NATURAL HISTORY, ORGANIZATION, AND LATE DEVELOPMENT OF THE TEREDINDÆ, OR SHIP-WORMS

By CHARLES P. SIGERFOOS

Professor of Zoology, University of Minnesota

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INTRODUCTION.

The ship-worms were favorite objects for study during the eighteenth century on account of the great damage they worked to the dikes of Holland in 1733 and in subsequent years. The first modern observations were those of Valisnieri (1715) and Deslandes (1720). After 1733 came Mossuet, J. Rousset, and especially Godfrey Sellius. These observers seem to have been unaware of the ancient observations mentioned by Theophrastus, Pliny, and Ovid, and it was supposed that the ship-worms were natives of India, whence they had been brought by shipping in modern times. It was Godfrey Sellius who first recognized their molluscan characters, but these were not recognized by Linnæus, who grouped the ship-worms, and *Dentalium*, along with *Serpula*. Cuvier and Lamarck adopted the view of Sellius, and since their time these animals have been put in their proper place.

The first reliable observations on the anatomy of the ship-worms were made by Deshayes, who gave a number of beautifully executed plates to *Teredo* in his "Mollusques d'Algerie", 1848. Like most of the plates of this great work, however, these are difficult to study and interpret. Supplementing the work of Deshayes is that of Quatrefages (1849), who began and completed his observations before he had access to the published results of Deshayes. This "Memoire sur le Genre Taret (*Teredo* Linn.)" is the one usually cited at the present time, although the paragraph with which Quatrefages prefaces his paper is almost as applicable now (with slight changes in the wording) as when it was written. "Naturalists up to the present time," he says, "have strangely neglected Teredo. This is not the place to review the anatomical researches of the last century, which are filled with errors excusable by the state of science of that period. But it is surprising that a mollusk with such remarkable external characters has not been the object of any special research from the foundation of comparative anatomy up to

[a] My work on the ship-worms was first suggested by Prof. W. K. Brooks. His constant interest throughout my stay at Johns Hopkins University was of great help to me and it gives me great pleasure to acknowledge my indebtedness to him. My material was collected at Beaufort, N. C., during the summers of 1895 and 1896, and my study was continued in the laboratory in Baltimore. To the authorities of Johns Hopkins University I am under deep obligations, both for the privileges of the marine laboratories at the seaside and for the facilities for work in the laboratory in Baltimore.

the present time. It is necessary to come to the year 1846 to find a naturalist who has taken for the subject of his observations this mollusk so unfortunately celebrated."

Since the appearance of this memoir of Quatrefages no detailed account of the whole organization of *Teredo* has appeared. Only in comparative treatises has it been taken up. The principal of these are the papers by Grobben (1888), on the pericardial glands in lamellibranchs; by Menegaux (1889), on the circulatory system in lamellibranchs, and by Pelseneer (1891), in his extensive comparative studies in the group. Grobben first observed the anterior adductor muscle in *Teredo* and proved the Teredinidæ to be dimyarians. Aside from this point, the figure of *Teredo* that he gives is wholly unreliable. Menegaux attempted to establish the homologies of the aortæ, and Pelseneer described the visceral ganglion and related structures. I shall have occasion to refer to these papers in special parts later, and it will be seen that the comparative method of study is not always satisfactory if the examination of the different forms be not made with sufficient thoroughness. My results differ from all of these. Unfortunately, the first two authors do not state the species on which their observations were made, and so I can not state that where my observations differ from theirs they were in error. There is, however, such great uniformity of organization in the various species that we may expect only differences in detail.

My observations have been based chiefly on *Xylotrya gouldi* Bartsch, and in the present paper except where otherwise stated this is the form described and figured. I have had specimens in all stages of development from the newly attached larva to the adult. I have also studied *Teredo dilatata* Stimpson and *T. navalis* Linnæus, and these have been used where they are essentially different or more favorable for description.

The object of my study of the ship-worms has been twofold. In the first place, I have endeavored, by the use of modern methods, to make a detailed study of the organization of this highly specialized lamellibranch and to correct some errors that have heretofore existed in the descriptions of it. In the second place, by the study of young stages, I have been able to trace the transformation of the typical lamellibranch larva into the very highly specialized ship-worm.

I have also traced the early embryology with the artificially fertilized eggs of *X. gouldi* and *T. dilatata*, in both of which the eggs are laid free into the water. Stages later than the typical early lamellibranch veliger, raised in aquaria, I have not been able to observe. The intermediate stages, between these and the newly attached larva, I hope to observe on the larvæ of some viviparous species at a future time, so as to complete my study of the development from the egg to the adult.

Methods of preserving material.—My preserved material was collected and prepared for study as follows: By hanging boxes and other structures of wood in the water at Beaufort, I was able to obtain all stages, from the newly attached larvæ to ship-worms 4 inches long, with adult organization. The youngest stages were collected from the surface of the wood. Later stages were dissected out of the wood into which they had bored. Early stages were narcotized with cocaine and afterwards fixed with mercuric chloride. Specimens 1 cm. or more in length were treated as follows: They were exposed quickly in their burrows and

immediately a quantity of Hermann's solution was dashed upon them. This reagent kills them instantly, before they have had time to contract appreciably. They were then immediately immersed in mercuric chloride or Perenyi's solution for fixation. After washing in weaker alcohols, specimens were preserved in 90 per cent alcohol. The early stages were stained in Kleinenberg's hematoxylin. For later stages, the best results were obtained by staining in bulk with borax-carmine, followed by staining sections with Lyons blue. For the examination of the younger stages as whole objects, the best results were obtained by staining in a weak solution of borax-carmine in acid (½ per cent HCl) 70 per cent alcohol, which decalcifies as well as stains.

With the exception of a few diagrams, which are indicated as such, the figures of sections have been drawn with the aid of a Zeiss camera lucida. In some cases, as in the series of transverse sections of the adult (fig. 28–35), they have been "touched up" afterwards. In no case, however, have they been essentially modified, and they are in no wise diagrams. The figures to illustrate the adult structure have been made from specimens about 10 cm. long, which I had raised, and which were killed almost perfectly extended. The siphons, however, have been filled in from life and from preserved specimens that had been narcotized before killing. In large specimens the body as a whole and the various organs are somewhat more elongated comparatively, but the relations remain the same as in younger specimens.

NATURAL HISTORY.

Any wooden structures that one may examine at Beaufort which have been in the water for some time and unprotected are found infested with ship-worms. These are of three species, which Dr. Paul Bartsch has kindly identified for me as *Xylotrya gouldi* Jeffreys, *Teredo navalis* Linnæus, and *T. dilatata* Spengler. *X. gouldi* and *T. dilatata* are very abundant, while *T. navalis* was found but rarely. *X. gouldi* is the most abundant of all, and is found everywhere. It may attain a length of 2 feet or more, though where it grows in large numbers it is so crowded that old specimens are often less than a foot in length. *T. dilatata* I have found mostly in the heavier piles of wharves, where specimens may attain the great size of 4 feet in length and an inch in diameter at the anterior end. *T. navalis* I have found very sparingly, not over a dozen specimens among the thousands of individuals I have examined. These in all cases were small specimens, from which it seems that the habitat at Beaufort is not favorable for them and is more favorable for the other two species, which fully occupy all of the available places for ship-worm life. The water contains a high percentage of salt, and the warm season is long. These factors may account wholly or in part for the comparative absence of *T. navalis*.

Of the thousands of young ship-worms (under 4 inches in length) I have taken from boxes, all except four specimens of *T. navalis* were *X. gouldi*. These were observed in June, July, and the first half of August. Whether the absence of younger specimens of *T. dilatata* during these three months was due to unfavorable locations, or the season for attachment is different from that of the other two species, I was not able to determine. I am inclined to think that the spawning season of *T. dilatata* is different from that of *Xylotrya*.

BREEDING HABITS.

As is well known, some species of ship-worms retain their eggs in the gills during their embryonic development. This is true of *T. navalis*, and even the small (an inch or two in length) specimens of this species I have taken have usually carried embryos in various stages of development. On the other hand, I have found that the eggs of the other two species are laid free into and fertilized in the water. If species of *T. dilatata* be taken from their tubes, they soon begin to extrude their sexual products, if these be mature. The eggs and spermatozoa are extruded from the anal or exhalent siphon in a slow, steady stream, which continues as long as the reproductive organs contain ripe sexual products. *Xylotrya gouldi* I have observed but rarely extruding its sexual products in this manner, but why there is a difference in this habit I have not determined.

In association with their character of free development in the water, the eggs of the ship-worm are very small and very numerous. While they vary somewhat in size, they have an average diameter of somewhat less than $\frac{1}{20}$ mm. ($\frac{1}{500}$ inch). Very large ship-worms may lay great numbers of eggs at one time. In one case I estimated the number laid by a large female of *T. dilatata* to be one hundred millions. The spermatozoa are very minute, and much more numerous than the eggs. The eggs of both species that lay their eggs into the water may be fertilized artificially, and develop with great uniformity and rapidity in aquaria. The eggs when first laid are of irregular shapes, but they soon become spherical and, if fertilized, the polar bodies are soon extruded and segmentation begins. Development is very rapid and on warm days the embryos become free-swimming within three hours after the eggs are laid. Within a day the shell has been formed and the typical lamellibranch veliger stage is reached. Beyond this stage I could not rear them in aquaria, though they may live for days afterwards. Hatschek has observed (1880) that the viviparous larvæ of a species studied by him (? *T. navalis*) are almost always present in only a few stages, and that transitional stages are but seldom found. It seems probable that the free-living larvæ of *Xylotrya* and *T. dilatata* attain one of these stages within a short time, and that the unusual conditions in aquaria prevent their advance beyond it.

The mode of life of the larvæ and the rate of development beyond the early stage attained so rapidly in aquaria have not been determined. What becomes of the larvæ after hatching from the eggs, how and where they live, it is difficult to surmise. Though the developed larvæ are settling on wooden structures constantly, I have not taken them and the intermediate stages in the tow-net, and where they develop I do not know. The rate of growth of larvæ of the marine lamellibranchs, however, is slow, and I think the larvæ of ship-worms when they attach themselves must be at least a month old. They may be more, for at this time their development is quite advanced and their organization complex. (See the description of the organization of the larva, p. 201.)

The breeding period of *X. gouldi* and *T. dilatata* seems to extend throughout the warm season. I have found ripe sexual products of both species from early in May till the middle of August. At the latter time there seemed no abatement in

their development. As will be described later, individuals become sexually mature in a month after they have attached, and those which attach in August must bear ripe sexual products later in the season, so that the breeding period would seem to extend throughout the warmer months.

ATTACHMENT OF THE LARVA.

During its free mode of life, the ship-worm larva has gradually developed into the larva typical of marine lamellibranchs. There is a bivalve shell into which the whole creature can be withdrawn for protection; a large swimming organ, the velum, by means of which the larva swims freely in the water; a long, powerful foot, by means of which it crawls actively over surfaces; and the internal organization peculiar to advanced lamellibranch larvæ. At the end of this larval development, in fact, the ship-worm larva is a typical small bivalve, except that it possesses the swimming organ.

Throughout the summer (or at least from May till the middle of August) at Beaufort, if one examines fairly clean, unprotected wooden structures submerged in the water, very small bivalves will be found crawling actively over the surfaces. These are very minute and are easily recognized as ship-worm larvæ that have just settled upon the wood. The larva moves rapidly in search of a favorable place for attachment, and this is usually in some minute depression or crevice in the wood, though it may become attached to perfectly smooth surfaces. It seems to possess no organ of special sense for the purpose, and yet it is able to determine what places are favorable for its future life and to avoid those which are not. Once it has chosen a point for attachment it throws out a single long byssus thread, thus securing itself to the surface of the wood, and very soon loses its velum, so that it can no longer lead a free-swimming life. Once attached, the larva begins to clear away a place for its burrow by scraping away the surface of the wood with the ventral edges of its shell valves. Such small particles of wood and other substances as are thus collected are cemented together over the larva so as to form a sort of conical covering for protection. This formed, the further transformation of the larva into the small ship-worm begins and progresses rapidly. The foot becomes a pestle-shaped organ which assists the shell in burrowing. The shell valves lose their power of opening at the ventral side and, by the development of knobs on the ventral and dorsal portions of both valves, are able to swing upon each other at right angles to the former direction. Meanwhile, because of the rapid growth of the valves on their ventral edges, the shell gapes at both anterior and posterior ends, for the protrusion of the foot in front and the siphons (and later the body) behind; and on the external surface of the valves at the anterior edges has been formed the first row of the small teeth which at this and later stages are the mechanical agents by which the animal bores into the wood. This transformation has taken place within two days from the time the larva has settled, and afterwards the animal rapidly becomes an elongate ship-worm, enlarging its burrow in the wood as it increases in size.

RATE OF GROWTH WITHIN THE WOOD.

The ship-worm in its larval stages develops slowly, but once in the wood it grows with remarkable rapidity. During its free life most of its energies are devoted to active locomotion and development; after attachment it leads a protected sedentary life and its growth is correspondingly rapid. The newly attached larva is somewhat less than 0.25 mm. long. In 12 days it has attained a length of about 3 mm.; 16 days, 6 mm.; 20 days, 11 mm.; 30 days, 63 mm., and 36 days, 100 mm. It is thus seen that within two weeks from the time it has settled, the ship-worm has increased hundreds of times in volume, and in five weeks thousands of times. Within two weeks it has developed its characteristic form. Even in a month specimens may contain ripe sexual elements, though normally these seem to be retained till larger quantities of spermatozoa and eggs are stored for extrusion at one time. I shall describe later what appears to be a change of sex from males to females, the male sex being developed in young specimens. I have found males four weeks old gorged with ripe spermatozoa, and in every way sexually mature.

The ages of larger specimens I have been able only to estimate from the time the piles and other wooden structures from which they were taken had been in the water. In one case I took specimens of *Teredo dilatata*, 4 feet long and an inch in diameter at the anterior end, from piles that had been in the water less than two years. This was in July, and in this case it seems the worms had entered the wood not earlier than the spring of the preceding year, and hence were little, if any, over a year old.

The rate of growth seems to depend but little, if at all, on the hardness or kind of wood. As is well known, ship-worms penetrate all kinds, whether it be soft white pine or hard oak. In India there are types that bore into stiff clay. None of our species adopt such a habitat, so far as I know, but I have found small, abnormal specimens of *Xylotrya* in very rotten wood, and I take it that their abnormal character was due to the unusual conditions. In this case they were associated with *Xylophaga dorsalis* and *Pholas dactylus*. I have observed, however, that in well-preserved wood they grow quite as rapidly if it is hard yellow pine as if it is soft white pine; so that the rate of growth seems conditioned by food supply and not by the ability of the animal, as regards the hardness of the wood, to form its burrow.

PROTECTIVE ADAPTATIONS.

The life of the ship-worm in the wood has led to profound changes in the character of its external parts and its means of protection. As it enters, the posterior part of the body projects more and more beyond the shell, which loses its protective character in large measure to take upon itself the purpose of burrowing. In specimens 2 mm. long the shell is still a quarter of the total length; in specimens 4 feet long, the shell is an inch or less in length. With the loss of protection of the soft body by the shell other means are acquired. In a general way the wooden wall of the burrow offers the protection afforded by the shell in other mollusks. But the very delicate tissues of the mantle would be injured by the slightest roughness in the surface of the wood. So, as the body elongates, the mantle secretes around

itself a constantly thickening calcareous tube which lines the whole burrow except the extreme anterior end, where the mantle is somewhat less delicate and where the tube fades out and the burrow is being constantly enlarged.

When the young "worm" enters the wood, it penetrates vertically to the surface, cutting across the grain. It soon bends its course, however, so that within 2 inches, usually, it takes a straight course in the direction of the grain. Individuals that enter the wood on end cut with the grain across the fibers from the start, so that their burrows are straight, unless they are turned from their course by obstructions of some sort. In such a case the course is changed so that the burrows may become exceedingly tortuous. When the ship-worm is in danger of burrowing into the tubes of its fellows or into other spaces, if its course can be no longer changed, it contracts the anterior part of the body slightly, secretes a closed calcareous lining in front of it, and ceases to burrow further or to grow. Otherwise, apparently, it may grow indefinitely, and it is difficult to say how large specimens might become were there not adverse conditions to stop their growth.

I believe that the calcareous lining of the burrow has been acquired primarily for the protection of the very delicate body from the rough surfaces of the wood, but it serves other purposes also. It prevents the diffusion of injurious substances into the burrow, and also prevents the intrusion of other creatures that live in the wood. Then, too, when the surrounding wood decays, or is eaten away by other animals inhabiting the wood, so as to endanger the life of the ship-worm, the tube may be so strengthened as to serve as the sole means of external protection. In this way the walls of the calcareous tubes, which, protected, are usually not over a quarter to a half millimeter thick, may become 2 mm. or more thick. This response to changed conditions on the outside is a very mysterious one and it is difficult to see by what means the animal recognizes its dangers.

The peculiar mode of life of ship-worms has led to the development of the pair of pallets (fig. 20). These are protective structures peculiar to the ship-worms. They differ somewhat in the various species, but are essentially calcareous paddle-shaped structures, attached one on either side of the posterior end of the body at the point of origin of the siphons. In *Xylotrya* the expanded part of the paddle consists of a series of funnel-shaped calcareous structures set one within the other upon a cylindrical handle, while in *Teredo* it is composed of a single piece. The handle of the paddle is embedded in a forward evagination of the mantle and the expanded part projects freely behind, where, by means of a set of muscles, they may be protracted forcibly so as completely to close the outer end of the burrow against the intrusion of any enemy from the outside. Also, when the burrow extends upward and its opening is more or less exposed at low tide, as sometimes happens, the pallets may so hermetically close the external opening as to retain the water in the burrow and to prevent the collapse of the body of the ship-worm. The action of the pallets is illustrated in figures 35 and 36. When the animal is undisturbed and feeding, the pallets are drawn forward and the siphons are extended freely into the water, as shown in figure 35. When it is disturbed in any way the siphons are contracted very quickly and the pallets forced into the end of the tube, as shown in figure 36.

MODE OF BURROWING.

The manner of mechanical formation of the burrow has been one of the most debated questions in the natural history of the ship-worms and their allies. In the former this work has been assigned by various observers to various structures. In some cases it was thought some chemical solvent assisted the mechanical action by softening the wood. Hancock thought there were siliceous particles in the mantle to do the work. Quatrefages thought it to be the "cephalic hood" (a thickened modification of the mantle at the anterior end on the dorsal side), aided by some chemical solvent. This structure he described as muscular, though it is but little muscular and could do no such important work as he assigned to it. Jeffreys ascribes this function to the foot, which by other observers was described as wholly absent. Osler, in 1826, had suspected the real mode of formation, though he did not actually observe it.

The shell is the agent, assisted by the foot, as I have actually observed in young specimens under the microscope; and the whole structure of the shell and the arrangement of its adductor muscles confirm this observation. The teeth on the anterior edges of the valves point outward and backward. On both dorsal and ventral portions of each shell valve (fig. 18 and 19) there are stout calcareous knobs which form a double pivot by which the valves are swung upon each other by the contraction of the adductor muscles. The mode of burrowing is as follows: While the foot performs a cupping action, thus drawing the shell close against the surface of the wood, the powerful posterior adductor muscle contracts, so that the teeth on the shell rasp away the wood. The valves are brought to the original position by the small anterior adductor. The comparatively very large posterior adductor is therefore the active agent that does the work, aided by the foot; the shell with its teeth is the tool with which the work is done.

INGESTION OF WOOD AND FOOD.

As in other lamellibranchs, a constant stream of water is passing through the siphons when they are extended from the outer end of the burrow into the water, and this serves for respiration and also contains the small organisms which serve for food. These consist mainly of diatoms and simple floating algæ, with other minute organisms. Small crustacea and other animal forms seem to be almost never eaten.

The particles of wood that are rasped away in forming the burrow are ingested, as the only means of getting rid of them. It has often been debated whether they undergo any digestion in the alimentary canal, and I am inclined to think that they contribute something to the nutrition of shipworms. Boring I believe to be a periodical function, perhaps alternating with more active ingestion of food. This is indicated by two facts. In the first place, it seems that while the new-formed teeth are being cemented to the anterior edges of the valves the shell could not be used. Also, the cæcum of the stomach contains almost wholly particles of wood, which indicates that while the animal is burrowing, the orifice into the cæcum is open. The very large fold of the internal mucous membrane of the cæcum (fig. 29–31) seems so eminently constructed for absorption that I think there must be some digestive action on the particles of wood within it.

ORGANIZATION AND LATE DEVELOPMENT.

In their form and general organization the adult ship-worms are the most peculiar and striking of all the lamellibranchs. Their newly attached larva has the form and essentially the organization of the larva typical of most of the marine lamellibranchs which are free-swimming during their larval development. The transformation of the typical larva into the highly specialized ship-worm is so striking and takes place with such great rapidity as properly to be called a metamorphosis.

THE LARVA.

ORGANIZATION.

