive bibliography.

76 Hatschek, Berthold. *Studien über Entwicklung des Amphioxus.* Arbeiten a. d. Zool. Institute. Wein, 1881. 88 pp. Nine plates.

77 Hatschek, Berthold. *Mittheilungen über Amphioxus.* Zoologischer Anzeiger, VII. 1884. pp. 517–520.

Olfactory pit, sense-organ of præoral pit, anterior præoral "nephridium."

78 Hatschek, Berthold. *Über den Schichtenbau von Amphioxus.* Anat. Anz. III. 1888. pp. 662–667. Five figures.

Origin of sclerotome, etc.

79 Kastschenko, N. *Zur Entwicklungsgeschichte des Selachierembryos.* Anat. Anz. III. 1888. pp. 445–467.

One of the first to bring forward definite embryological facts to prove that the anterior (præ-auditory) head-cavities of van Wijhe (Ueber die Mesodermsegmente, etc., des Selachierkopfes. Amsterdam, 1882) are not homodynamous with the true somites. He was followed in this respect by Rabl (Theorie des Mesoderms. Morphologisches Jahrbuch, XV. 1889).

80 Korschelt, E., und Heider, K. *Lehrbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere.* 3d Heft. Jena, 1893.

81 Kowalevsky, Alexander. *Entwicklungsgeschichte des Amphioxus lanceolatus.* Mém. de l'Acad. Imp. des Sciences de St. Pétersbourg. VII. Series. T. XI. No. 4. 1867. Three plates.

82 Kowalevsky, Alexander. *Weitere Studien über die Entwicklungsgeschichte des Amphioxus lanceolatus, nebst einem Beitrage zur Homologie des Nervensystems der Würmer und Wirbelthiere.* Arch. f. Mikr. Anat. XIII. 1877. pp. 181–204. Two plates.

Among the definite discoveries communicated by Kowalevsky in these two memoirs may be mentioned the following: General features of segmentation and gastrulation, origin of mesoderm from archenteric pouches, unique method of formation of nerve-tube (see text), origin of notochord, neurenteric canal, asymmetrical origin of gill-slits and mouth, and *in part* the metamorphosis.

83 Kupffer, Carl von. *Die Entwicklung von Petromyzon Planeri.* Arch. f. Mikr. Anat. XXXV. 1890. pp. 469–558. Six plates.

Origin of head-cavities, hypophysis, etc.

84 Kupffer, Carl von. *Die Entwicklung der Kopfnerven der Vertebraten.* Verhandl. Anat. Gesellschaft in München. 1891. pp. 22–55. Eleven figures. (Ergänzungsheft zum Anat. Anz. VI. 1891.)

Ammocœtes (see Fig. 92 in text).

85 Kupffer, Carl von. *Studien zur vergleichende Entwicklungsgeschichte des Kopfes der Kranioten I. Die Entwicklung des Kopfes von Acipenser sturio an Medianschnitten untersucht.* pp. 95. Nine plates. Seven figures in text. *München* and *Leipzig*, 1893.

Important contribution to the delimitation of the wall of the brain. On page 84 is a reconstruction of head-cavities of Ammocœtes (see Fig. 72). Figs. 21 and 22 in the plates represent cerebral vesicle of Amphioxus. (Cf. Fig. 51.)

86 Lankester, E. Ray, and Willey, A. *The Development of the Atrial Chamber of Amphioxus.* Quarterly Jour. Micro. Sc. XXXI. 1890. pp. 445–466. Four plates.

87 LEUCKART, RUDOLPH, und PAGENSTECHER, ALEX. *Untersuchungen über niedere Seethiere. Amphioxus lanceolatus.* Müller's Archiv f. Anat. u. Physiol. 1858. pp. 558–569. Taf. XVIII.

Description of larvæ of Amphioxus taken off Heligoland. Drew attention to larval asymmetry, and to the existence of the brain-ventricle (cerebral vesicle). In absence of knowledge of early development their interpretation of many of the structures (especially præoral pit, mouth, and gill-slits) was incorrect. Latter applies also to Schultze's observations.