The general shape of the newly attached larva (fig. 1) is that of a small clam, with equal shell valves. These latter are broader dorso-ventrally than long, so that this lamellibranch, which is more elongated as an adult, as a larva is more foreshortened, perhaps, than any other form. The youngest specimens I found were creeping over the surface of the wood by means of the very active tongue-shaped foot. The velum was in all cases retracted into the large velar cavity (*vc*), a large space in the anterior dorsal part of the shell cavity. This is best shown in figure 24, which represents a sagittal section of a newly attached larva. The foot (fig. 1, 7, 22) at this stage is very long, ciliated over most of its extent, and angular at its posterior end. This angular portion is occupied by a well-developed though simple byssus apparatus which throws out a single simple byssus thread several times as long as the diameter of the larva. This serves to anchor the larva in the early stages of attachment, so that after the velum has been lost it may still return to its mooring if from any cause it lose its footing.

The siphons are already well developed in the larva, the ventral inhalent or respiratory (*is* fig. 1, 7, 22) with ciliated sensory papillæ; the dorsal exhalent (*es*), a simple nonciliated tube. The gills have advanced but little beyond the stage figured by Hatschek (1880) for the viviparous larva studied by him. On each side of the body there are two large gill-slits, and in the gill membrane the rudiment of a third. The shipworm larva is a typical dimyarian. Both adductor muscles are present in their usual positions, the posterior (fig. 22, *ap*) already considerably larger than the anterior (*aa*). The posterior retractor muscles of the foot at this stage are attached in the umbonal region of the shell, just in front of the posterior adductor muscle.

The alimentary canal is already highly specialized (fig. 7, 22, 23, 24). A comparatively long œsophagus (*oe*) leads into the stomach, from which a single comparatively large liver vesicle projects as a diverticulum on each side. The sheath of the crystalline style (*ss*) projects from the posterior ventral portion of the stomach on the midline. The intestine leaves the stomach from the right side, anteriorly. The cæcum of the stomach, peculiar to the Pholadacea, is present as a small hemispherical rudiment on the right side, just posterior to the opening of the intestine.

The nervous system of the larva (fig. 7 and 59) is already highly specialized. At the sides of the œsophagus are the two cerebral ganglia, separated from each other

by only a snort connective. The pleural ganglia (*pl*) are still separate from the cerebral (*c*) and lie lateral to them. The pedal ganglia (*p*) are high up in the foot and are closely fused together, as in the adult. The two visceral ganglia (*v*) are still wide apart and lie against the anterior face of the posterior adductor muscle. In front of each is a separate respiratory ganglion (*r g*). From each pleural ganglion a pleuro-visceral connective (*pv*) extends to the corresponding visceral ganglion, and from the cerebral ganglion a very short cerebro-pedal connective (*cp*) to the pedal. I think there is still a distinct pleuro-pedal connective, but this I can not state positively. The ganglia contain the ganglion cells and the connectives contain only nerve fibers.

The kidneys (*k*, fig. 7) consist of large vacuolated cells, and open externally in front of the posterior adductor. The internal pericardial openings I have not been able to find. Lying around the cerebral ganglion is a gland which, so far as known, is peculiar to ship-worms and which, in later stages, becomes so greatly developed in connection with the gills. The glandular portion (*g D*, fig. 24) contains spherical cells, and from it a duct opens to the exterior (*d D*) under the cerebral ganglion.

METAMORPHOSIS.

The duration of the free-swimming life of the larva is not known, but it is perhaps a month, more or less. In a very much shorter period after attachment, the peculiar ship-worm has been developed, with the adult organization essentially completed. The first change is the sudden entire loss of the velum. Within a few hours after the larva has settled, the velum begins to disintegrate and its constituent cells are cast off and eaten by the larva. The lower lip is projected forward under the cavity of the velum, and as the cells are cast off they can not pass to the exterior, and so are eaten. The basement membrane of the velar epithelium contracts rapidly and the cavity of the velum is very quickly obliterated (within a few hours).

Accompanying the loss of the velum, the long byssus thread has been secreted. As soon as the larva is secured by means of the byssus it seeks a place to burrow, and, in preparation for its future life, its whole organization begins to change. The fusion of the two sides of the mantle ventrally progresses rapidly, and within two or three days (fig. 2) only the opening for the foot is left. The siphons elongate rapidly, and very early (within three days) the mantle grows out posteriorly so as to project beyond the shell. The shell grows and changes rapidly after attachment. Within two days the first row of teeth has been formed on the anterior edge of each valve; the greater growth on the ventral edges causes the two valves to gape, to permit the protrusion of the foot in front and the growth of body behind; the knobs have been formed on dorsal and ventral portions; the apophyses have been formed and the retractor muscles of the foot have become attached to them instead of to the umbonal region of the shell. The foot, meanwhile, has become pestle-shaped.

The alimentary canal takes an important part in the general change. The cæcum of the stomach, present in the larva as a rudiment, enlarges very rapidly and, even before woody material has been ingested in quantity, projects as a large vesicle into the foot. In the early stage shown in figure 8 (four days attached, a half millimeter long) it already forms a large part of the visceral mass. As the ingestion

of woody materials progresses, the cæcum projects more and more posteriorly, and in specimens 2 mm. long (fig. 9) extends much beyond the posterior adductor muscle. The gills soon grow around the foot posteriorly, and in specimens 2 mm. long, 10 to 12 days old, project much beyond the visceral mass (fig. 9). This same stage also shows the pericardial space, with its contained and associated structures, in the position which it occupies in the adult, distinctly posterior to the larger adductor. And in this, as in subsequent stages, the visceral ganglion lies at the posterior end of the pericardial cavity.

There are a number of features in the organization and metamorphosis of the larva that seem to have a wider significance. One of these is the sudden and complete loss of the velum. Lovén thought that, in forms of lamellibranchs studied by him, it entered into the formation of the labial palps. These structures are present in the adult *X. gouldi* only as the small ridges on the sides of a slight groove around the mouth; so that this form, in which they may be said to be absent, does not give evidence necessarily against the derivation of the palps of the adult from the velum of the larva in forms in which the palps are well developed. The velum in various lamellibranch larvæ, however, is very much larger than the palps in early stages, so that most of it must be cast off or absorbed. In the newly attached oyster I have observed that the cells of the velum are absorbed more slowly, though the palps are developed somewhat later merely as ridges at the sides of the mouth. The evidence from *X. gouldi* and *Ostrea virginiana*, it seems to me, shows conclusively that the palps are not derived from the velum. The loss of the velum is an event not confined to the lamellibranchs. Wilson (1890) has observed that the trochal cells of *Polygordius* are suddenly cast off and eaten, as in *X. gouldi*, and Pruvot has described the loss of the test in *Dondersia*. These all seem to be phases of one and the same phenomenon and indicate that the loss of a part of the ectodermal covering during metamorphosis in these and many other forms is a very primitive and general occurrence.

The addition of the ship-worms to the forms which have heretofore been known to possess a byssus apparatus indicates that this structure is perhaps universal in lamellibranch larvæ, though in the adult it may become degenerate. I may add that in *Ostrea virginiana* a byssus apparatus is present in the newly attached larvæ, though here a secretion is thrown out for the attachment of the left valve and does not form a byssus thread. In forms like *Teredo* and *Ostrea* the byssus serves for the attachment of the young bivalves, and apparently it has the same purpose in other forms in which it is present in the young (e. g., *Pecten*) but is lost in the adult. In *Sphærium* and allied forms it serves to attach the viviparous larva to the wall of the brood chamber in the gill of the mother. All the known facts go to show that the byssus apparatus was developed to assist in the transformation of the free-swimming pelagic larva into the lamellibranch with an attached or other settled mode of life. Then, this transformation having taken place, the byssus may be lost, or it may be retained in forms which are permanently attached but lack other means than the byssus for attachment.

The sheath of the crystalline style is well developed in the newly attached larva. Everything, however, indicates its derivation by transformation of the posterior end of the stomach. If we imagine the intestine leaving the blind end of the

sheath, we get an arrangement very like that in *Nucula* and *Yoldia*, in which the posterior half of the stomach has the same structure and function as the sheath in other forms, though no style is formed. Having left, in the development of more specialized forms, its point of origin in the median position at the extreme posterior end of the stomach, the intestine has remained attached to various parts of the sheath of the style, as in *Cardium*, and has reached its greatest displacement in forms like *Teredo* and *Pholas*, in which it leaves the stomach from one side and in which the sheath of the style forms a large blind pouch. If this view of the relations of the stomach, intestine, and sheath be the correct one, then the sheath is not a structure which has been acquired in the more highly specialized forms. It is homologous with the posterior part of the stomach of primitive forms like *Nucula* and *Yoldia*. The intestine has left its original median attachment to the posterior end of the stomach and has become attached to one side of it.

THE ADULT.

After the preceding description of the larva and its metamorphosis, the general plan of organization of the adult ship-worm will be easily understood. This is illustrated for *Xylotrya* in figures 5, 6, 10. Figure 5 represents a left view of a young specimen 4 inches long, as it is taken from its tube. At the anterior end (on the left) the "head" is covered by the small shell, over whose dorsal and posterior portions duplicatures (the "cephalic hood") of the mantle project. Behind the shell extends the long, naked body, tapering so that the whole "worm" forms a very long truncated cone. At the posterior end are shown the points of attachment to the calcareous tube, and from it project the palettes and siphons. From the anterior end, between the gaping shell valves, projects the pestle-shaped foot.

The outer wall of the naked, projecting part of the body is the mantle. If it is removed, as represented in figure 6, the long gills are exposed posteriorly and the large visceral mass anteriorly. The latter is continuous with the foot and extends about two-fifths of the length of the body. It contains the viscera (alimentary canal, genital organs, etc.). Dorsal to it (fig. 10) lies the large pericardial cavity with its contained and associated structures (heart, kidneys, visceral ganglion). Dorsal to the pericardial cavity is the long, narrow anal canal, into which the rectum opens above the posterior adductor muscle, and which is continued into the epibranchial cavity posterior to the visceral ganglion. The shell cavity is occupied mostly by the foot, the cæcum and anterior part of the stomach, and the two adductor muscles which are common to most lamellibranchs.

SHELL.

The newly attached ship-worm larva possesses a typical bivalve shell. The valves are equal in size and united dorsally by a well-developed hinge apparatus. The shell in side view is wider than long; the transverse diameter is about equal to the longitudinal. The right valve (fig. 11) bears three equal hinge teeth; the left, two. Dorsal to the teeth is an external hinge ligament. In each valve the apophysis of later stages is present as a rudiment. Up to this time growth has taken place along concentric lines. From this time on rapid, very unequal growth in different parts

of the valves causes a sudden transformation of the shell, which becomes very different from that of the typical bivalve. The initial stages in this change are shown in figure 14, which is an anterior view of the shell of a ship-worm which has been in the wood a day, more or less. After growing a small amount, the anterior border has cemented to it a row of teeth which have been secreted separately in small pockets in the epithelium of the anterior edge of the mantle. The first row of teeth, as well as those formed through life, are cemented to the shell so as to point almost straight outward and very slightly backward. The apophysis, present as a small rudiment in the larval shell, has grown out into the shell cavity, pushing the mantle before it; and, in this very rapidly attained stage, is almost as large comparatively as in the adult. Meanwhile the ventral edge of the valve has grown rapidly, and there have been formed on the dorsal and ventral portions the two knobs upon which, in this and subsequent stages, the two valves swing during the mechanical process of boring. During these changes the hinge teeth present in the larval shell have disappeared, probably by absorption. The valves which, during larval life, have swung at the hinge so as to open and close the shell cavity on the ventral side, come to swing upon the knobs along a median transverse axis vertical to the main axis of the animal. The greater growth of the valves on their ventral edges causes them to gape before and behind for the protrusion of the foot in front, and the siphons, later the body, behind.

Growth of the valves continues with great rapidity. The left valve of a specimen 1 mm. long is shown in oblique view in figure 15. The chief features that have been introduced are as follows: The point of greatest growth is on the ventral edge. The lines of growth, and hence the rows of teeth, are wider apart on the dorsal half of the anterior border than on the ventral. In this way an angle is formed in the anterior edge, which soon (fig. 16) becomes a right angle. Meanwhile, the posterior border has grown rapidly and flares outward so as to give better purchase for the posterior adductor muscle during its contraction. Likewise, a much smaller portion of the dorsal anterior edge flares outward for the attachment of the anterior adductor (fig. 18).

There is little modification in form, structure, and relations of the shell after the stage shown in figure 16, which is a side view of the left valve from a specimen 5 mm. long. As growth on the ventral edge takes place, the knob is constantly being added to toward the midline and absorbed on the side toward the concavity of the valve. And as growth at the posterior border takes place, the posterior adductor muscle is constantly moving backward. In the larval and subsequent stages, the whole shell, including the teeth, is covered externally by delicate epidermis.

PALLETS.

These structures are peculiar to the ship-worms and have been acquired for closing the outer ends of the burrow against intruders and for other purposes. The structure of one of these is shown in figure 20, which represents the left pallet of a specimen 5 mm. long. It consists of a series of seven funnel-shaped structures which have been formed and cemented, in succession, to the handle. The formation of the pallet is as follows: In specimens still less than 1 mm. long, the mantle

of the posterior region has formed a duplicature (fig. 8, 9), which projects like a collar over the base of the siphons. At the anterior portions of the sides of the space thus formed the epithelium of either side evaginates forward. In the pocket thus formed the handle of the pallet is secreted and projects backward into the "collar" space. The lining walls of the sides of the "collar" space secrete the funnel-shaped pieces which are cemented to the handle. New larger pieces are added in succession at the anterior end, and those first formed may be broken off. In species of *Teredo* the paddle part of the pallet is a solid piece and not divided into a series of pieces, as has just been described for *Xylotrya*. Strictly speaking, the segments of a pallet are semicircular when seen on end. When the two pallets are brought together in closing the outer opening of the cylindrical tube they thus form a truncated cone.

MANTLE AND SIPHONS.

In the adult ship-worm (fig. 5) the mantle forms a very long and very delicate tube, which stretches from the anterior edge of the shell to the base of the siphons. These latter are modifications of the mantle, as in other forms of lamellibranchs. The tube is open only at the anterior end, the pedal opening for the protrusion of the foot; and at the ends of the siphons, the inhalent and exhalent openings. It was formerly a much debated question how much of this tube should be considered body proper and how much siphons. In the light of present knowledge it is easy to see that the muscular collar marks off the end of the body and the beginning of the siphons.

The mantle in ship-worms has undergone more differentiation, perhaps, than in any other lamellibranch. The anterior edge is thickened, as in other forms, and secretes the teeth, the edges of the valves, and the epidermis. The very delicate part underlying the shell, and stretching beyond it to the siphons, secretes the inner layers of the shell and the calcareous tube lining the burrow. Within the shell cavity induplicatures secrete the apophyses, and at the same time absorb part of them as they change shape and position. Also, other parts secrete the two pairs of knobs on the valves. The posterior edge of the shell is not marked by the thickened mantle edge as in other types, but the mantle forms a duplicature around the whole posterior edge of the shell, which stretches forward. On the dorsal side the whole umbonal region of the valves is covered by this duplicature, and to this special part Quatrefages gave the name of "cephalic hood" (*c h*, figs. 9, 26). To it he assigned the function of forming the burrow. It is somewhat, but not very muscular, and no such important work could be done by it. It probably serves as an elastic washer around the "head," which prevents the fine particles of wood grated off by the shell from passing posteriorly to lodge between the mantle and calcareous tube.

In the collar region it has been seen that the mantle forms the duplicature or collar, which projects posteriorly over the base of the siphons, and within the cavity of which the handles and paddles of the palettes are formed separately (fig. 9, 10). The siphons, specializations of the mantle, form two long tubes (fig. 5, 6, 9) whose walls are slightly fused together through half or more of their extent. The anal

or exhalent siphon is without papillæ or tentacles and is shorter and less muscular than the respiratory or inhalent siphon, which bears a number of tentacles (fig. 5, 6, 9). These are sensory structures, but they also serve mechanically to close very quickly the entrance of the respiratory siphon against the entrance of enemies and injurious objects from the outside.

Between the duplicature at the posterior edge of the shell and the collar the mantle is very uniform. Its structure is as follows: Externally, the surface epithelium is composed of flattened, nonciliated cells, which secrete the calcareous lining of the burrow. Internal to the outer epithelium are the weak muscles of the mantle, consisting of the longitudinal layer; a layer in which the fibers cross obliquely to the longitudinal fibers; and internal to these the circular layer. The internal surface of the mantle is lined by cells which in general are columnar and ciliated. Opposite the ends of the gills, the mantle is strongly ciliated and contains numerous mucous gland cells which empty into the internal surface of the mantle cavity. This region is indicated diagrammatically in figures 27–32, where on either side ventral to and outside the ciliated, glandular area the mantle wall is thickened so as to form a groove opposite the groove of the gill. In life these two grooves are in apposition and together form a canal along which the food is swept forward to the mouth by the ciliated cells lining the canal.

Between the two epithelial layers of the mantle there is a reticular network formed of connective tissue, with a small amount of muscle and nerve fibers, etc. The spaces so formed are filled by a peculiar substance whose nature I have not been able to determine. In living specimens the mantle is of a light grayish, translucent appearance. But specimens in alcohol become of almost a chalky whiteness, due to the masses of this peculiar material. Each lacunar space is filled by a more or less spherical nodule, which is just visible to the naked eye. Examined by transmitted light, these nodules are very opaque and seem composed of granular particles; by reflected light they are white. They are insoluble in acids, but soluble in water and quickly disappear in aqueous solutions. Deshayes described them as nonnucleated mucous cells. They are apparently the "siliceous particles" which Hancock observed, and with which he supposed the burrow to be formed. They are not cells, but deposits of some sort. They are probably to be regarded as constituting a reserve of calcium, containing material of some sort for rapid use, as occasion may require, in the formation and thickening of the calcareous tube which lines the burrow.

Special gland of the mantle.—Lying between the two epidermal layers of the mantle, in the middorsal region near the extreme posterior end of the body, there is a small special gland which seems to be peculiar to the ship-worms. The extent and the details of structure of this organ are shown in figure 21, which represents a transverse section of the whole gland in a specimen about a half a centimeter long. The gland consists of numerous more or less spherical, vesicular acini whose average diameter is about a fortieth millimeter. They are lined by flattened, nonciliated, slightly granular cells. From the gland a median duct passes posteriorly to open on the dorsal outer surface.

This gland appears in the young ship-worm soon after attachment as a single median small vesicle of apparently ectodermal derivation. As the animal grows,

new vesicles are formed as outgrowths from those already present. What the function of the gland is has not been determined, but its position indicates that it may be the secretion of some material noxious to enemies that may get into the end of the ship-worm burrow.

MUSCULAR SYSTEM.

Early in this century it was a much debated question whether the muscle then known in the shipworms was homologous with the anterior or the posterior adductor of other lamellibranchs, or with both combined. It was Grobben who established the homology of the muscles when he discovered (1888) the small anterior adductor, which had been overlooked previously.

In the general transformation of the larva into the ship-worm the ligament, which in the larva opposes the two adductor muscles and opens the shell, comes to serve only to keep the two valves from separating from each other. And the two muscles which together, in the larva, oppose the action of the ligament and close the shell come to cause the two valves to swing upon each other on the dorsal and ventral knobs of the shell valves during the process of boring. So the two adductors become antagonistic to each other.

In the newly attached larva both adductor muscles are present, the posterior (*ap*, fig. 7, 22,) already considerably larger than the anterior (*aa*). Both are attached to the valves within the concavity of the shell and well toward the dorsal side. In the general transformation these muscles, as the active mechanical agents in excavating the burrow, undergo considerable change. The posterior adductor, as the one that really does the work, becomes very large (fig. 6, 9, 10) and passes posteriorly to be attached to the outwardly turned edges of the shell (fig. 15–17), so as to give it better purchase during its contraction. The anterior adductor muscle, whose only work is to bring the shell valves back to their original position, after contraction of the posterior adductor, is comparatively very small (fig. 6, 9, 10, *aa*), and moves forward from its original position in the larva to be attached to the outwardly turned anterior edges of the shell valves.

In minute structure all of the muscle fibers of both adductors are apparently striated, due to a more or less regular deposit of granular material on their surface. This structure seems to support the view as to the function of the two parts of the adductor in forms like *Pecten*, where one part is tendinous and is supposed to prevent the shell valves from separating too far. The other part, composed of striated fibers which contract quickly, is for active adduction of the valves. In ship-worms, where it is not necessary to oppose the action of a hinge ligament, all parts of both muscles are of the same character as that part in *Pecten* which is supposed to serve for active adduction.

The pedal muscles in the larva are those typical of lamellibranchs with a foot. A pair of anterior retractors and a pair of protractors of the foot are attached in the anterior umbonal region of the shell valves; and a pair of posterior retractors, in the posterior umbonal region, anterior to the attachment of the posterior adductor muscle. With the remarkable growth of the apophyses of the shell, the posterior retractor muscles suddenly lose their old attachment in the umbonal region, to become attached to the apophyses through almost the whole length of the latter.

After this shifting, which takes place as the young ship-worm begins to bore, these muscles no longer are sharply defined, but form wide bands which run from the apophyses to be distributed around the sides of the foot

In ship-worms the posterior end of the body, which has usually been described as the "muscular collar," contains a number of highly specialized muscles, some of which are peculiar to the ship-worms. Their general arrangement and their relations to the pallets, to the calcareous tube, and to the siphons are shown in figures 35 and 36. They are divided into two sets, those which manipulate the pallets and those which are distributed to the siphons. The first set consists of a pair of protractors of the pallets (*pp*), two pairs of retractors of the pallets (*rp*), and a single adductor of the pallets (*ap*). On each side the protractor of the pallet is inserted along the handle of the pallet, whence it radiates to be attached to the side of the calcareous tube along a broad line, its origin. On each side there are two retractors of the pallet. One is inserted on the end of the handle and passes forward to be distributed in the mantle along the sides of the body. The other is inserted near the outer end of the handle, whence it runs forward to be attached to the wall of the calcareous tube along with the siphonal muscles. The adductor of the pallets is a stout, cylindrical muscle stretching between the anterior ends of the two pallet handles, and lying in the septum which divides the mantle cavity into epi and hypo branchial cavities posteriorly. The muscles of the siphons are attached on each side to a triangular area of the calcareous tube, slightly anterior and ventral to the attachment of the pallet muscles. From this origin the siphonal muscles are distributed to the siphons, mostly to the respiratory.

The action of the muscles of the pallets and siphons is as follows: When the ship-worm is undisturbed, the siphons are widely extended into the water and the pallets are drawn forward, as represented in figure 35. If the animal is disturbed the siphons are retracted with great rapidity by the contraction of their muscles. At the same time, by the action of the protractors of the pallets, the pallets are pushed forcibly into the end of the tube so as completely to close the latter. The outer ends of the paddles are brought together by pushing against the sides of the tube. The pallets are dislodged by the more powerful ventral retractors, and retraction seems to be completed by the long muscles attached to the ends of the handles. At the same time, by the action of the adductor of the pallets, their paddles are separated so as to permit the extension of the siphons by an inflow of blood.

From this description it is seen that the end of the tube of *Teredo* is homologous with the pallial sinus of typical lamellibranchs. The same siphonal muscles are present as in other forms, but the muscles of the pallets are peculiar to the ship-worms.

RESPIRATORY SYSTEM.

The gills of *Teredo* are perhaps more highly specialized than those of any other type of lamellibranch, for they possess a membranous, nonperforate portion which reminds one of the gill structure in the Septibranchia, and they are otherwise sharply marked off from those of forms most nearly related to the ship-worms and of other lamellibranchs.

Development and general structure of the gills.—The embryonic development of the gills of *Teredo* has been observed by Hatschek (1880) in the viviparous larva of the unidentified species he studied. Here the rudimentary gill of each side is a fold in which perforations appear in succession, new ones being added posterior to those already formed. In the newly attached larva of *X. gouldi*, the gills have advanced but little beyond the stage described by Hatschek. On each side there are two slits and the rudiment of a third. The slits, however, have so increased in size as to occupy most of the space on the upper sides of the foot and the gill-fold has fused to the sides of the foot by its ventral edge. In this way, the gill-slits come to separate bars or filaments attached at both ends (fig. 24); and as the fold, when it appears, is attached dorsally along the line of attachment of the mantle on the sides of the body and the ventral edge fuses with the upper part of the foot, the gill-bars or filaments lie almost horizontally in the mantle chamber.

This mode of differentiation of the gill by the formation of gill-slits in a fold whose ventral edge fuses continuously, at first with the sides of the body and visceral mass (fig. 2) and later with its fellow of the opposite side (fig. 3), is kept up during life. Beginning, however, with a stage still less than 1 mm. long, the process is modified as follows: In specimens less than 1 mm. long (fig. 2) the gill of either side consists of a membrane with a single series of gill-slits which decrease in size from before backwards. When, however, there are about fifteen slits in the series, a perforation in the gill-fold or membrane appears opposite and internal to the tenth (rarely ninth or eleventh) slit of the first series. New ones are added in succession posterior to it, so that a second series of slits comes to be formed internal to the first (fig. 3). At the posterior end the slits of the inner series always lag slightly behind those of the external in their development. As shown in figure 3, there are no slits in the inner series internal to the ten first formed in the outer series, and none ever appear, a fact of significance, as will be shown in describing the gill of the adult, where the first formed part of the gill, with its outer series of ten gill-slits, becomes widely separated from the rest of the gill.

The gill-fold and gill in the young *Teredo* represent the *internal half of the molluskan ctenidium*. From the resemblance of the mode of development to that in *Cyclas* (Ziegler) and *Mytilus* (Lacaze-Duthiers), it is seen that the slits of the first formed series separate the descending limbs of the lamellibranch gill filaments, and that the second series separate the ascending limbs. The anterior ten filaments, then, never develop the ascending limbs. Likewise, the other (the outer) half of the ctenidium is never developed in *Teredo*—contrary to the belief of Deshayes and Quatrefages, who believed the whole ctenidium, or "pair" of gills, to be present on either side of the body.

The term "gill-fold" I have used to designate the posterior end or growing point of the gill, and "gill-filaments" the elements that are formed from it. In later stages, however, soon after that shown in figure 2, the growing point forms a more or less cylindrical hollow tube, filled by a blood space, which fuses continuously on the midline with its fellow of the opposite side, and dorsally over a wide area (between the two points indicated in fig. 37) with the mantle. In this way the epibranchial cavity is separated from the rest of the mantle cavity. Meanwhile,

the free portion of the growing point has become angular, and at the sides of the angle the two series of perforations are formed progressively (fig. 3), the outer always slightly in advance of the inner. The corresponding slits of the two series push in (in the direction of the lower arrows in fig. 37) till they meet each other and till they push through to the epibranchial cavity. These in-pushings divide the original blood space of the growing point into flat spaces separated from each other except at two points, the openings into the afferent and efferent branchial veins. The median portion of the original blood space remains undivided as the afferent vein, and by the disappearance of the median part of the walls of the two growing points as they fuse together, the afferent veins of the two sides unite, posterior to the visceral mass, to form the single large, median, afferent branchial vein. The undivided outer dorsal portion persists as the efferent branchial vein on each side. The walls of adjacent slits are connected by numerous connective-tissue cells (fig. 38) so as to form the gill laminæ, the name given to them by Quatrefages and more appropriate for the gill elements in ship-worms which (except the anterior eleven) do not form filaments. From the mode of formation it is seen that there is a large flat blood space in each lamina and that there is a free flow of blood through the lamina (in the direction of the arrows, fig. 37) between the afferent and efferent branchial veins.

In a young ship-worm a half centimeter in length (somewhat later than the stage represented in fig. 3) there is on each side a continuous series of seventy-five or more gill filaments (filaments and laminæ), stretching from the mouth region around the sides of the body and posterior to the visceral mass. Soon afterwards the "filament" between the tenth and eleventh (usually) gill-slits broadens from before backward. This growth increases till, in large specimens of the adult, the anterior eleven filaments (it may rarely be ten or twelve) are separated from the rest of the gill by a space of 10 cm. or more. They retain the structure, however, and doubtless the function, of gill elements, though in the adult they form a series of simple bars attached at both ends on the sides of the "head" (fig. 6). In reality the first and eleventh filaments are but half filaments.

In ship-worms the epibranchial cavity forms a single long canal posteriorly (fig. 10, 31, 32), but is divided anteriorly where the gills of the two sides diverge from each other. As the anterior eleven filaments become separated from the rest of the gill, the epibranchial cavity between these two parts of the gill becomes a long, very narrow canal (*ep ca*, fig. 26–29), which lies in the mantle on each side, external to the afferent branchial vein and adjacent to the groove described below.

The two limbs of a gill lamina (fig. 37) form almost a right angle with each other. At the angle there is a ciliated groove (fig. 30–32, 37) which extends the full length of the gill in young specimens (fig. 3), and in adults, in addition, connects the anterior eleven filaments with the rest of the gill (fig. 6, 26–29). In the adult the connecting part of the groove, then, is really a part of the gill and is homologous with the groove of one filament in other parts of the gill. The minute structure of the groove is as follows: The lining cells are in the main strongly ciliated and columnar (fig. 44), but there are distributed among them numerous mucous gland cells. As already noted, the internal surface of the mantle opposite the edge of the gill

also forms a groove lined by strongly ciliated cells with many mucous gland cells among them, and this, with the groove of the gill, forms a very long tube which conveys food to the mouth.

Minute structure of the gills.—It has been seen that, by their mode of formation, the "intrafilamentar union" between the two limbs of a lamina is so complete that blood may flow freely through the wide, flat blood space of the lamina from the afferent to the efferent branchial vein. The "interfilamentar" or, better, interlaminar connection between adjacent laminæ, is also very extensive, but serves only for support and does not permit the full interchange of blood. The general plan of the interlaminar connections is shown in figure 39, which is a tangential section of a gill almost in the line of the letters *ifj* in figure 38. It is seen that the points of union in adjacent laminæ are arranged in regular rows. At each point the supporting rod (*s r*, fig. 40) projects through a perforation, so as to bind together adjacent laminæ. Attached to adjacent rods are fiber-like cells, which are apparently muscular and contractile.

The minute structure of the edge of a lamina is similar to that of the filaments in forms like *Mytilus*, though the various types of cells are more sharply marked off from each other. At each side there are two rows of large "lateral cells" (*l c*, fig. 40), bearing long, dense cilia. External to these are small nonciliated gland cells, and at the angles the small, flattened "latero-frontal" cells (*lfc*, fig. 40), each with a single row of stiff cilia. The outer edge of the laminæ is occupied by numerous small "frontal cells" (*fc*) which bear numerous weaker cilia. The two broad sides of the lamina are composed of very flat cells without cell outlines or regular arrangement, and are connected together by numerous connective-tissue cells which penetrate the blood space of the lamina (*bs*, fig. 38, 40). In their minute structure (fig. 41) the anterior eleven filaments which are separated from the rest of the gill are essentially like the rest of the gill, except that the "frontal cells" are more numerous, and the middle ones seem to bear no cilia. The first and eleventh filaments are only half filaments, indicating that the filaments are formed by perforations in a gill membrane which is primitive, and not that the membrane is formed by the precocious fusion of gill filaments. The long epibranchial canal is sparsely ciliated, and it seems that the special function of the anterior eleven filaments is to get rid of superfluous water in the anterior end of the burrow.

Glands of Deshayes.—Closely associated with the gills of the adult is a pair of very complicated structures which, so far as known, are peculiar to ship-worms, and which constitute one of the most important features which distinguish the ship-worms from other types of lamellibranchs. In honor of the observer who first called attention to them, I have called them the "glands of Deshayes." Though he pointed them out they have never been fully described as to character, structure, and relations.

Deshayes observed a peculiar structure in the umbonal region on each side of the shell cavity. He described it as of glandular nature and supposed its function to be the secretion of a fluid to soften wood in the formation of the burrow. In the gill laminæ he described peculiar modifications of the tissues, which he supposed to be mucous glands and to serve for the nutrition of the viviparous embryos of ship-worms. He also described a third structure as invading a part of the walls of

the afferent branchial vein, and of unknown function. These three glands described by Deshayes are parts of one and the same structure, which is present, in different degrees of development, in all of the three species I have studied. In all three the part in the gill is well developed. In *T. dilatata* the umbonal portion of the gland is so large as to occupy a considerable part of the umbonal region of the shell cavity; in *X. gouldi* it is small, and in *T. navalis* apparently rudimentary. In his studies of the pericardial glands in lamellibranchs, Grobben sought in *Teredo* for the gland described by Deshayes in the umbonal region, thinking it might represent a part of the pericardial gland of other forms which possess this organ. He failed to find it and supposed it to be absent. However, though he apparently had none of the forms with which I have worked, I think it was doubtless present in his species.

In the larva this peculiar structure is present on each side in front of the cerebral ganglion, though still comparatively simple (*g D*, fig. 7). It is vesicular and filled with spherical *cells* of apparently mucous nature. A duct leads to the exterior, opening at the side of the mouth on the ventral side of the velum.

The structure of subsequent stages of the gland will be best understood by first describing that part in the gill. An examination of figure 38 will show that this modified portion contains elements of two very different types of structure. Their distribution and relations are best shown in figure 37, which represents a lamina from the gill of *T. navalis*, in which species they are most strikingly developed. This figure also shows the distribution of the gland in the branchial vein, and that this portion is of the same nature as that lying in the lamina adjacent to it. Still farther from the vein is the second type of structure. Ramifying in all directions from the latter are dentritic processes which penetrate the epithelial walls of the lamina. These ramified portions are the primary structures, apparently, and the other two are derived from them. The structure of the dentritic portion is shown in figures 46 and 47, which were drawn under a magnification of 1,900 diameters. The processes seem devoid of any membrane. The contents consist of very minute filamentous structures arranged lengthwise in the direction of the process. Lying in the mass thus formed are nuclei which vary in number and position. The middle one in figure 48 indicates that they may change position, and that the whole structure forms a syncytium. The enlarged portions of the processes, shown in figure 37, become surrounded by a specialized epithelial covering, apparently derived from the lining cells of the gill lamina. This stage is represented in figures 46 and 47. The minute filamentous structures have taken on a more irregular arrangement, and lying within the mass are spherical cells of varying appearance. While some (fig. 45) are coarsely granular, others are almost homogeneous. The nuclei lie on one side of the cells.

The other type of structure (fig. 49–51) I am confident, though not perfectly sure, is also derived from the dentritic processes along with a modification of the surrounding epithelium. The developed structure is of remarkable appearance (fig. 51). The base is composed of modified epithelium cells of the wall of the lamina. The nuclei stain lightly and lie in a granular protoplasm, from which deeply staining rods project toward the blood space of the gill lamina, but from which they are separated by a membrane formed of very flat cells. The development of this structure seems to be as follows: When the dentritic processes penetrate

among the epithelial cells (fig. 48), the filaments are arranged lengthwise; soon they take on a vertical position (fig. 49), enlarge, and become covered by the caplike membrane (fig. 49–51). If this derivation be the correct one, then the rods in figure 51 have been formed by the enlargement of the filaments of the dentritic structures. In the lamina the rods project toward the blood space; in the afferent branchial vein, away from the blood space. Why the difference I do not know.

The development of the gland of the adult, so far as I can determine, is as follows: When the small ship-worm has been in the wood for a day or so, the gland of the larva sends out processes which invade the surrounding ectodermal tissues (the mantle, sides of the body). As the side of the body becomes enlarged, it fuses with the dorsal sides of the gill filaments (fig. 25). From the first there is close association between the gland and the gill. As the latter grows, the filaments become invaded by the gland; and, as the anterior ten filaments become separated from the rest of the gill, the two parts of the gland thus differentiated remain connected by a long, narrow duct which accompanies the epibranchial canal and lies in the afferent branchial vein (fig. 26–30). With the separation of the two parts of the gill, the intervening part of the gland disappears in *X. gouldi* and *T. navalis*, but persists in *T. dilatata*. As the gland enters each gill lamina, it remains connected by a small duct with the main duct, and may send the granular cells into the latter. The main duct may become gorged with granular cells (fig. 37). In most cases, however, there are few cells in it, and I am inclined to regard the main duct (at least in *X. gouldi*) as degenerate and perhaps essentially functionless. Likewise, I am inclined to regard the formation of the spherical cells in the one part as not the chief function of this part of the gland. The origin and fate of the cells I have not been able to determine. Their contents suggest that they may be modified mucous gland cells.

What the special function of this remarkable structure is I am not able even to guess. The rudimentary character of the anterior part in the "head" of *T. navalis* indicates that it can not be the formation of a secretion to soften wood. Its development in the gill, in small as well as large individuals, in male and female, and in forms that do not retain the eggs in the gills, proves that this part can not be for the nutrition of viviparous embryos. The close connection with the gill indicates, it seems to me, that its function may be the elaboration of some internal secretion or other material for whose formation the presence of both blood and water is necessary.

CIRCULATORY SYSTEM.

The circulatory system of the shipworms is highly modified in relation to the peculiar form of the body. The growth of the visceral mass ventrally at first, and afterwards its great elongation posteriorly, along with the elongation of the rest of the body, accounts for the changes that have taken place. Doubtless the ancestors of ship-worms were lamellibranchs with typical circulation, in which on either side in the pericardial cavity lay an auricle lateral to, and emptying into, the median ventricle which surrounded the intestine; and from the ventricle the anterior aorta passed forward above the intestine and the posterior aorta backward below the intestine. In ship-worms the pericardial cavity, with its contained parts, has come

to lie on the morphological ventral side of the intestine, though apparently on its dorsal side, and the relations of the various parts of the circulatory system to each other and of the system as a whole to associated parts have been radically changed.

The youngest stage of the circulatory system I have observed in detail is in specimens 2 mm. long, in which the heart consists of two almost completely separated halves (fig. 52). On each side a more or less spherical auricle (*au*) lies lateral and slightly ventral to, and leads into, a more or less spherical half of the ventricle (*ve*). Each half of the ventricle sends a very narrow, vessel-like portion toward the midline, where the two sides unite. In this middle portion there are two semilunar valves (fig. 55) on the dorsal and ventral sides, and from this point two vessels emerge. One runs anteriorly, and, bending around the posterior adductor muscle, is continued posteriorly in the mantle. At this stage the visceral mass has projected but little posteriorly (fig. 3), and the second vessel from the heart, somewhat smaller than the other, runs ventrally into the visceral mass. These structures are shown in section in figure 54, which is of a longitudinal section through the median part of the ventricles and aortæ in a specimen 4 mm. long.

In the stage in which the heart is developing the stomach and cæcum already occupy most of the visceral mass and the gills are very wide apart. This may account for the wide separation of the two halves of the heart. In development posteriorly the gills advance ahead of the other structures and, accompanying them, the two sides of the heart are drawn out backward so as to lie side by side. In the adult (fig. 53) the two halves of the ventricle (*ve*) have fused on the midline, except at the posterior end, where the two sides still project as somewhat hemispherical masses. Internally, however, the lumen remains divided (fig. 29) through half of the extent of the ventricles. At the anterior end the ventricle has the shape of an elongated cone. The two auricles accompany the gills in the posterior development of the latter and come to lie side by side like two large vessels in the posterior half of the pericardial cavity. Each projects into the ventricle on its own side and valves separate the cavities of the auricles from that of the ventricle (fig. 53).

The pericardial cavity of the ship-worms (fig. 10, 29, 30) lies on the apparent dorsal, but really on the morphological ventral, side of the visceral mass. It is very large, extending from the posterior adductor to the visceral ganglion through a quarter of the length of the animal. In *Xylotrya gouldi* it narrows in front to form a canal which projects beyond the wider part to the posterior adductor muscle. About two-thirds of the distance from the visceral ganglion to the posterior adductor (fig. 10) the anterior end of the ventricle dips down through the pericardium into the visceral mass. This point is the end of the ventricle and the beginning of the aortæ, the end of the ventricle being marked off by two semilunar valves which project forward on its dorsal and ventral sides (*val*, fig. 55). From the end of the ventricle two vessels are given off. The larger (*avp*, fig. 10, 56) runs forward (fig. 26–28) in the visceral mass and passes ventral to and in front of the posterior adductor, to bend over the latter and enter the mantle as the large dorsal or posterior pallial artery. This runs posteriorly as a single vessel in *Xylotrya*, at the right side of the anal canal and epibranchial cavity (fig. 26–32, *da*) to the posterior end of the body, where it divides into the two paired arteries of the siphons.

This aorta I have just described is the morphological posterior aorta, though its course at first is anterior. The second aorta leaving the ventricle runs posteriorly in the visceral mass, which it supplies, and is the morphological anterior aorta.

The venous system consists of three important parts. Blood from the viscera and anterior part of the body is gathered into a system of afferent branchial veins consisting anteriorly of a pair of large vessels (*ba*, fig. 27–29) which in the region of the visceral ganglion unite to form the single very large afferent branchial vein that runs between the fused gills (fig. 10, 30–32). Passing from this vein through the gill lamellæ, the aerated blood enters the large paired efferent branchial veins, from which it passes to the auricles. Blood from the posterior part of the body is gathered into an afferent renal vein (*arv*, fig. 31, 32), which runs forward and enters the perinephridial spaces at the posterior end of the kidneys.

The description I have just given applies specially to *X. gouldi* and *T. navalis*. In *T. dilatata*, while the relations are somewhat different, the homologies remain the same. In this species the principal part of the visceral mass has remained more anterior and the posterior part of the body is longer in proportion. In following the gills the heart has become much more elongated, and this elongation has taken place principally in the aorta-like part of the ventricle which runs forward from the more thickened portion of the ventricle. In this species the pericardial cavity extends much farther forward than in *X. gouldi*, passing under and anterior to the posterior adductor muscle as a long canal to end under the œsophagus. In this canal the ventricle runs to the anterior side of the posterior adductor and then dips into the visceral mass. Valves mark the anterior end of the very long ventricle, from which two vessels pass forward. The larger, after giving off branches in its course, bends around the adductor and divides into paired pallial arteries which supply the posterior part of the body. This is the posterior aorta. The other, the anterior aorta, also runs forward a short distance, but soon breaks up into arteries which supply the visceral mass.

I have gone into details in describing the aortæ, because the posterior aorta has been described as fused with the anterior in *Teredo*. This observation was first made by Grobben (1888) who described as aorta a part of the ventricle which is distinctly muscular and contractile. The parts which should have been described as aortæ he has not figured at all. Menegaux has also maintained that the two aortæ are fused (1889). Unfortunately neither of these authors names the species with which he worked, but their descriptions of other parts are faulty and indicate that there is little doubt that they have been in error in this regard also.

ALIMENTARY CANAL.

In adaptation to their burrowing mode of life, the alimentary canal of all the Pholadacea has become more highly specialized, perhaps, than in any other type of lamellibranch. This specialization is most accentuated in the ship-worms, apparently in association with the ingestion of the particles of the wood grated off in burrowing.