88 LWOFF, BASILIUS. *Über Bau und Entwicklung der Chorda von Amphioxus.* Mittheilungen a. d. Zool. Station. Neapel. IX. 1891. pp. 483–502. One plate.

Consult this memoir for previous literature on histology of notochord.

89 LWOFF, BASILIUS. *Ueber einige wichtige Punkte in der Entwicklung des Amphioxus.* Biologisches Centralblatt, XII. 1892. pp. 729–744. Eight figures.

Notes absence of mesodermal "pole-cells." From frequency of mitoses in dorsal ectoderm of gastrula, concludes that the material destined to form dorsal wall of archenteron, from which notochord and myocœlomic pouches arise, grows in from the *ectoderm* round dorsal lip of blastopore. Hence notochord and mesoderm are essentially derived from ectoderm!

90 MARSHALL, A. MILNES. *Vertebrate Embryology.* London, 1893.

91 MÜLLER, JOHANNES. *Über die Jugendzustände einiger Seethiere.* Monatsbericht der königl. preuss. Akad. der Wissenschaften zu Berlin. 1851. pp. 468–474.

First accurate description of larva of Amphioxus, p. 474. In 1847 Johannes Müller obtained a young Amphioxus of 2½ mm. at Helsingfors. He says that the appearance of the gill-slits was peculiar, in that there were two rows of slits in the pharyngeal wall, placed one above the other. In the upper row were *five* round slits, while the lower slits were vertically elongated and were *fourteen* in number. He adds that it was doubtful whether it represented the young "Branchiostoma lubricum" or belonged to a new species.

92 MÜLLER, WILHELM. *Ueber die Hypobranchialrinne der Tunikaten und deren Vorhandensein bei Amphioxus und den Cyklostomen.* Jenaische Zeitschrift f. Naturwiss. VII. 1873. pp. 327–332.

93 PLATT, JULIA B. *Further Contribution to the Morphology of the Vertebrate Head.* Anat. Anz. VI. 1891. pp. 251–265.

94 RABL, CARL. *Über die Differenzierung des Mesoderms.* Anat. Anz. III. 1888. pp. 667–673. Eight figures.

Discovery of the sclerotome-diverticulum in embryo of Pristiurus.

95 RICE, HENRY J. *Observations upon the Habits, Structure, and Development of Amphioxus lanceolatus.* American Nat. XIV. 1880. pp. 171–210. Plates 14 and 15.

Author was the first to find Amphioxus in Chesapeake Bay. With regard to development, he gives some fairly good figures of larvæ, and observed some of the more obvious features of the metamorphosis, as already described by Kowalevsky.

96 RÜCKERT, JOHANNES. *Ueber der Entstehung der Excretionsorgane bei Selachiern.* Arch. für Anat. u. Physiol. (Anatomische Abtheilung). 1888. pp. 205–278. Three plates.

Contains also the discovery of segmental origin of gonads.

97 SCHNEIDER, ANTON. *Beiträge zur vergleichenden Anatomie und Entwicklungsgeschichte der Wirbelthiere, II. Anatomie und Entwickl. von Petromyzon und Ammocœtes.* 4°. Ten plates. Berlin, 1879.

Figure of the ciliated grooves in pharynx of Ammocœtes, at page 84.

98 SCHULTZE, MAX. *Beobachtung junger Exemplare von Amphioxus.* Zeit. f. Wiss. Zool. III. 1851–2. pp. 416–419.

Two larvæ from Heligoland. Good description of structure of notochord.

99 VAN WIJHE, J. W. *Ueber Amphioxus.* Anat. Anz. VIII. 1893. pp. 152–172.

100 WILLEY, A. *On the Development of the Atrial Chamber of Amphioxus.* (Preliminary communication.) Proceedings of the Royal Society, XLVIII. 1890. pp. 80–89.

101 WILLEY, A. *The Later Larval Development of Amphioxus.* Quarterly Jour. Micro. Sc. XXXII. 1891. pp. 183–234. Three plates.

102 WILSON, EDMUND B. *On Multiple and Partial Development in Amphioxus.* Anat. Anz. VII. 1892. pp. 732–740. Eleven figures.