Most of the parts of the alimentary canal of the adult are already present in the newly attached larva, though their relations to each other and their relative

development are very different from the adult condition. The general plan is shown in figure 7, which represents a newly attached larva from the right side, with the shell, mantle, and gills removed. A long, ciliated œsophagus (fig. 7, 22 *oe*) leads into a rather small stomach, from which projects on each side a large, simple, almost spherical liver lobule. The wall of the liver is composed of large, coarsely granular, pigmented, nonciliated cells (fig. 7, 23). The intestine leaves the right side of the stomach (fig. 7, 24) and after forming a single loop passes over the posterior adductor muscle as the rectum. Just posterior to the point of origin of the intestine is a small hemispherical diverticulum of the stomach, the cæcum (*ce*, fig. 7, 23, 24), composed of densely granular, nonciliated cells. The posterior ventral part of the stomach is occupied by the opening of a large conical diverticulum, which is median in position, the sheath of the crystalline style (*s s*, fig. 7, 22). Its walls are composed of large, coarsely granular, densely ciliated cells characteristic of this structure, except at the blind end, where the cells are smaller, more finely granular, and nonciliated (fig. 22).

The alimentary canal of the larva is interesting because of the advanced development of some parts and the retarded development of others. The liver has advanced but little in form beyond a stage reached two or three days after hatching. On the other hand, the cæcum of the stomach, which is peculiar to the members of the Pholadacea, is already present as a rudiment, although it is not to become functional till after the adoption of the burrowing mode of life in the wood.

As the larva develops into the ship-worm, the size and relations of the parts of the alimentary canal change greatly. The œsophagus becomes, in the adult, very short in comparison with other parts (fig. 10). The stomach elongates posteriorly more and more (fig. 8, 9, *s*) till, in the adult, it projects far beyond the posterior adductor muscle and forms a long, irregular, more or less cylindrical tube (fig. 10). As is well known, the wood grated away in boring is ingested and stored in the cæcum of the stomach. Even before the ingestion of the wood begins, the cæcum projects into the foot as a large hollow vesicle lined by clear, ciliated cells; but as soon as wood is ingested it enlarges rapidly and soon forms the largest part of the digestive system (fig. 8, 9, 10, *ce*). With its increase in size, it comes to leave the posterior end of the stomach and crowds the sheath of the crystalline style to the left side (fig. 8, 9, 10). In young specimens the cæcum occupies almost the whole mass of the foot, and its blind end points forward (fig. 8, 9). As the visceral mass elongates, the cæcum is gradually drawn backward, till in the adult it forms a very long cylindrical tube, stretching to the posterior end of the visceral mass (fig. 10, *ce*). In ship-worms that are boring and growing the cæcum is always completely filled with ingested particles of wood. The scarcity of diatoms and other food materials seems to indicate that in the ship-worm boring an ingestion of wood alternates with ingestion of food, and that in feeding the food is guided into the intestines, and in boring the particles of wood into the cæcum. The cæcum of the adult is, then, a long blind tube, opening only at its anterior end into the stomach. Internally it is lined with a ciliated mucous membrane, which is infolded on the ventral side like a complex typhlosole (fig. 30, 31). This fold

seems of independent origin, and not at all homologous with the fold in the intestine. The long retention of woody particles in the cæcum, along with the greatly increased absorbent surface of the latter, indicates that the wood is at least in part digested and serves as food.

In elongating posteriorly, the cæcum pushes the intestine ahead of it, so that the latter always forms a very long loop around the posterior end of it. In the adult the intestine, because of the great development of the cæcum and the greater development of the liver on the right side, leaves the stomach slightly to the left of the midline, near the posterior end (fig. 10). Bending forward it forms a single short loop and then passes backward to form the loop around the cæcum. Then passing forward dorsal to the stomach it bends over the posterior adductor as the rectum (*r*), which projects slightly into the anal canal. Throughout its whole extent the intestine possesses a typhlosole, but slightly developed except in that part next to the stomach. Here it is so greatly developed as to form several coils (fig. 27), which are analogous to the spiral valve of the intestine of elasmobranchs. Because of this the diameter of the intestine in this region is greatly enlarged (fig. 10). The intestine of *X. gouldi* is very much shorter than in other shipworms. This shortening is doubtless connected with the greatly increased absorbent surface because of the coiled typhlosole. In most shipworms the intestine forms several coils before it passes around the cæcum, and in such forms there is no greatly developed typhlosole.

In ship-worms, as in *Pholas*, there is a second small, quill-shaped cæcum of the stomach on the dorsal side to the left, under the posterior adductor muscle (*ce'*, fig. 9, 10, 26). It is lined by columnar, ciliated cells and generally contains particles of sand. It is small and seems rudimentary, but it may have some function unknown at the present time. Pelseneer has observed an apparently homologous structure in *Nucula*, where it is said to secrete a small style.

The sheath of the crystalline style, present on the midline of the larva, comes to arise from the left side of the stomach near the anterior end of the latter (*ss*, fig. 9, 10), and hangs toward the right side. Its blind end forms a vermiform tube, which is very different from the rest of the sheath. The latter has its walls composed of large, coarsely granular cells, which bear long, very heavy, dense cilia (fig. 56). The tubular portion, on the other hand, has its walls composed of elongated, densely granular and deeply staining, nonciliated cells. In adults the walls of the tube may become very thin (fig. 57), in parts. What the function of this tubular portion is I am not able to state, though it is perhaps the secretion of some constituent of the style. Barrois (1889) has figured a *pair* of diverticula at the ends of the sheath of *Pholas dactylus*, lined by cells similar to those of the rest of the sheath. On examining sections of specimens of *Pholas* of apparently the same species as those studied by Barrois I find a single tube, as in ship-worms, lined by cells of the same character as in the latter. I am inclined to believe that Barrois's description and figures are faulty.

The liver, composed of a single spherical lobule on either side of the stomach in the larva, soon divides into several lobules on either side (*l*, fig. 8, 9). As growth takes place, the duct of the right half of the liver divides (in specimens 4–5 mm. long) and as the shipworm elongates, the posterior part of the right half of the

liver passes backward, so that in the adult its duct opens into the posterior end of the stomach. These anterior and posterior portions of the liver are completely separated from each other, forming separate liver masses (fig. 10). The anterior remains in the foot and sends its duct to open into the lateral anterior portion of the stomach. There seems little doubt that it was this part which Frey and Leuckart observed and described as the salivary glands peculiar to ship-worms. The posterior part of the liver is the larger of the two and opens by a very large duct into the ventral part of the stomach. It is differentiated into two portions, which in structure and apparently in function are quite distinct from each other, though they open into the stomach by the same duct. The more elongated, slightly larger portion (fig. 28) lies on the right side, and in structure is like the anterior liver mass of ship-worms and the whole liver in other forms of lamellibranchs. The second portion (fig. 28), lying more on the left side, is different in appearance. Its lobules are larger, with larger lumens and thinner walls, which are composed of flattened cells glandular in appearance. The presence of large quantities of woody materials in these larger, thin-walled lobules suggests that this portion of the liver may be specialized for the digestion of cellulose, and this view is strengthened by the long retention of woody materials in the cæcum. This portion of the liver is adjacent to the opening of the cæcum, and it may be that it secretes a ferment for cellulose digestion which is continued in the cæcum. As has been pointed out already, the latter by its structure seems adapted to absorption on a large scale.

NERVOUS SYSTEM.

The nervous system of ship-worms I have studied in the larval and subsequent stages to the adult of *Xylotrya gouldi*, and in the adult of *T. navalis* and *T. dilatata*. While my description applies especially to the first of these, the others are in such close agreement that we seem justified in believing that there is great uniformity in this regard in all of the species of the Teredinidæ, and that the descriptions heretofore given have been somewhat erroneous.

Nervous system of the larva.—In the newly attached larva the principal elements of the adult nervous system are present. In their relations to each other, however, the embryonic development of these is not complete; and in their relation to other structures great changes take place along with the change in the general organization. The general plan is shown in figures 7 and 59, the latter representing a dorsal view of the nervous system of a larva just attached. In front of and on the sides of the mouth are the two cerebral ganglia (*c*), separated from each other by a very short commissure, and each sending a connective to the pedal ganglion (*p*) of the same side. Lateral to the cerebral ganglion of each side is the pleural ganglion, still distinctly separate from it and sending a connective posteriorly to the visceral ganglion. I think there is also a pleuro-pedal connective at this stage, but this I am not able to state positively. The two pedal ganglia are as completely fused together as in the adult, and lie just posterior to the beginning of the œsophagus (fig. 22). Lying immediately in front of the posterior adductor muscle (fig. 7, 22, 24), the two visceral ganglia together form a long cylinder enlarged at both ends. The commissure connecting the two ganglia contains ganglion cells. The two sides rapidly become more closely fused and, in the early stage represented

in figure 8, the concentration is almost as great as in the adult. Each visceral ganglion of the larva gives off a respiratory nerve which bears a respiratory ganglion still far apart from the visceral. While the visceral ganglia are becoming more closely fused, the commissures between the cerebral and pleural ganglia are becoming obliterated. The pleural ganglia persist as separate masses in the young ship-worm of three or four days (fig. 8), but soon afterwards fuse completely with the cerebral, though sections of later stages still indicate by their structure the double origin of the so-called cerebral ganglia.

While these concentrations of the visceral ganglia with each other and of the pleural with the cerebral have been taking place, the cerebral commissure is constantly elongating, along with the growth of the œsophagus, so that in the adult the cerebral ganglia are separated from each other by a comparatively long commissure.

Nervous system of the adult.—Along with the great change in the general relations of the various systems that has taken place during the transformation from the larva to the adult ship-worm, the nervous system has changed principally in the altered position of the visceral ganglia, which lose their place in front of the posterior adductor muscle, and come to lie much posterior to it. The same three pairs of ganglia are present in the ship-worms, however, as in other types of lamellibranchs. The general arrangement is shown in figure 60. Lying almost at the sides of the mouth are the two cerebral ganglia (*c*, fig. 10, 60), well developed and separated from each other by a long commissure (*c c*), which is composed only of nerve fibers. From near the outer end of each a single large pallial nerve passes, to be distributed to the parts of the mantle which underlie the shell and form the cephalic hood. From near the inner ends of the ganglia large connectives pass around the sides of the mouth to the pedal ganglia (*p*); and from the posterior outer ends the cerebro-visceral connectives pass posteriorly to the visceral ganglia. The pedal ganglia give off several pairs of large nerves to the foot.

Visceral ganglia.—The two visceral ganglia of the larva fuse into the single mass which lies very far posteriorly in the adult (*v*, fig. 10, 60). After leaving the cerebro-pleural ganglia, the cerebro-visceral connectives pass along the sides of the "head" under the anterior gill filaments; but posterior to the large adductor muscle they take up a more median position, among the tissues of the liver and reproductive organs. In front of the visceral ganglia they come to lie close together, internal to the large, ductlike portions of the reproductive organs. But before entering the visceral ganglia, they pass dorsal to a small "anterior ganglion" which lies just in front of the latter. In passing through they give to it a small number of nerve fibers (fig. 63), which are lost in it. Then the connectives enter the visceral ganglion but little diminished in size. This anterior ganglion was first described by Pelseneer (1888) for the ship-worms, and seems peculiar to them and their allies. It is a small ganglionic mass lying distinctly in front of the visceral ganglion in well-preserved specimens. From the fact that fibers cross between the sides, it seems composed of two halves, quite completely fused together. As has been stated, the cerebro-visceral connectives in passing send fibers ventrally into it, to be completely lost there. From this ganglion several pairs of nerves are

given off which innervate the kidneys and other viscera, the genital papillæ and the osphradium, at least in part (fig. 60). From the anterior end a pair passes forward to supply the genital organs and perhaps other viscera. From the middle of the ganglion a pair passes laterally to innervate the genital papillæ and the kidneys (fig. 63). Leaving the posterior lateral angles of the ganglion, the largest pair of nerves pass backward under the visceral, and divide each into two parts. The one, somewhat larger than the other, passes dorsally to enter and be lost in the mass of the visceral ganglion. The other passes laterally to innervate the osphradium.

The visceral ganglion proper of the adult (fig. 10, 60), because of the great development of the posterior part of the body innervated by it, has attained greater comparative size than the cerebral and pedal. It forms a somewhat three-lobed mass, in which the larger central part consists of the completely fused pair of visceral ganglia of the larva, while the lobe on either side consists of the respiratory ganglia of young stages which have come to lie adjacent to the visceral proper.

From the visceral ganglion several pairs of nerves are given off, whose connection with the visceral is through the lateral masses (fig. 60). Passing forward on either side are two small nerves (fig. 60, 1 and 2) which accompany the kidneys and anal canal and innervate the posterior adductor muscle and the mantle anteriorly. Given off slightly posterior to them, a large nerve (3) goes directly to the middle part of the mantle. Posteriorly, a pair of large pallial nerves (*pn*, fig. 31–33, 60) passes backward to innervate the posterior part of the mantle, including the siphons and the muscles of the palettes. The branchial nerves (fig. 60, *bn*) pass laterally, closely associated with the osphradium, and then innervate the gills.

This description of the nervous system differs essentially from that of Quatrefages (1849) which has heretofore been accepted. He thought the two cerebral ganglia closely fused, and the pedal rudimentary and separate. I have no doubt that he mistook the pedal ganglia for the cerebral; his figures seem to show this. But what he observed and figured as the two very small pedal ganglia I do not know. It has been seen that while the pedal ganglia are not so large as in forms with a large foot, they are not at all rudimentary.

Otolithic vesicles.—The larva leads an active, free-swimming life, and some means of orientation is very essential. This is the function of a pair of otolithic vesicles in the usual position in the foot. But the adult ship-worm may assume any position and the otolithic vesicles become useless and degenerate. After attachment they soon cease to grow and, in specimens 2 or 3 mm. long, their function seems lost. They persist as small masses of cells in the adult, though without a lumen and without the otolithic concretions.

Sense organ of the genital papilla.—One of the pairs of nerves of the anterior ganglion has been described as going to the kidneys and genital papillæ. Situated just at the junction of the ectodermal genital duct with the sexual organ there is an organ which, by its structure, seems to be for special sensation. The nerve to it (fig. 63, 64), after a very short course, is distributed to sensory cells which lie adjacent to the epithelial lining of the genital duct. The sensory cells are long spindle-shaped, and send their peripheral ends to terminate among the epithelial cells lining the

genital duct. Their central ends I have not traced distinctly into the nerve to the anterior ganglion, but it seems justifiable to suppose that this is their connection. What the function of this organ is I can not state. While the figures apparently show it some distance from the exterior, it should be remembered that, in ship-worms 30 mm. long, the sexual duct is less than a half millimeter long, and that the sense organ is really very near to and, for purposes of sensation, practically at the surface.

Osphradia.—In the ship-worm these molluskan organs of special sense form large masses of complex tissues at either side of the visceral ganglion (fig. 60). Their general shape is elliptical and they are in close association with the branchial nerves. Each organ (fig. 65) is composed of two parts. At the ventral (outer) surface there is a part of the body epithelium, which in this region is specially differentiated from the surrounding cells. While the epithelium of the epibranchial cavity is ciliated, the osphradial epithelium is quite devoid of cilia. Besides, the cells composing the osphradial epithelium seem to have quite lost their cell walls, so that the spherical nuclei lie in a common mass of protoplasm. The outer surface of the epithelial layer is covered by a very delicate membrane, and at its internal surface there is a stouter basal membrane. Underlying the surface epithelium is a mass of nervous elements, composed of both cells and nerve fibers. The cells, however, are sensory and stain somewhat differently from the ordinary ganglion cells. They are of two kinds, both spindle-shaped, and sending their peripheral ends through the basement membrane of the overlying epithelium, to break up into brushlike terminations just inside the delicate outer membrane of the epithelium. These structures are shown in figures 65 and 66. In figure 65 both types of cells are shown, the larger one to the left representing the type much less numerous than the other, staining differently from them, and penetrating the osphradial mass to terminate centrally differently from the smaller, more numerous cells. The internal or central connections I have not been able to determine, but this much it seems justifiable to state: The osphradial nerve from the anterior ganglion becomes so closely associated with the respiratory nerve that it can not be stated that the anterior ganglion alone supplies the osphradium. Also, the large sensory cells penetrate through the osphradial mass, and especially it can not be stated that their connection is with the osphradial nerve.

These structures I have described in some detail for two reasons. In the first place, the epithelium of the osphradium is usually described as consisting of columnar cells, which form the sensory part of the structure. This I have found to consist of a layer in which cell outlines are not distinguishable, and in which the spherical nuclei lie as in syncytium. The real sensory cells are the spindle-shaped cells lying in the deeper part of the osphradium.

In the second place, Pelseneer (1891) has described the osphradium in ship-worms and *Pholas* as innervated by a nerve from the anterior ganglion, and the latter as connected with the cerebral ganglia through the connectives. From this he concludes that the osphradia, as well as the other organs of special sense, are innervated from the cerebral ganglia. The organization of the nervous system in ship-worms, it seems to me, lends no evidence whatever to this view. The nerve fibers received from the connectives by the anterior ganglion are quite lost in the latter, and can not be traced into any of the nerves which leave it. Moreover, the anterior ganglion may, with much more reason, be said to be connected with the visceral ganglion, for

the branch of the so-called osphradial nerve from the visceral ganglion to the anterior ganglion is much larger than the nervous elements received by the anterior ganglion from the cerebro-visceral connectives. Pelseneer seems not to have seen the other nerves that leave the anterior ganglion. With as much reason it might be said that the structures they supply also are innervated from the cerebral ganglia. Nerve fibers, it may be, pass from these structures through the anterior ganglion to the cerebral, but that the latter are the only centers in which reflexes may be established seems not in accordance with the structure of the nervous system in *Teredo*. It seems more plausible to regard the anterior ganglion as a part of the visceral which has been separated from the latter. It receives a part of the cerebro-visceral connective, and gives off some of the nerves that formerly were given off by the visceral.

From a theoretical standpoint, too, one would expect elongated forms like *Teredo* and *Pholas* to have a more direct connection between the osphradia and the reflex centers. If the osphradia test the character of the water flowing over the gills, then it is difficult to believe that in a large ship-worm the nervous impulse should travel from them to the cerebral ganglia and back again through the visceral ganglion to the pallial nerves before the siphons can be contracted and the inhalent current stopped. This would necessitate a course of almost two meters in very large specimens. The more direct connection through the visceral ganglion is the one it seems reasonable to expect.

KIDNEYS.

The kidneys (organs of Bojanus, nephridia) of *Teredo* were observed, apparently, by Deshayes, but mistaken for veins. Quatrefages also observed them, but gave no adequate description. Pelseneer (1891) has noted the position and relations of the openings of the two ducts.

In the adult ship-worm the paired kidneys lie on the dorsal side of the large pericardial cavity and ventral to the anal canal, extending through the long distance between the posterior adductor muscle and the visceral ganglion. Each kidney consists of what may be termed the body, which lies around the posterior face of the posterior adductor muscle (*k*, fig. 10), and two very long ducts, one of which puts the body of the kidney in communication with the pericardial cavity, while the other leads to the exterior. The body is a massive, much pouched structure, in which the lining secretory epithelium is vacuolated and in part ciliated. From the body the very long, narrow, cylindrical afferent duct passes posteriorly (*ka*, fig. 27–29) near the midline. Just in front of the visceral ganglion it enlarges, becomes convoluted internally, diverges from its fellow of the opposite side (*k a*, fig. 62), and dips under the end of the efferent duct (fig. 61) to open into the posterior angles of the pericardial cavity (fig. 30) by a large funnel-shaped opening. The lining cells of the afferent duct are not vacuolated and apparently not excretory; and not ciliated except in the enlarged, funnel-shaped portion, in which they bear strikingly long, dense cilia (fig. 64).

The efferent duct, leading from the body of the kidney to the exterior, is also a cylindrical tube, of much larger diameter than the afferent duct. It runs with the latter near the midline (*ke*, fig. 10, 27–29), and in front of the visceral ganglia, after diverging slightly from its fellow of the opposite side (fig. 62), it crosses dorsal

to the end of the afferent duct. Then it passes ventrally and posteriorly (fig. 61, 62, 66) to open near the midline into the epibranchial cavity, under the visceral ganglion. The efferent duct is lined with columnar, vacuolated and apparently secretory cells, which are not ciliated except at the anterior end and near the external opening.

Venous blood from the posterior end of the body returns by the afferent renal vein (fig. 31, 32, *a r v*) which runs in the mantle, and on a level with the posterior ends of the duct, enters the peri-renal blood spaces (fig. 27–29, 31). After bathing the kidneys, it enters the general venous circulation.

Pelseneer, who, it seems, observed only the posterior ends of the kidney duct, described them as much pouched. In properly prepared specimens of *X. gouldi* I find that, while the body of the kidney is much pouched, the ducts form straight cylindrical tubes. Preserved ship-worms are almost always very greatly contracted and shrunken, and I am inclined to believe that this fact accounts for Pelseneer's results. Also, contrary to the statements in text-books (Lang), I find that the two kidneys of *X. gouldi* do not communicate with each other, as they do in *Pholas* and other forms. In the larva the kidneys lie anterior to the posterior adductor muscle and lateral to the visceral ganglion (fig. 7, 24, 26). As the visceral ganglion passes under and posterior to the muscle, the kidneys accompany it (fig. 9). In the early stages each kidney consists of a simple loop (fig. 9), of which the branch opening to the exterior seems to be excretory. As the ship-worm elongates, the chief secretory portion of the kidney remains with the muscle, while the two ducts become very long and their openings accompany the visceral ganglion.

REPRODUCTIVE ORGANS.

The first stage in which I have observed the reproductive organs is in specimens 2 mm. long, in which there is a mass of undifferentiated primordial germ cells under the visceral ganglion. As growth takes place processes grow out from the original organ till, in the adult, the sexual organs occupy a large part of the posterior portion of the visceral mass (fig. 10, 29–31). As the sexual products develop, they are stored in the cavities of the organ, and especially of that part first formed (fig. 63, 64, *ov*), which serves as a duct for the rest of the organ. The real sexual duct is remarkably short. It is formed as an ectodermal invagination which is already present in specimens 2 mm. long, but which does not break through into the sexual organ till sexual maturity.

In the adult ship-worm the sexes are separate. Young specimens (1–4 cm. long) of *X. gouldi*, however, are very frequently hermaphrodite. As in all such cases the sperms are developed first, it appears that the species may be protandrous. In the adults I have observed no external differences between the sexes. In the male there is, however, a remarkable development of mucous gland cells on the dorsal side of the epibranchial cavity, while in the female they are not usually developed in this region.

SUMMARY.

The results of my work on ship-worms may be summarized as follows:

(1) The larva is a typical free-swimming marine lamellibranch larva.

(2) The whole velum is suddenly cast off and eaten, soon after the attachment of the larva. After the loss of the velum the young ship-worm is, in its general organization, essentially a typical small bivalve.

(3) The loss of the velum in ship-worms and in *Ostrea* (which I have also observed) indicates that the formation of the palps in lamellibranchs has no connection with the velum.

(4) A byssus apparatus is present in the newly attached larva, but is functional for only a few hours.

(5) The position and relations of the sheath of the crystalline style in the larva indicate that this structure, in the more highly specialized lamellibranchs, is homologous with the posterior half of the stomach of forms like *Yoldia* and *Nucula*.

(6) The pleural ganglion of the larva is separate from the cerebral.

(7) The transformation of the larva into the small ship-worm is so rapid as to amount to a metamorphosis. Almost the whole organization is involved—shell, mantle, foot, alimentary canal.

(8) The posterior adductor muscle is the effective agent in forming the burrow, and the shell is the tool with which it works.

(9) In the ship-worms there is a peculiar gland of unknown function in the mantle of the posterior part of the body.

(10) A system of highly specialized muscles manipulate the pallets and are peculiar to ship-worms.

(11) There is on either side but a half ctenidium. The anterior eleven gill filaments form small "plications" on the side of the "head," separated by a wide space from the rest of the gill.

(12) In close association with the gills is a prominent glandular structure of unknown function, which I have called the "gland of Deshayes." It consists of two types of elements of remarkable character.

(13) Through the elongation of the visceral mass, the positions of the two aortæ have been reversed; i. e., the apparent posterior aorta is the real anterior and the apparent anterior the real posterior.

(14) The cæcum of the stomach is very large and apparently an important absorbent organ. The blind end of the style sheath is tubular and of very different character from the outer part. In *Xylotrya* the typhlosole of the anterior part of the intestine is remarkably developed into a complicated in-rolled duplicature.

(15) The nervous system of the adult contains the three pairs of ganglia, well developed, as in typical lamellibranchs. The pedal ganglia are fused together; the cerebral are separated from each other by a long commissure. The "anterior ganglion" is a small ganglion separated from the visceral ganglion, and nerves from it innervate the kidneys, the genital organs, and the osphradium in part.

(16) On the genital duct is an organ of special sense of unknown function. The sensory cells of the osphradium lie beneath the surface epithelium. Their peripheral

ends penetrate the epithelial layer, and break up into brush-like terminations on its surface.

(17) The kidneys lie dorsal to the pericardial cavity. The main secretory part of each kidney is much pouched and lies on the posterior adductor muscle. It is connected with the posterior ends of the pericardial cavity by a very long, narrow duct, and with the exterior by a very long, larger duct which opens under the visceral ganglion.

(18) In the adult ship-worm the sexes are separate. Young individuals (1–4 cm. long) of *X. gouldi*, however, are very frequently hermaphrodite. In all such cases the male cells are developed first, indicating that the species may be protandrous. The sexual duct is very short and is formed as an ectodermal invagination.

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EXPLANATION OF PLATES.

KEY TO LETTERING.

an	Anus.
a a	Anterior adductor muscle.
a c	Anal canal.
a g	Anterior ganglion.
ao a	Anterior aorta.
ao p	Posterior aorta.
a p	Posterior adductor muscle.
a pa	Adductor muscle of palette.
a r v	Afferent renal vein.
au	Auricle.
b a	Afferent branchial vein
b e	Efferent branchial vein.
b n	Branchial nerve.
b s	Blood space of gill lamina.
by	Byssus.
b g	Branchial groove.
c	Cerebral ganglion.
c c	Cerebral commissure.
c s	Crystalline style.
ce	Cæcum of stomach.
ce'	Secondary cæcum of stomach.
c h	Cephalic hood of mantle.
col	Collar
c p	Cerebro-pedal connective.
c v	Cerebro-visceral connective.
d D	Duct of the gland of Deshayes.
d a	Dorsal artery.
d k	Dorsal pivotal knob of the shell.
ep c	Epibranchial cavity.
ep ca	Epibranchial canal.
e s	Exhalent or anal siphon.
f	Foot.
f c	Frontal cells of gill.
g	Ctenidium or gill.
g'	Anterior gill filaments.
g a	Ascending limb of gill filament.
g d	Descending limb of gill filament.
g du	Genital duct.
g D	Gland of Deshayes.
gl ep	Gland cells of epidermis.
g o	Genital organ.
i	Intestine.
i f j	Inter-filamentar junction of gill.
i l s	Inter-laminar spaces of gill.
i s	Inhalent or respiratory siphon.
k	Kidney.
k a	Afferent tube of kidney.
k e	Efferent tube of kidney.
l	Liver.
l c	Lateral cells of gill.
l d	Liver duct.
lf c	Latero-frontal cells of gill.
lig	Shell ligament.
m	Mantle.
m c	Mantle cavity.
m g	Mantle groove.
m u	Muscle fibers.
o	Mouth.
œ	Œsophagus.
o n	Osphradial nerve.
o s	Osphradium.
o t	Otolithic vesicle.
ov	Ovary.
p	Pedal ganglion.
pa	Pallet.
p c	Pericardial cavity.
p gl	Gland cells of foot.
p l	Pleural ganglion.
p n	Pallial nerve.
p p	Protractor muscle of pallet.
r	Rectum.
r f	Retractor muscle of pallet.
r g	Respiratory ganglion.
r p	Retractor muscle of pallet.
s	Stomach.
sh	Shell.
s r	Supporting rod of gill filament.
s s	Sheath of crystalline style.
v	Visceral ganglion.
vl	Valve of anterior end of ventricle.
v c	Velar cavity.
v e	Ventricle.
v k	Ventral pivotal knob of the shell valve.
v m	Visceral mass.

DESCRIPTION OF FIGURES.

PLATE VII.

FIG. 1. Newly attached larva of *X. gouldi*. Sketched from life. The foot is shown fully extended. × 110.

FIG. 2. Young shipworm of about 3 days' attachment, from the ventral side. The shell is represented as transparent, with its outline shown faintly, to show the underlying gills at the sides of the visceral mass. × 125.

FIG. 3. Specimen of about 1 week in the wood, slightly contracted, ventral view. To show especially the arrangement of the gills and the extent of the visceral mass. × 95.

FIG. 4. Same stage as figure 3, from the left side. The worm-like form is being rapidly assumed. × 95.

PLATE VIII.

FIG. 5. Young adult, from left side. The extension of the mantle over the shell, as the "cephalic hood," shown on the dorsal side of the latter. The mantle also extends forward over the posterior margin of the shell for a short distance. The siphons are represented as fully extended, but the pallets are not quite fully retracted. The mantle extends over the bases of the pallets as a collar. The attachments to the calcareous lining of the burrow of the muscles of the pallets (*pp*) and of the siphons (*rs*) are shown. The drawing was made from a slightly contracted specimen 10 cm. long.

FIG. 6. Same as 5, the mantle removed to its line of attachment dorsally, at the two ends, removed to the midline. Lines with figures indicate the position of the sections from which figures 28–35, inclusive, were drawn.

PLATE IX.

FIG. 7. Larva a few hours after attachment, from the right side. The velar membrane has shrunken and the cells of the velum have been ingested. The shell, mantle, gill and liver lobe of the right side removed. The cells of the disintegrating velum are not represented. The foot not fully extended. × 213.

FIG. 8. About the same stage as figure 2, from the left side. The left shell, mantle, and gill represented as removed. The double origin of the cerebral ganglion is still shown. The visceral ganglion and kidney still lie in front of the posterior adductor. The cæcum largely fills the foot, and has crowded the crystalline style and intestine to the left side. × 167.

PLATE X.

FIG. 9. Same as figure 4, the left shell, mantle, and gill removed. The pericardial space, with the included and associated parts, has taken up a position posterior to the adductor muscle. The secondary cæcum of the stomach has been formed. The gills project posterior to the visceral mass. × 95.

FIG. 10. Adult, anterior half of the body, with the left shell valve, mantle, and gill removed, and the pericardial cavity laid open. Half of the posterior adductor removed.

PLATE XI.

FIG. 11. Right shell valve of newly attached larva, internal view. The rudimentary apophyses are shown below the teeth. × 110.

FIG. 12. Same, left shell valve.

FIG. 13. Shell of newly attached larva, end view. × 110.

FIG. 14. Shell of shipworm that has been in the wood about 1 day, front view. The first row of teeth upon the shell, the apophyses and the pivotal knobs have been formed. The shell gapes at both ends. × 110.

FIG. 15. Left shell valve of specimen about 1 mm. long. Oblique view. The larval shell still shown. × 110.

FIG. 16. Left shell valve of specimen 5 mm. long. × 23.

FIG. 17. Left shell valve of large adult. The lines of growth are shown natural size and relations, but the teeth are omitted. × 10.

FIG. 18. Front view of shell of adult. × 7.

FIG. 19. Internal view of right valve, *apo*, apophysis; *aa* and *ap*, attachment of anterior and posterior adductor muscles. × 7.

FIG. 20. Left pallet of specimen 5 mm. long. × 70.

PLATE XII.

FIG. 21. Dorsal gland of the posterior part of the mantle. Section of whole gland of specimen 5 mm. long. The letters are placed in the epibranchial cavity; *fol* are secretory follicles; *du*, duct. × 700.

FIG. 22. Sagittal section of a newly attached larva. The very large glands of the foot occupy a large part of the mass of the latter. A large quantity of material derived from these glands lies adjacent to the byssus gland. The disintegrating cells of velum, some of which have been eaten, are not represented. × 540.

PLATE XIII.

FIG. 23. Transverse section of larva. From a specimen in which the foot was more protracted than shown in figure 22. The ventral mantle edge is filled with cells gorged with material, evidently for the rapid growth of the shell during its transformation. × 440.

FIG. 24. Horizontal section of newly attached larva in which the cavity of the velum was partially obliterated. On the left side the contents of the gland of Deshayes are shown; on the right side, the duct. × 440.

PLATE XIV.

FIG. 25. Transverse section of a specimen 1 mm. long, to show especially the extent and relations of the gland of Deshayes. × 125.

[NOTE.—Figs. 26–33 are a series of transverse sections of a specimen 10 cm. long, along the lines indicated in figure 6. The drawings were made with the aid of a camera and afterwards touched up, though not essentially changed. The details of structure are semidiagrammatic. The right side in the sections is on the left side of the observer. All × 15.]

FIG. 26. Section through the posterior adductor muscle and cephalic hood. Tubular part of style sheath to the right side. Posterior aorta asymmetrical, on the right side.

FIG. 27. Section through the wound typhosole, the canal-like anterior end of the pericardial cavity and the posterior end of the body of the kidney.

FIG. 28. Section through the large posterior liver mass. Shows the distribution and character of the two different parts of the liver.

FIG. 29. Section through the large ventricle and the ovary.

FIG. 30. Section through the opening of the kidney into the pericardial cavity, the anterior ganglion, and the posterior ends of the auricles. The two arrows from the right indicate the course of the water currents between the gill laminæ, the one pointed dorsally, that of blood through the gill lamina. The number and distribution of the interlaminar connections indicated by dots.

PLATE XV.

FIG. 31. Section near the posterior end of the visceral mass.

FIG. 32. Section to illustrate the structure in the long region between the visceral mass and the muscular collar. In this figure, but not in the other transverse sections, the corpuscles of the blood are represented in the blood vessels.

FIG. 33. Section through the "collar," pallet handles, and base of siphons.

FIG. 34. Section of a pallet handle and its sheath. The attachment of the ventral retractor muscle is shown. × 272.

FIGS. 35, 36. Diagrams of the posterior end of body of adult, left side, to show the arrangement of the siphons and pallets and their muscles. In figure 35 the siphons are represented as extended, the pallets as retracted; in figure 36 the siphons are represented as contracted, the pallets as protracted. *Ca*, calcareous lining of burrow.

PLATE XVI.

FIG. 37. Lamina of gill of young *T. navalis*, to show especially the distribution of the gland of Deshayes, in which the elements are represented semidiagrammatically. The arrows indicate the course of the water over and blood currents through the gill lamina. The epibranchial cavity and the blood vessels are indicated by the letters which are placed in these spaces. × 208.

FIG. 38. Transverse section of three laminæ of *Xylotrya gouldi* almost in the line of the lower arrow in figure 30. Two interlaminar junctions are shown. The two elements of the gland of Deshayes are shown, both as to character and distribution. × 208.

PLATE XVII.

FIG. 39. Tangential section of a gill of *Xylotrya gouldi* to show the distribution of the interlaminar junctions. × 156.

FIG. 40. Transverse section of three gill laminæ, along the line shown in figure 37, near the tip of the lamina, so as to show the interlaminar junctions on one side. × 180.

FIG. 41. Section of the three most anterior gill filaments at the side of the "head." The one to the left is the first one and only a half filament. The letters are placed in the epibranchial canal. × 430.

FIG. 42. Group of cells from the branchial groove at the edge of the gill, showing the character of the ciliated cells and the mucous cells among them. × 950.

FIG. 43. Section of that part of the branchial groove which connects the two parts of the gill. × 430.

FIG. 44. Section of the duct of the gland of Deshayes between the two parts of the gill (i. e., between the main part of the gill and the anterior separated filaments of the head). The epibranchial canal is shown to the left and the afferent branchial vein to the right. The great variety in the cells in the duct is represented. × 695.

PLATE XVIII.

FIG. 45. Section of two tubes of the gland of Deshayes from a gill lamina. In the walls of the gill lamina are shown sections of the dendritic processes which penetrate among all portions of the glandular structures. × 925.

FIGS. 46 and 47. Coarser and finer portions of the dendritic processes from the gill lamina of *T. navalis* represented in figure 37. The distribution and contents of these structures are represented in detail. × 1267.

FIGS. 48–51. Four stages in the development of the structures of the second factor of the gland of Deshayes. × 1267.

PLATE XIX.

FIG. 52. Heart of specimen 2 mm. long, dorsal view. Openings from auricles show through the walls of the ventricle. × 180.

FIG. 53. Heart of young adult. The anterior aorta is represented as turned to one side and the auriculoventricular valves as showing through the wall of the ventricle. About × 10.

FIG. 54. Longitudinal section of the ventricle and vessels of a specimen 4 mm. long. The arrows indicate the course of the blood. The posterior adductor muscle and the wall of the stomach represented in part. The anterior end is to the right of the figure. The letters are in pericardial cavity and stomach. × 272.

FIG. 55. Longitudinal section of the anterior part of the ventricle and vessels of a specimen 10 cm. long. × 272.

FIG. 56. Group of cells from the main portion of the style sheath. × 575.

FIG. 57. Same from tubular portion. × 575.

FIG. 58 A. Group of cells from the liver, which show the usual liver structure, and 58 B, from its modified portion. × 575.

PLATE XX.

FIG. 59. Nervous system of newly attached larva, showing the pleural ganglion still separate from the cerebral, and the visceral ganglia still wide apart. The details of the nerves are not shown. × 430.

FIG. 60. Nervous system of adult, dorsal view, except that the pedal ganglion is shown more from behind.

FIGS. 61 and 62. Diagrams to show the relations of the ends of the kidneys, genital duct, pericardial cavity, and visceral ganglion. Figure 61 lateral and figure 62 dorsal view.

PLATE XXI.

FIG. 63. Transverse section of the anterior ganglion and genital duct, to show the connection between the cerebro-visceral connective and anterior ganglion and the origin of the sensory nerve and its distribution to the genital duct. Only a part of the sense organ was included in the section, which is from *T. navalis*, though it might represent *X. gouldi* equally well. × 272.

FIG. 64. Longitudinal section of the genital duct to show its extent and character and the sense organ of the genital duct. The end of the ovary is shown, as also the folded kidney near its pericardial opening. × 272.

FIG. 65. Section of the osphradium, vertical to the surface, to show the structure of the osphradium and the two types of sensory cells, with their brushlike terminations. × 1210.

FIG. 66. Tangential section of the osphradium, to show the distribution of the processes of the sensory cells among the nuclei of the epithelial layer. × 950.

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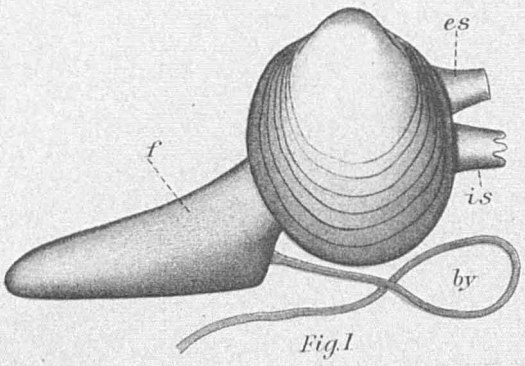