In this and the following more detailed paper, the author describes and interprets a remarkable series of experiments on the artificial production of twins and dwarfs. Besides this, there are many important observations on the normal cleavage of the egg.

103 WILSON, EDMUND B. *Amphioxus and the Mosaic Theory of Development.* Journal of Morphology, VIII. 1893. pp. 579–638. Ten plates.

104 Ziegler, H. Ernst. *Der Ursprung der mesenchymatischen Gewebe bei den Selachiern.* Archiv f. Mikr. Anat. XXXII. 1888. pp. 378–400. One plate.

Independent discovery of sclerotome-diverticulum. (See Rabl.)

IV.

ASCIDIANS.

For bibliography relating to the Ascidians, see Professor W. A. Herdman's Reports on the Tunicata collected during the "Challenger" expedition — Parts I.–III. 1882–88; and also Korschelt und Heider, "Lerhbuch der vergleichenden Entwicklungsgeschichte der wirbellosen Thiere." Heft III. Jena, 1893.

V.

PROTOCHORDATES, ETC.

105 Ayers, Howard. *Concerning Vertebrate Cephalogenesis.* Jour. Morph. IV. 1890–91. pp. 221–245.

106 Bateson, William. *Memoirs on the Development of Balanoglossus.* Quarterly Jour. Micro. Sc. Vols. XXIV.–XXVI. 1884–86.

107 Brooks, W. K. *The Systematic Affinity of Salpa in its Relation to the Conditions of Primitive Pelagic Life; the Phylogeny of the Tunicata; and the Ancestry of the Chordata.* Part II. of Monograph of the Genus Salpa. Johns Hopkins University. Baltimore, 1893.

108 Burckhardt, Rudolf. *Die Homologieen des Zwischenhirndaches und ihre Bedeutung für die Morphologie des Hirns bei niederen Vertebraten.* Anat. Anz. IX. 1894. pp. 152–155 and 320–324.

Relates to neuropore of craniate Vertebrates. Author calls the lobus olfactorius impar of Kupffer, the *recessus neuroporicus.*

109 Clapp, Cornelia M. *Some Points in the Development of the Toad-fish (Batrachus Tau).* Jour. Morph. V. 1891. pp. 494–501.

Observations on the double origin of mouth, made in 1889, not published in this paper.

110 Davidoff, M. von. *Ueber den "Canalis neurentericus anterior bei den Ascidien."* Anat. Anz. VIII. 1893. pp. 301–303.

111 DOHRN, ANTON. *Studien zur Urgeschichte des Wirbelthierkörpers, I. Der Mund der Knochenfische.* Mitth. Zool. Stat. Neapel. III. 1881–2. pp. 253–263.

112 FIELD, GEORGE W. *The Larva of Asterias vulgaris.* Quarterly Jour. Micro. Sc. XXXIV. 1892. pp. 105–128.

113 FOWLER, G. HERBERT. *The Morphology of Rhabdopleura Normani Allman.* Festschrift für Rudolf Leuckart. pp. 293–297. Leipzig, 1892.

114 HARMER, S. F. See M'INTOSH.

115 HERDMAN, W. A. *Article "Tunicata."* Ency. Brit. 9th ed., republished in "Zoölogical Articles" by Lankester, etc.

116 HUBRECHT, A. A. W. *Article "Nemertines."* Ency. Brit. 9th ed., republished in "Zoölogical Articles" by Lankester, etc.

116 *bis*. HUBRECHT, A. A. W. *On the Ancestral Form of the Chordata.* Quarterly Jour. Micro. Sc. XXIII. 1883. pp. 349–368.

For later works on this subject see Notes to Chap. V.

117 KUPFFER, C. VON. *Entwickelungsgeschichte des Kopfes.* In Merkel and Bonnet's Ergebnisse der Anatomie und Entwickelungsgeschichte, II. 1893. pp. 501–564.

118 LANG, ARNOLD. *Zum Verständnis der Organisation von Cephalodiscus dodecalophus M'Int.* Jenaische Zeitschrift f. Naturwiss. XXV. 1891.