Fig.1

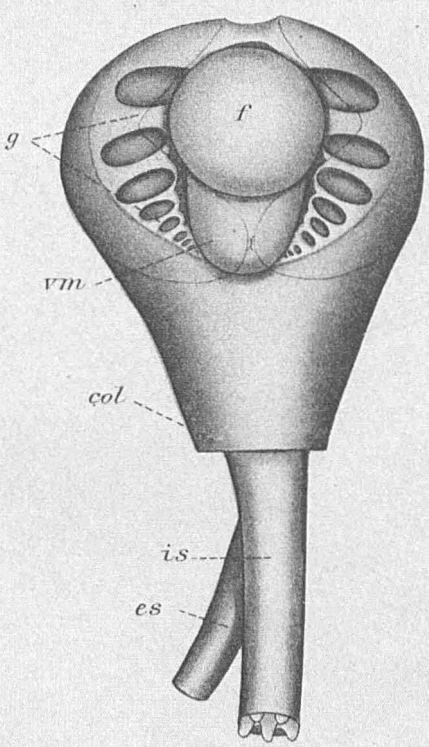


Fig.2

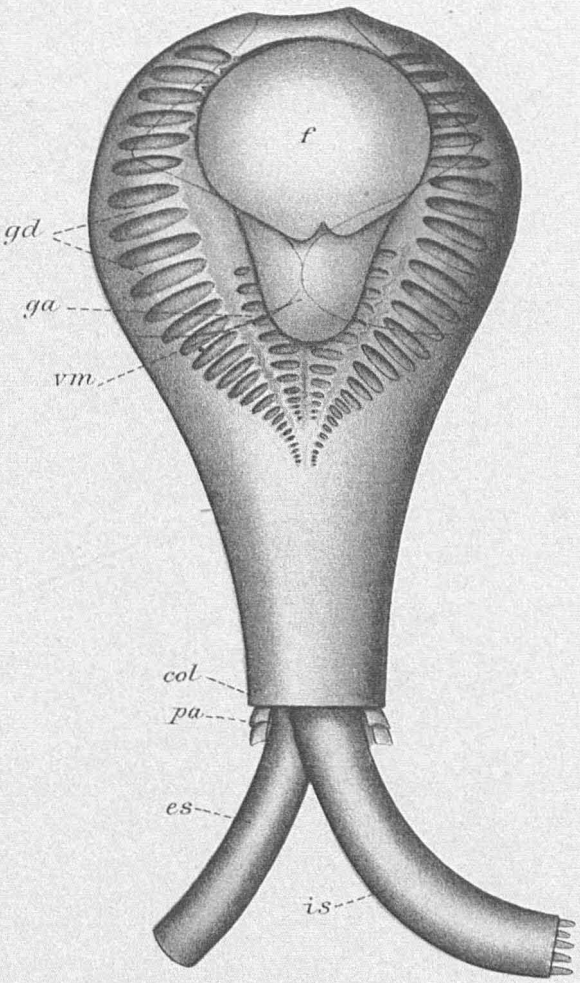


Fig.3

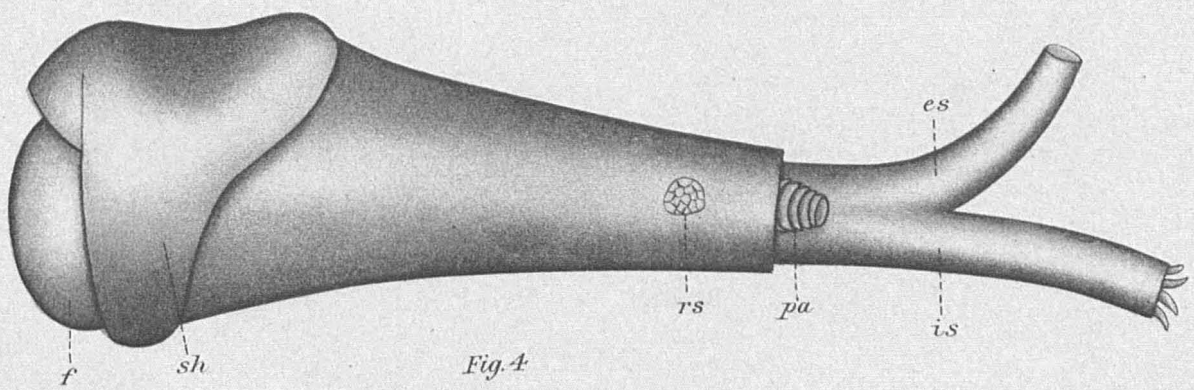


Fig.4

A. HOEN & CO. BALTIMORE

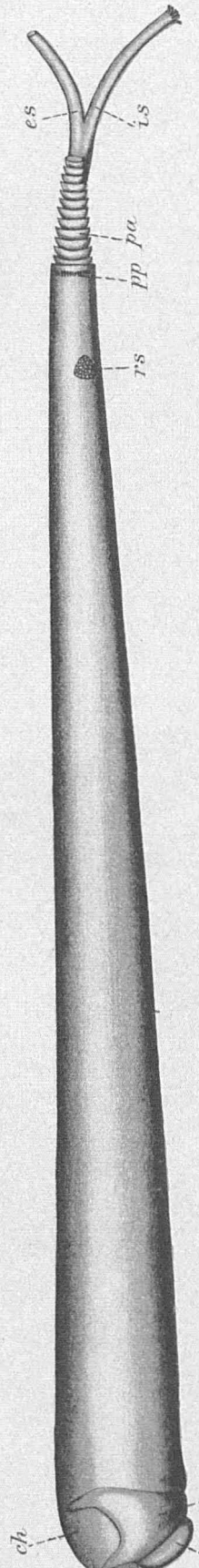


Fig.5

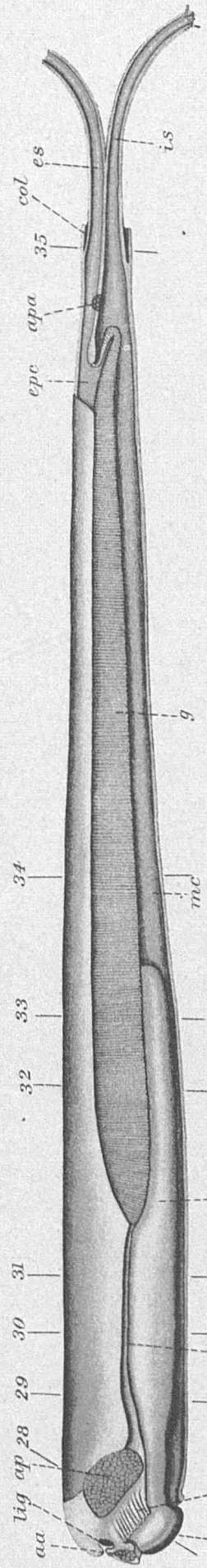


Fig.6

A. HOEN & CO. BALTIMORE

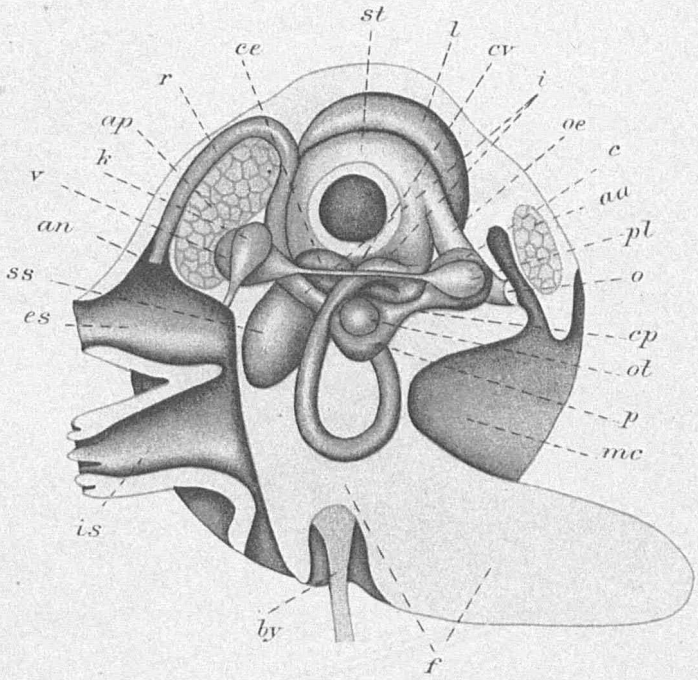


Fig.7

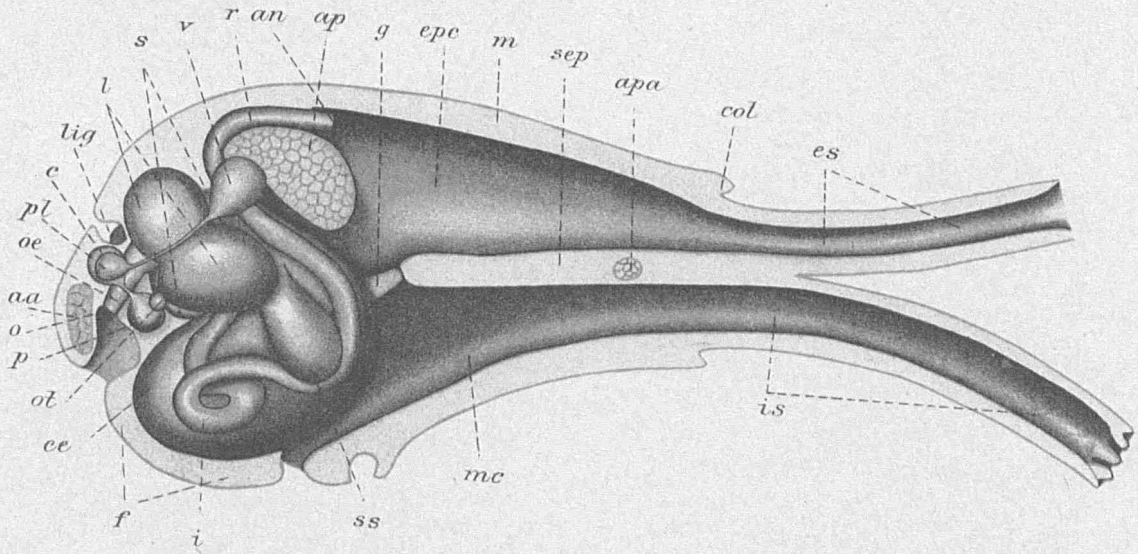


Fig.8

A. HOEN & CO. BALTIMORE.

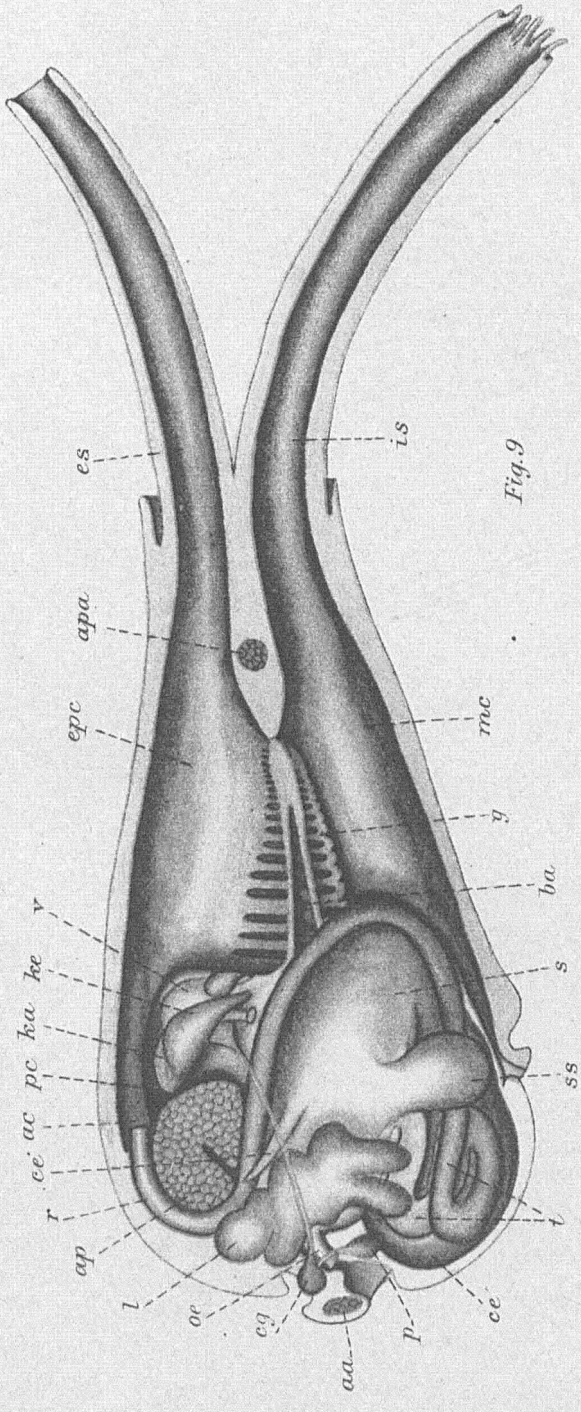


Fig. 9

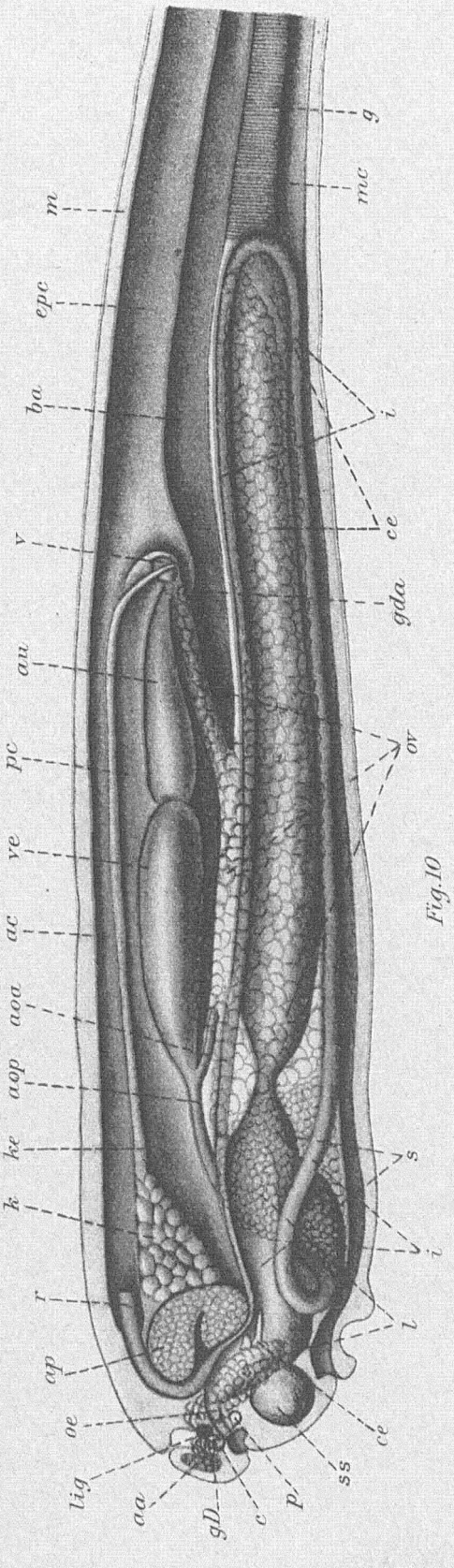


Fig. 10

A. HOEN & CO. BALTIMORE

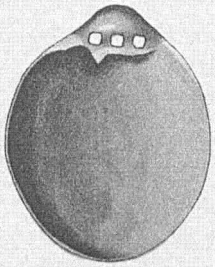


Fig.11

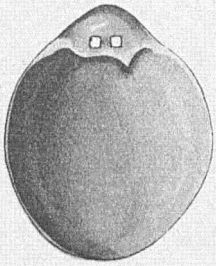


Fig.12

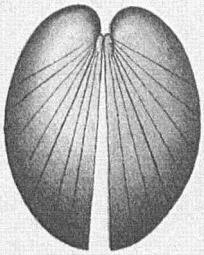


Fig.13

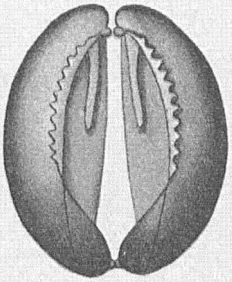
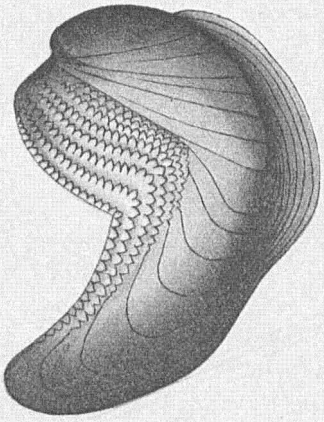


Fig.14



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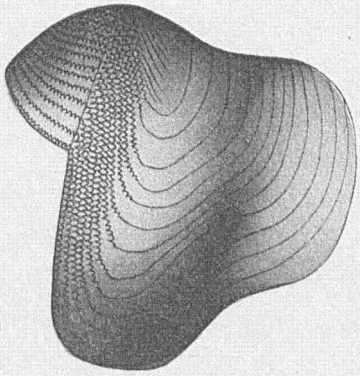
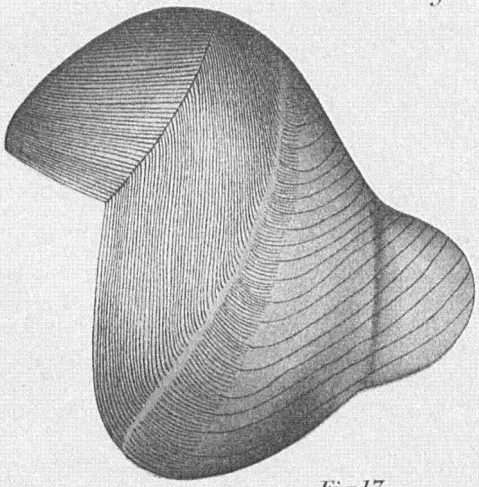


Fig.16



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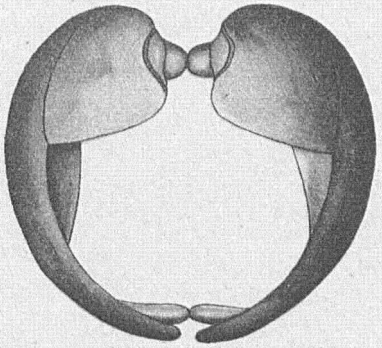

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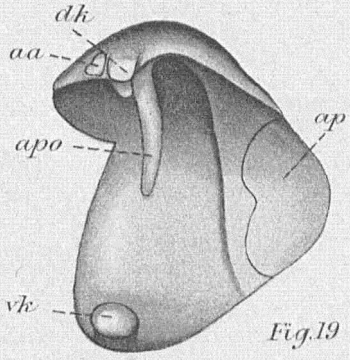


Fig.19

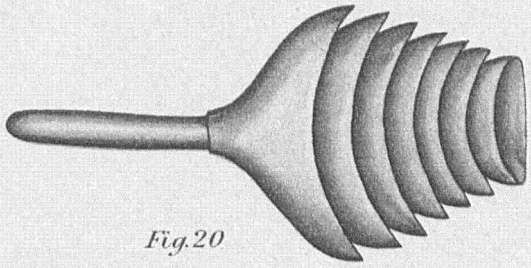


Fig.20

A. HOEN & CO. BALTIMORE

Fig. 21

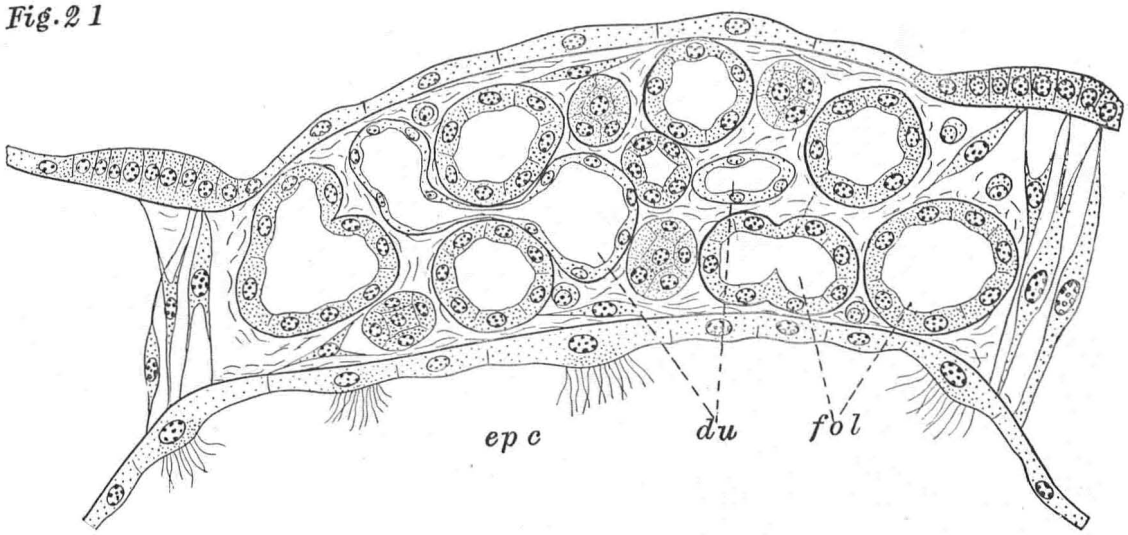


Fig. 22

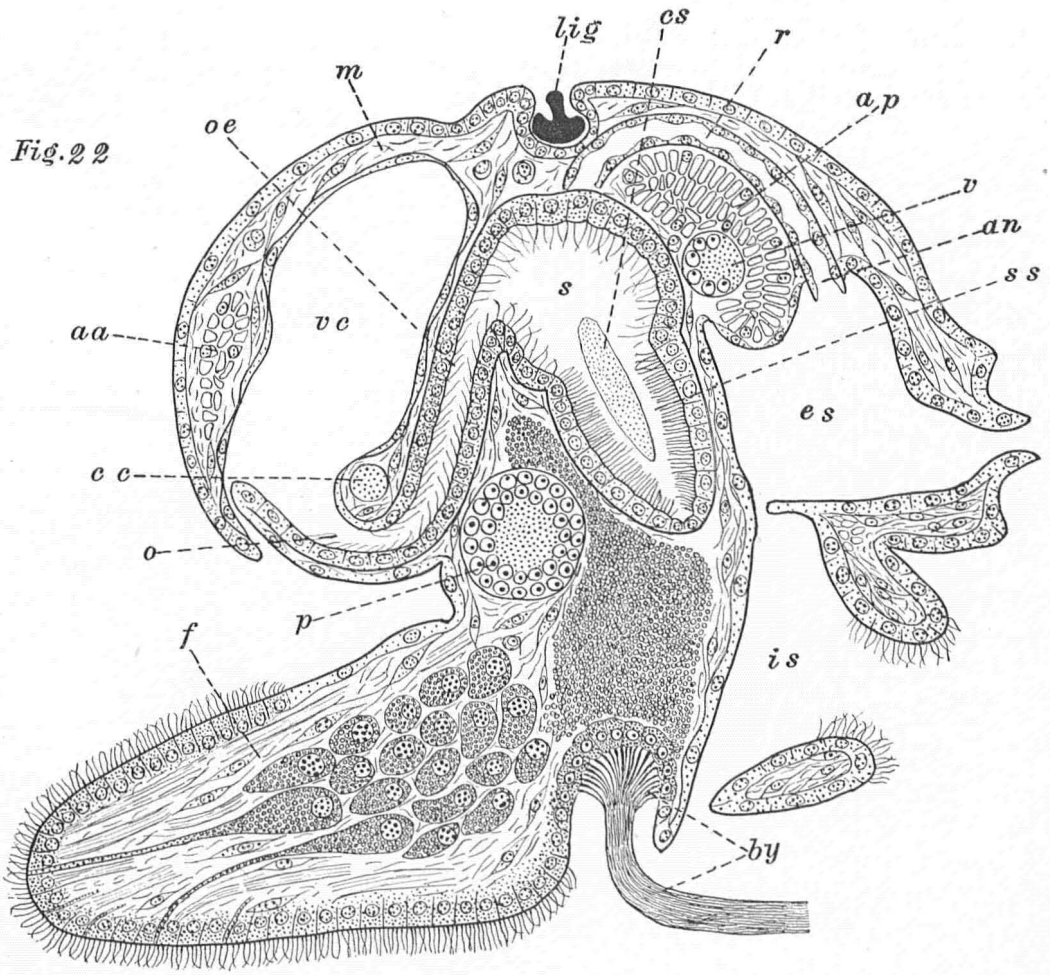
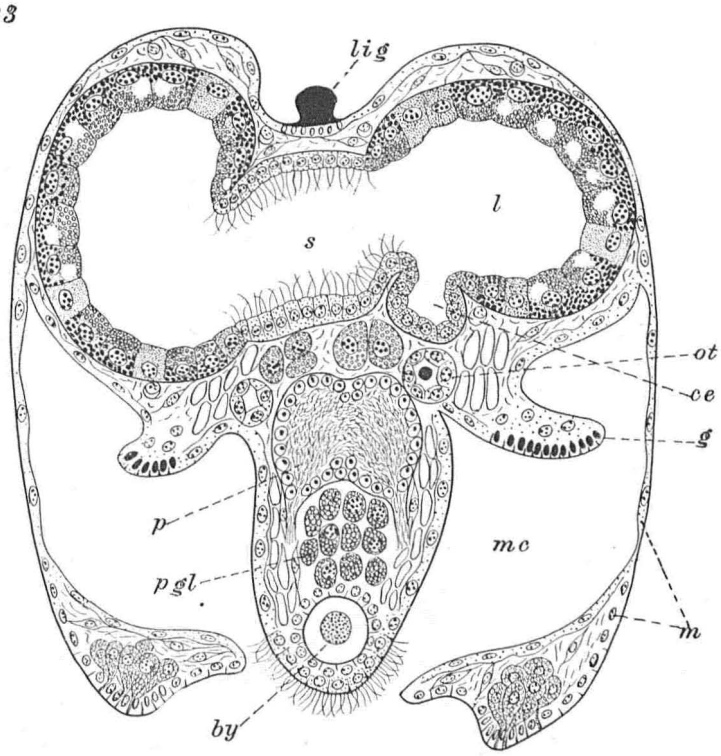


Fig.23



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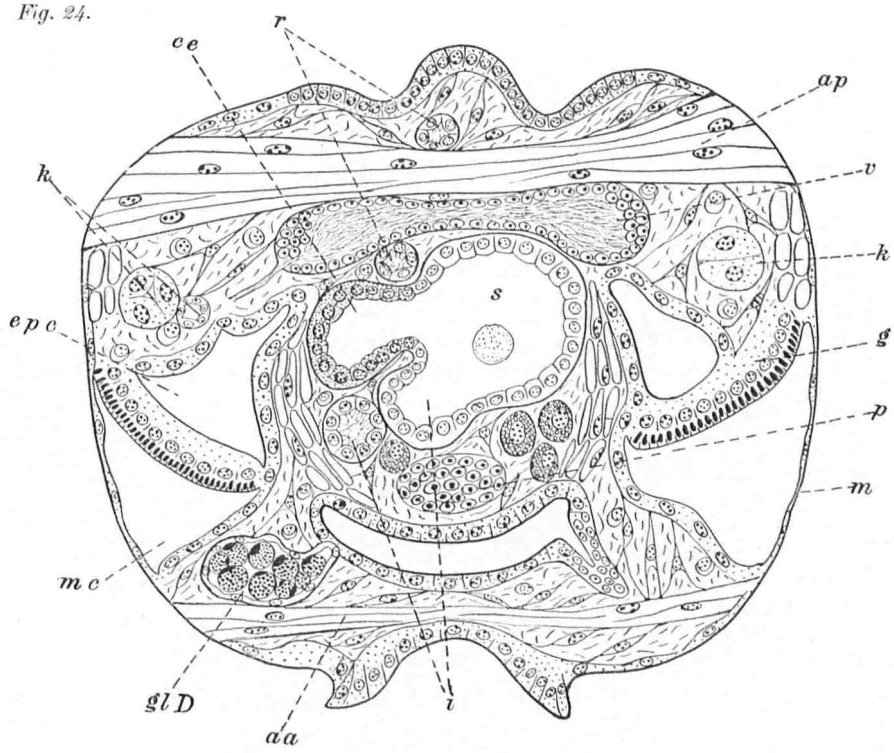

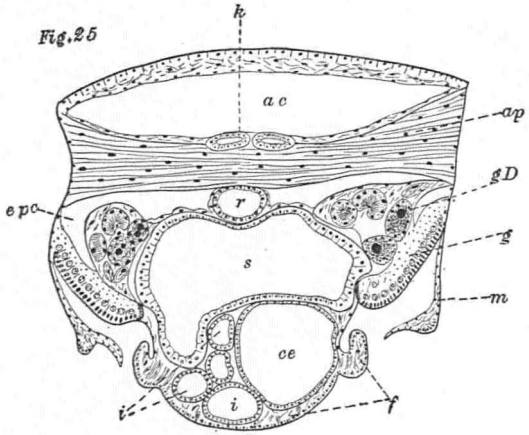
Fig. 25
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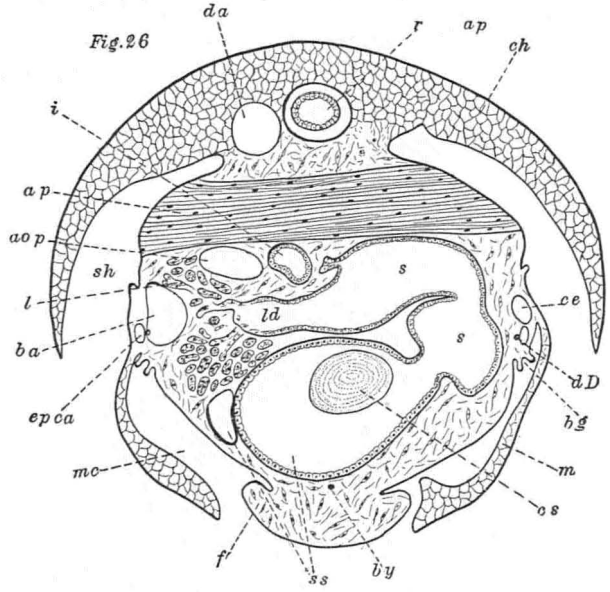
Fig. 26
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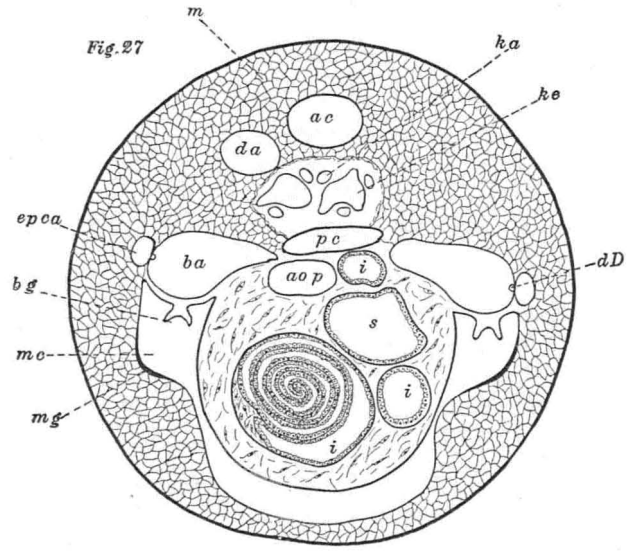
Fig. 27
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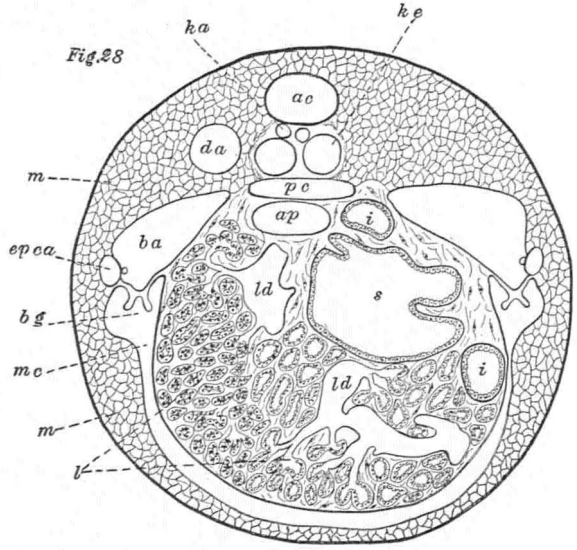
Fig. 28
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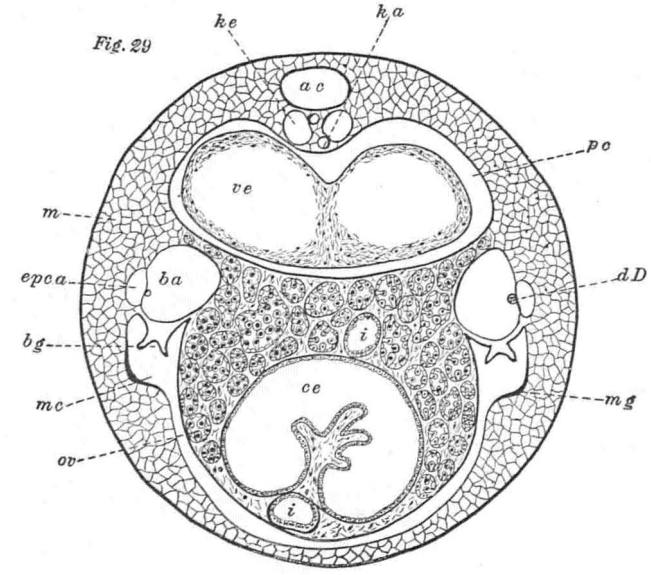
Fig. 29
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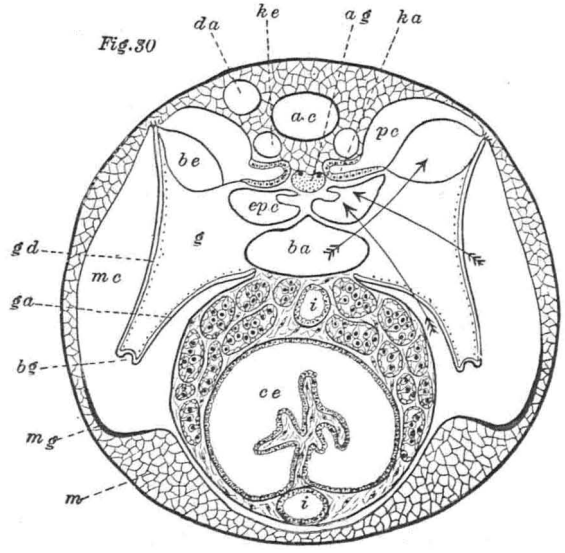
Fig. 30
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Fig. 31

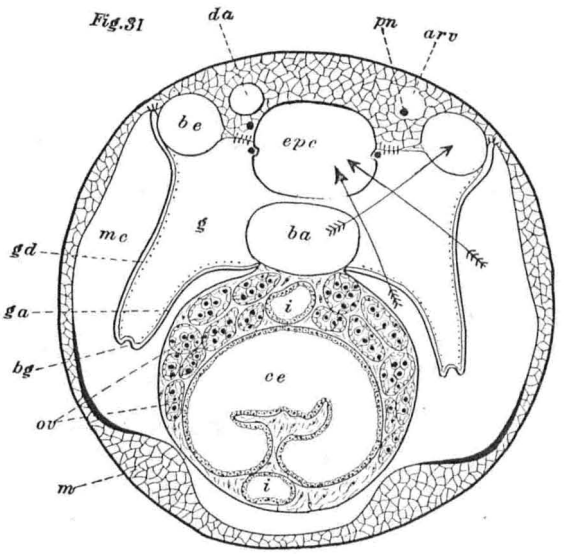


Fig. 32

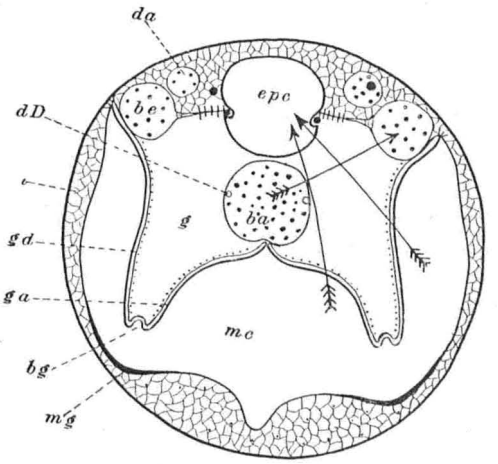
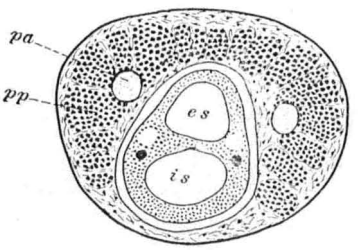


Fig. 33



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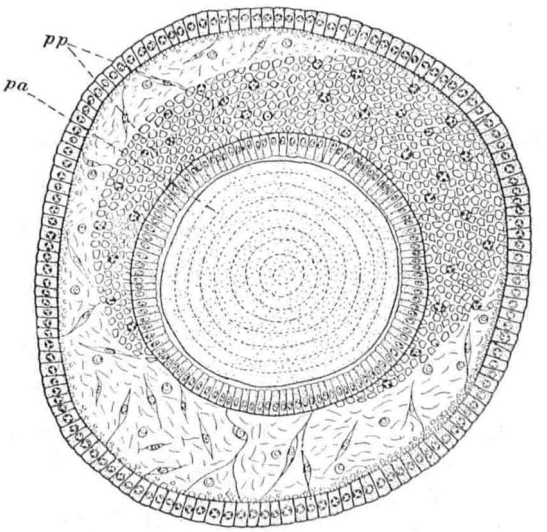


Fig. 35

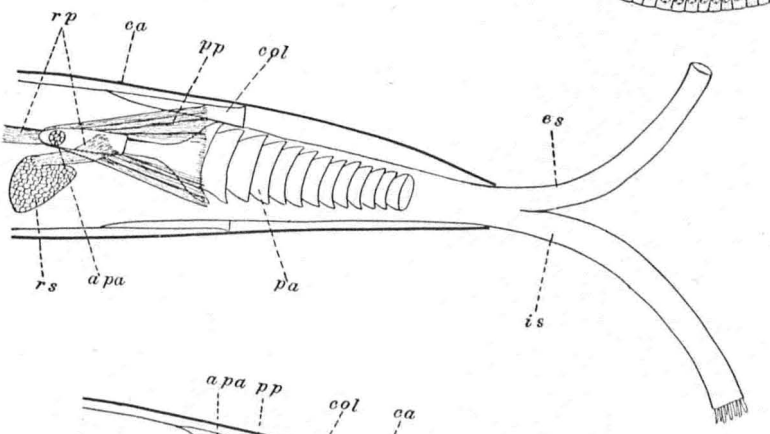


Fig. 36

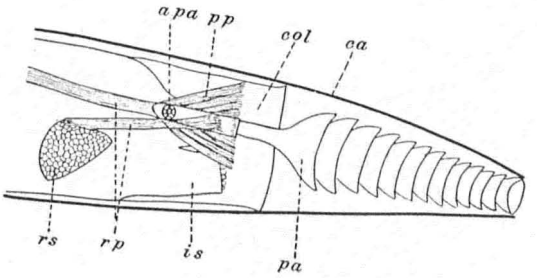


PLATE XVI.

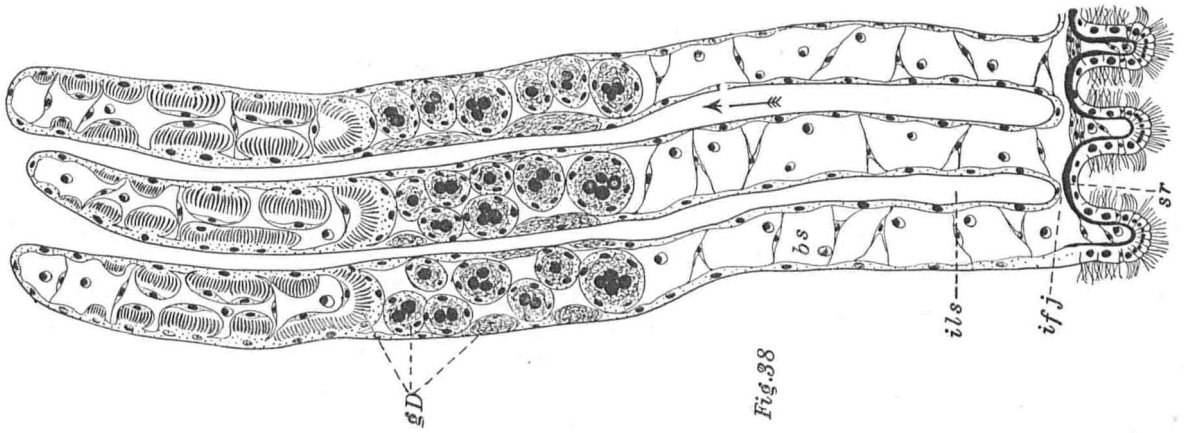


Fig. 38

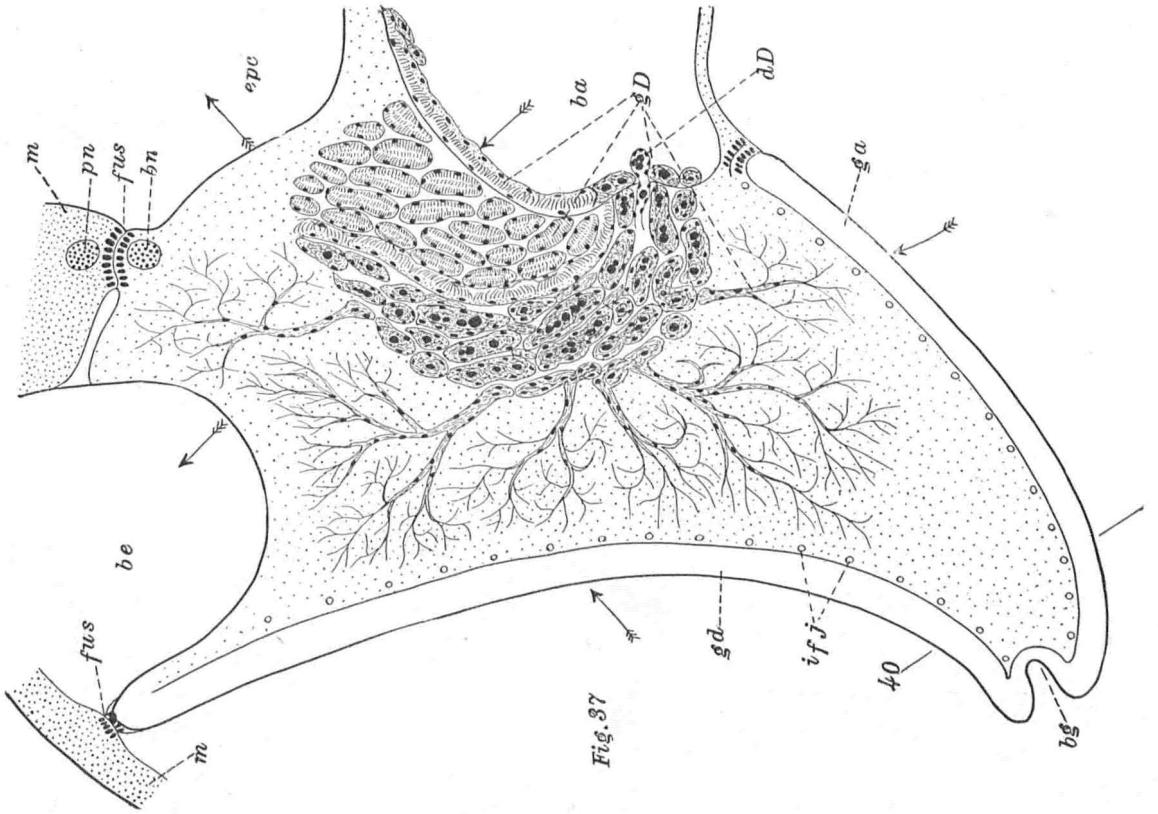


Fig. 37

Bul. U. S. B. F. 1907.