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120 LANKESTER, E. RAY. *Degeneration: a Chapter in Darwinism.* Nature Series. London, 1880. Republished in "The Advancement of Science; Occasional Essays and Addresses." London, 1890.

121 LANKESTER, E. RAY. *A Contribution to the Knowledge of Rhabdopleura.* Quarterly Jour. Micro. Sc. XXIV. 1884. pp. 622–647.

122 MACBRIDE, E. W. *The Organogeny of Asterina Gibbosa.* Proceedings Royal Society. Vol. 54. 1893. pp. 431–436.

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124 MORGAN, T. H. *The Growth and Metamorphosis of Tornaria.* Jour. Morph. V. 1891. pp. 407–458.

125 MORGAN, T. H. *The Development of Balanoglossus.* Jour. Morph. IX. 1894. pp. 1–86.

126 PLATT, JULIA B. *Further Contribution to the Morphology of the Vertebrate Head.* Anat. Anz. VI. 1891. pp. 251–265.

Describes the double origin of mouth in Batrachus.

127 Pollard, H. B. *Observations on the Development of the Head in Gobius capito.* Quarterly Jour. Micro. Sc. XXXV. 1894. pp. 335–352.

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129 Sedgwick, Adam. *The Original Function of the Canal of the Central Nervous System of Vertebrata.* Studies from Morph. Lab. Cambridge, II. 1884. pp. 160–164.

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Contains important observations on the first appearance of the mouth, and its relation to the pituitary body.

131 Seeliger, Oswald. *Studien zur Entwicklungsgeschichte der Crinoiden.* (*Antedon rosacea.*) Zoologische Jahrbücher. Abth. f. Anat. VI. 1892. pp. 161–444.

132 van Wijhe, J. W. *Ueber den vorderen Neuroporus und die phylogenetische Function des Canalis Neurentericus der Wirbelthiere.* Zool. Anz. VII. 1884. pp. 683–687.

133 Willey, A. *Studies on the Protochordata, I.–III.* Quarterly Jour. Micro. Sc. XXXIV.–XXXV. 1893.

Contain further bibliographical references.

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ARTHUR WILLEY, B.Sc. Lond.,

Tutor in Biology, Columbia College ; Balfour Student of the University of Cambridge.

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The purpose of this volume is to consider the problem of the ancestry of the Vertebrates from the standpoint of the anatomy and development of Amphioxus and other members of the group Protochordata. The work opens with an Introduction, in which is given a brief historical sketch of the speculations of the celebrated anatomists and embryologists, from Étienne Geoffroy St. Hilaire down to our own day, upon this problem. The remainder of the first and the whole of the second chapter is devoted to a detailed account of the anatomy of Amphioxus as compared with that of higher Vertebrates. The third chapter deals with the embryonic and larval development of Amphioxus, while the fourth deals more briefly with the anatomy, embryology, and relationships of the Ascidians; then the other allied forms, Balanoglossus, Cephalodiscus, are described.

The work concludes with a series of discussions touching the problem proposed in the Introduction, in which it is attempted to define certain general principles of Evolution by which the descent of the Vertebrates from Invertebrate ancestors may be supposed to have taken place.

The work contains an extensive bibliography, full notes, and 135 illustrations.

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AN INTRODUCTORY STUDY.

BY

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Instructor in Biology, Columbia College.

This work has been prepared to meet the needs of the general student for a concise knowledge of the Fishes. It contains a review of the four larger groups of the strictly fishlike forms, Sharks, Chimaeroids, Teleostomes, and the Dipnoans, and adds to this a chapter on the Lampreys. It presents in figures the prominent members, living and fossil, of each group; illustrates characteristic structures; adds notes upon the important phases of development, and formulates the views of investigators as to relationships and descent.

The recent contributions to the knowledge of extinct Fishes are taken into special account in the treatment of the entire subject, and restorations have been attempted, as of Dinichthys, Ctenodus, and Cladoselache.

The writer has also indicated diagrammatically, as far as generally accepted, the genetic relationships of fossil and living forms.

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