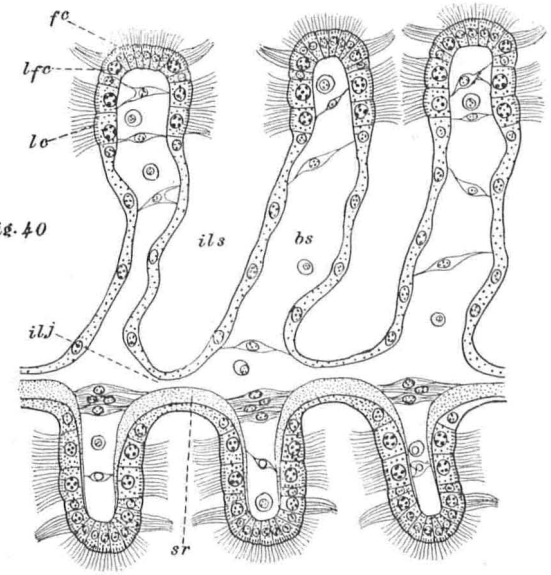


Fig. 40

Fig. 39

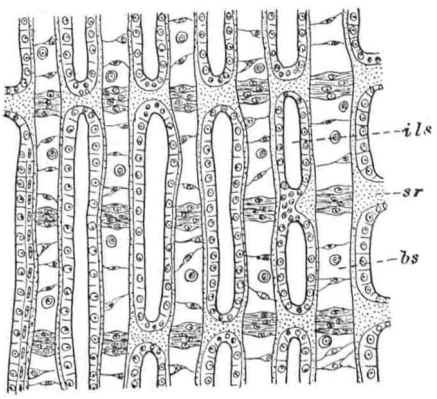


Fig. 41

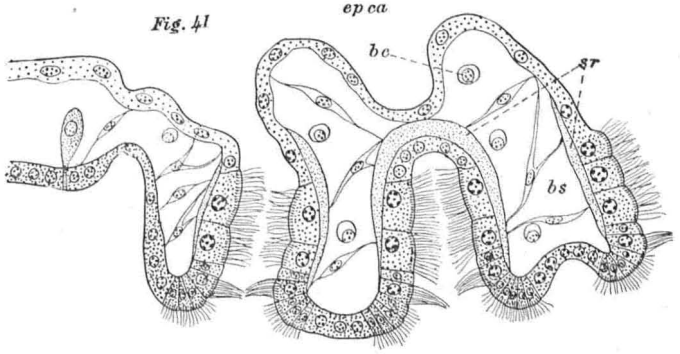


Fig. 42

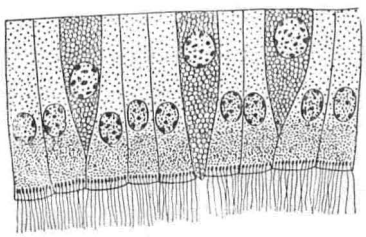


Fig. 43

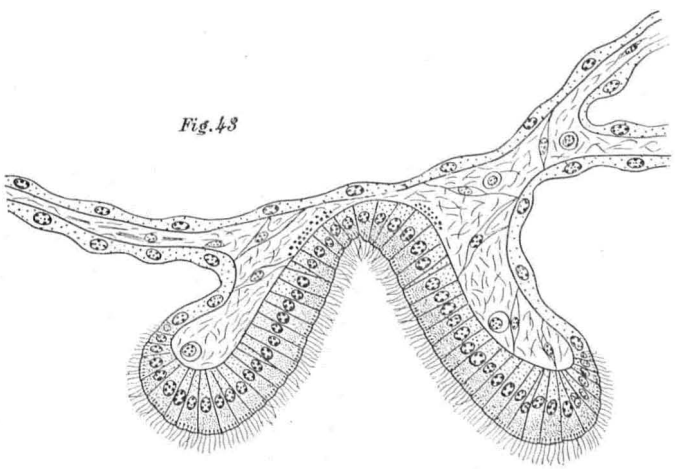
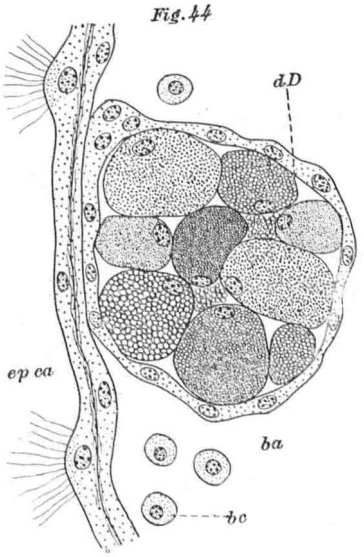


Fig. 44



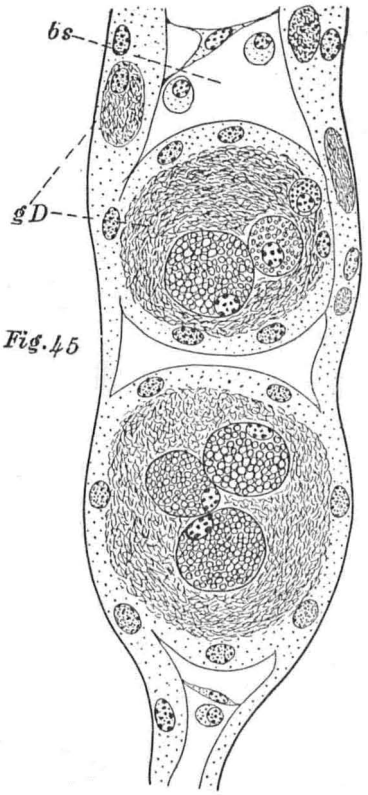


Fig. 45

Fig. 46

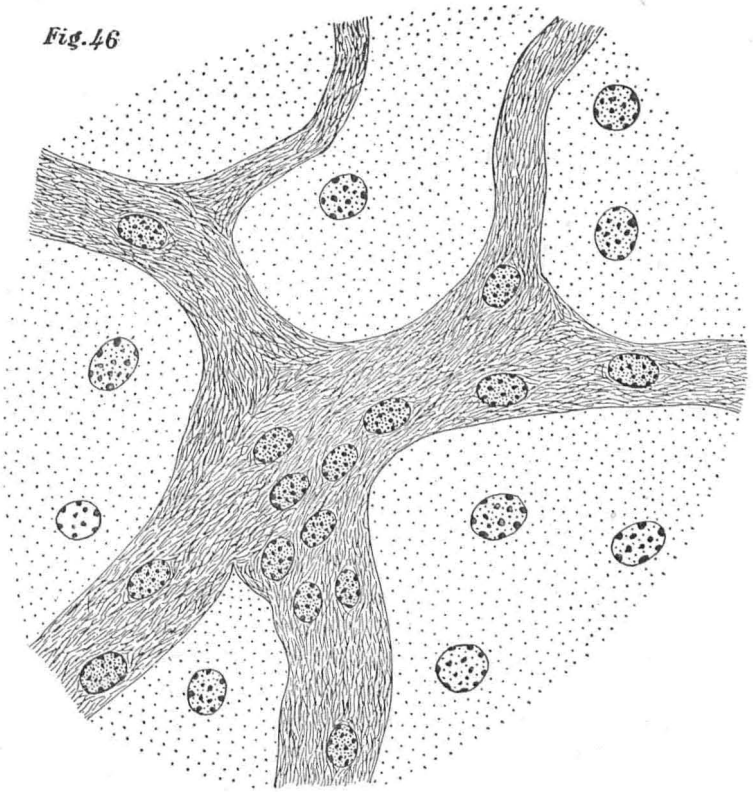
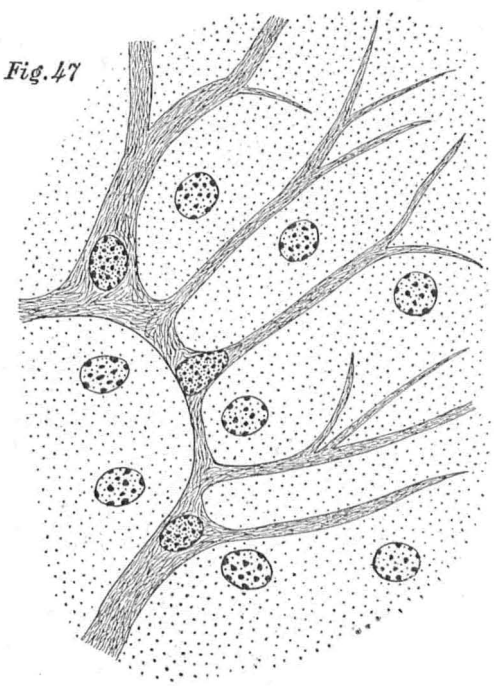


Fig. 47



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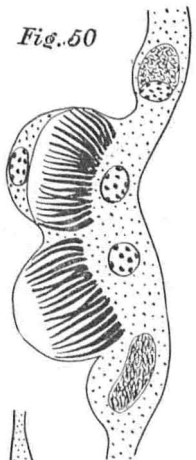


Fig. 51

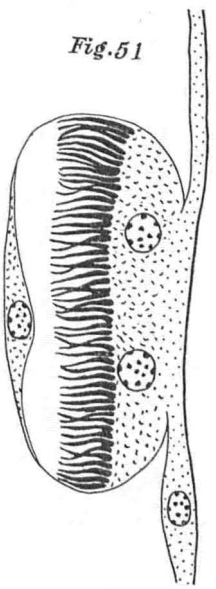


Fig. 49

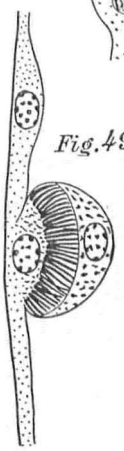


Fig. 48

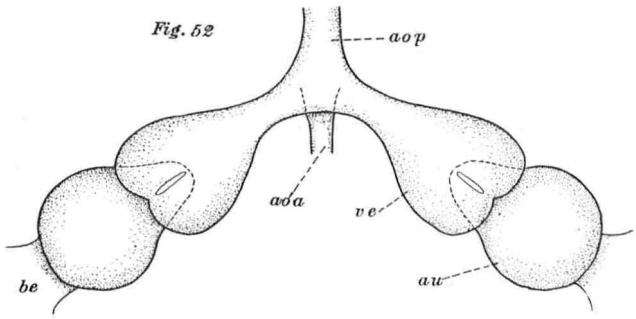


Fig. 52

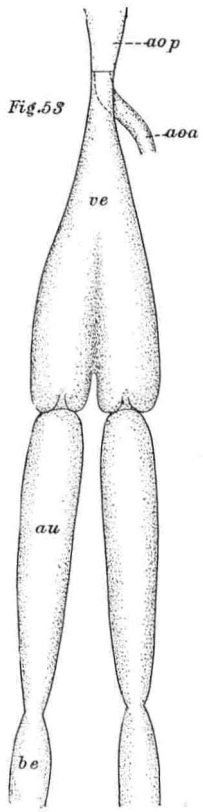


Fig. 53

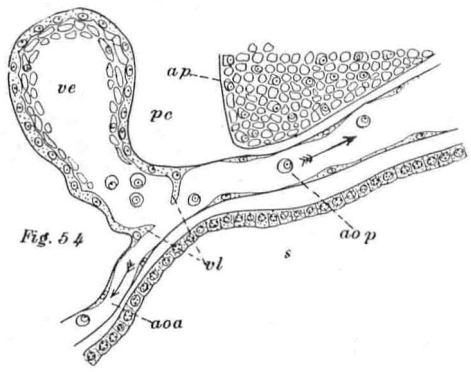


Fig. 54

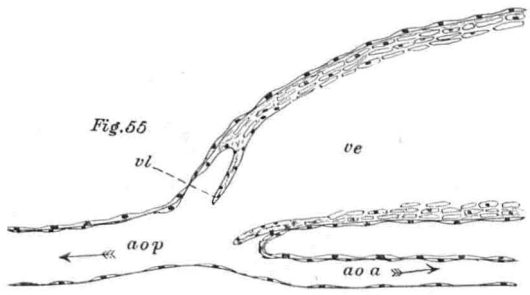


Fig. 55

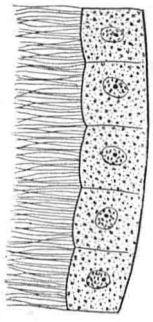


Fig. 56

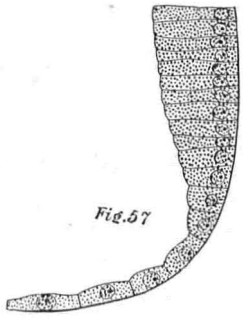


Fig. 57

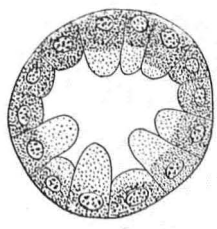


Fig. 58 A

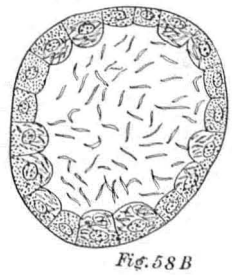


Fig. 58 B

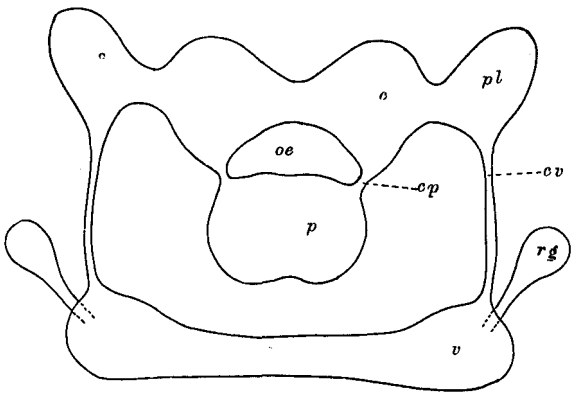


Fig. 59

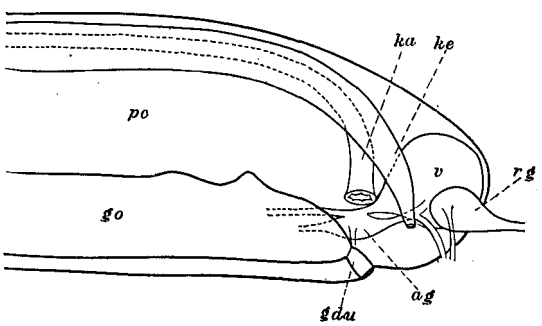


Fig. 61

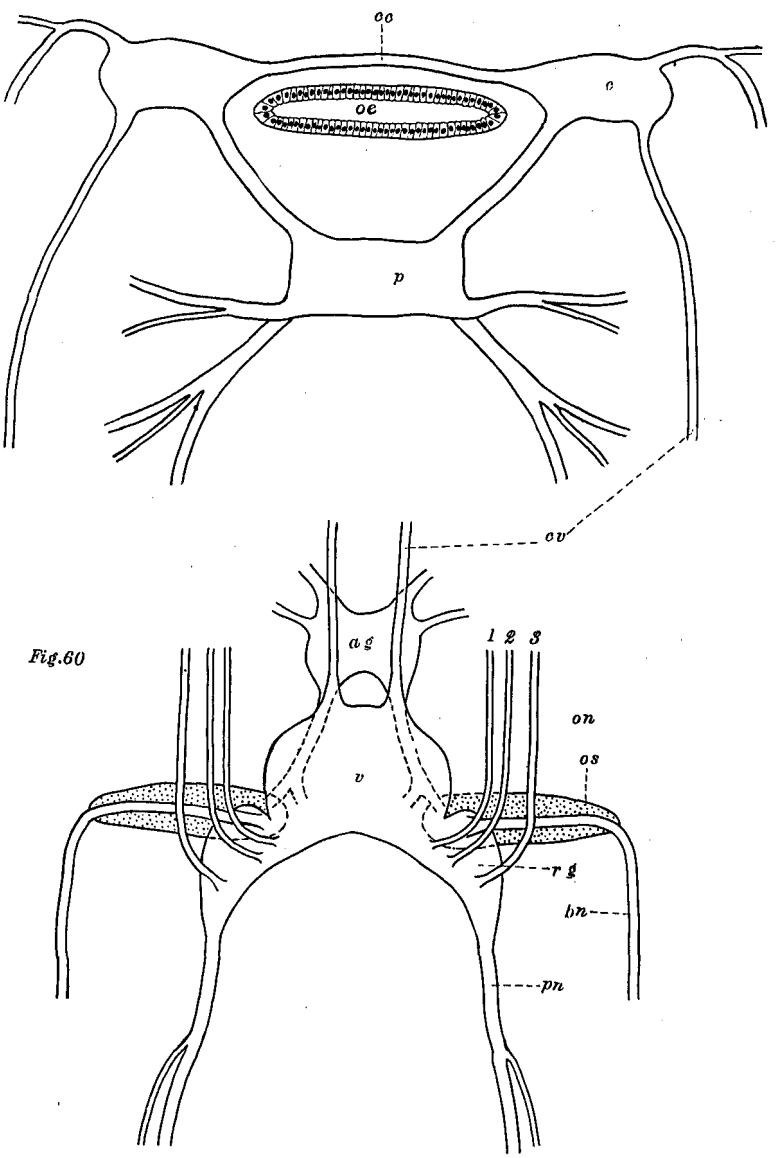


Fig.60

Fig.62

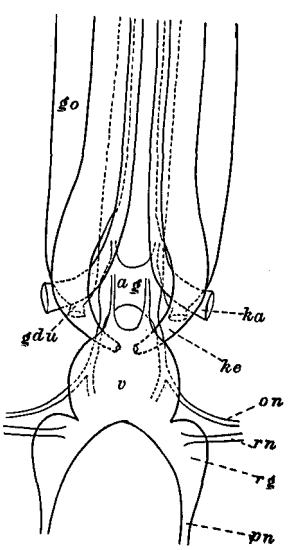
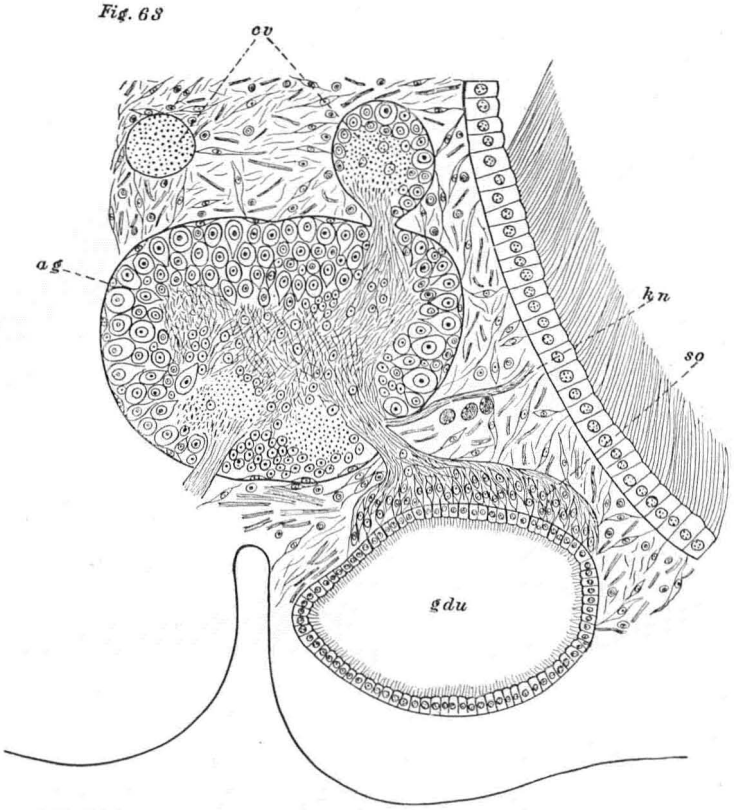


Fig. 63



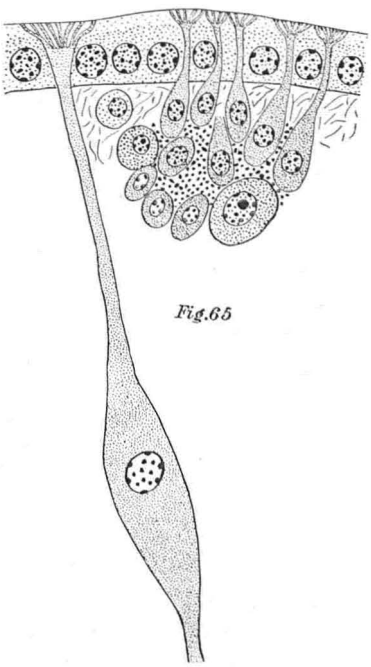


Fig. 65

Fig. 66

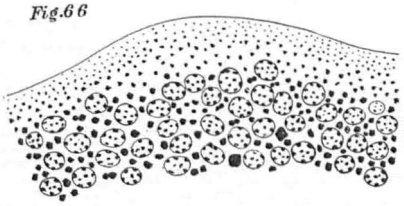
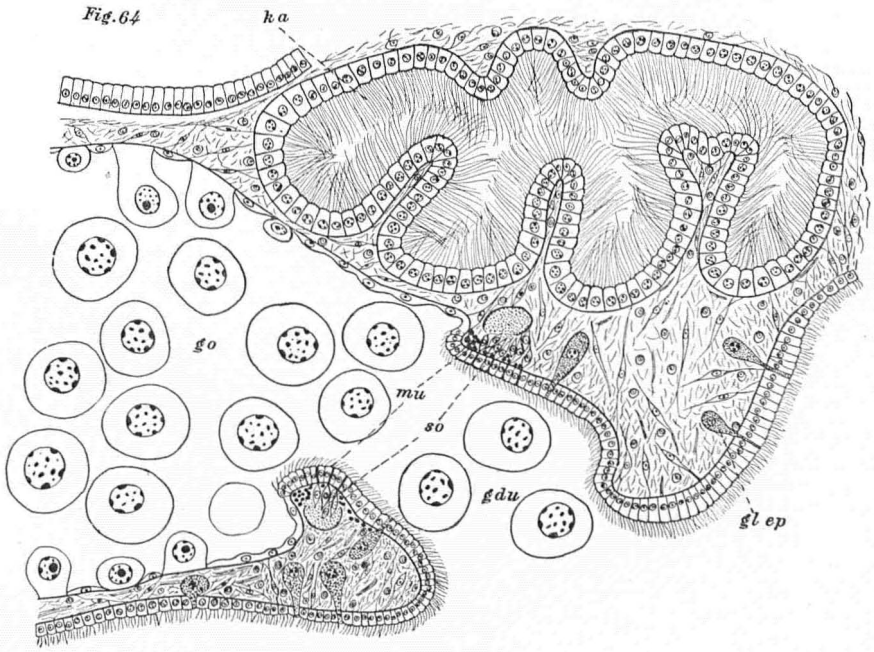



Fig. 64