ON THE

ANATOMY AND HISTOLOGY

OF

Cymbuliopsis Calceola

BY

J. I. PECK.

Reprinted from "Studies from the Biological Laboratory, Johns Hopkins University," Vol. IV., No. 6.

1890

BALTIMORE:
PRESS OF ISAAC FRIEDENWALD,
32 S. Paca Street.

ON THE ANATOMY AND HISTOLOGY OF CYMBULIOPSIS CALCEOLA.

By J. I. PECK. With Plates XXXVI–XXXIX.

The specimens upon which the following researches were made were collected in the Gulf Stream, off Cape Charles, in October, 1888, by the Fish Commission schooner Grampus, and my thanks are due to the U. S. Fish Commissioner Prof. M. McDonald for affording me the opportunity to make the expedition, and also for putting the vessel and her crew at my service during the cruise.

It is the purpose of the present paper to give the anatomy of the pteropod *Cymbuliopsis calceola*, as obtained from a study of serial sections of the entire animal; also to indicate the histological elements of some of the principal tissues as they appear in their anatomical connection. The molluscs were taken at the surface of a moderately rough sea, at lat. 37° 11′ N., long. 74° 15′ W., in an early morning at the beginning of October, 1888. The specimens were killed in Perenyi's fluid and hardened in alcohol, by which process the tissues generally were well preserved, with some shrinking of the delicate connective tissue network, however, in the process of imbedding. A successful double-staining *in toto* was realized with dilute Kleinenberg's haematoxylin, followed by borax carmine.

The systematic position of the pteropod has been given by the new classification of the family Cymbuliidae as proposed by Pelseneer,[1] according to whom the new genus *Cymbuliopsis* is established, to include two species, which are distinct from Cymbulia on the one hand in having no "ventral lobe of the foot," nor "lash-like appendage" below the fin, also in having the flattened proboscis free from the upper surface of the base of the fin, and differing especially in the shape of the "slipper" or

[1] *Report on the Pteropoda collected by H. M. S. Challenger during the years* 1873–1876, Part LXV, p. 96.

"shell," which in Cymbulia is pointed at the aboral end and truncated at the anterior end, with long pointed tubercles along the margin. The genus also differs on the other hand from Gleba (Tiedmannia), inasmuch as the latter has a "shell" with a much more widely open cavity. The true shell, with operculum, of these forms, however, the homologue of the ordinary molluscan structure, only exists during larval stages,[1] having nothing in common with this secondary thickening of the mantle of the adult Cymbuliidae. I have therefore, referring to its present protective nature as a thick leathery armor into which the body of the animal slips as a helmet encloses the head, called this later structure in Cymbuliopsis—formed within the mantle—the *casque*, distinguishing it from the true shell of the mollusc, which was doubtless present in larval life.

The general form of the pteropod from a dorsal view is shown in Pl. XXXVI, Fig. 1, and that of the casque in Fig. 2, both drawn from a specimen in alcohol, in which the casque has slipped out of the mantle in which it was secreted, leaving the frayed portions of the exterior layer of the same still hanging from the body of the animal. The wide flattened proboscis, *p*, —the head region—is in contact with, yet free from, the upper surface of the fin. It is in fact in this case asymmetrical in form; a result perhaps of its shrinking in alcohol. Its edges are rolled outward to form a ciliated groove, which is, no doubt, sensory in function. Directly at the front part of the proboscis is the mouth, a large distensible opening regulated by loose lip-like folds. The position of the rudimentary tentacles—one upon either side of a median line over the oesophagus—is shown at *t*, and they are ordinarily discernible in surface views, although they are not shown in the figure. They are sometimes wholly absent, for in a very complete series of sections of one specimen they do not appear, while in another series they are well defined through at least ten sections, having a retractor muscle underneath and a nerve supply. But at best the tentacles are mere knob-like structures, with rudimentary sensory structure at their base, however, and they may be retracted to the general surface level of the proboscis. The oesophagus leads backward and

[1] See *Klassen und Ordnungen des Thierreichs*, Bronn und Keferstein—Malacozoa, pp. 630–632.

downward to the visceral mass or nucleus, seen through below and displaced to the left. All the tissues of the animal are exceedingly translucent, so that the course of the oesophagus may be followed from surface view. In perfect specimens the visceral nucleus is still enclosed in the pallial cavity by the internal layer of the mantle, represented in the figure by a circle drawn a little way exterior to the visceral nucleus, but this latter is generally more or less torn in the loss of the casque at the capture of the animal. This dark-brown rounded "nucleus" contains the digestive and reproductive organs, and on its dorsal surface the heart and nephridium are laid. The primitive molluscan foot cannot be recognized in the adult animal, while its successor, the fin, has attained very large relative proportions, and is moved by muscles which are laid in regular intercrossing bands a little beneath the epithelial surface of either side, both dorsal and ventral alike; the thickness of the fin being made by the branching network of connective tissue cells so characteristic of molluscan histology. The structure and disposition of these muscle bands has been recently described for other pteropods by Paneth,[1] and in comparison with the heteropods by Kalide,[2] but without especial reference to Cymbuliopsis. In the latter genus there are three definite layers of bands controlling the fin, Fig. 1, 1, 2 and 3. Of these the most exterior bands are (1) the narrowest, and are distributed nearly parallel to each other over the whole surface of the fin in an antero-posterior direction. These lie directly upon and across the next layer beneath them (2), which is made up of thicker and much broader bands running across the fin from one side to the other in arcs of circles. And finally the innermost bundles (3) are distributed radially from beneath the proboscis in such a way that the two lateral portions of the fin are supplied by them, a few bands a little to the right and left of the median line in front of the proboscis being omitted. All the muscle bands as they near the edge of the fin become small and branch out to anastomose with each other. The edge

[1] *Beiträge zur Histologie der Pteropoden und Heteropoden*, Archiv für mik. Anat., Bd. XXIV, pp. 235, 262.

[2] *Beitrag zur Kentniss der Muskulatur der Heteropoden und Pteropoden*, Zeit. für Wiss. Zoöl., Bd. XLVI.

of the fin also contains branched connective tissue cells and processes passing from a central cell nucleus to both surfaces. In the general interior of the fin, of course, is the network of connective tissue cell processes, and the branching nerve trunks and blood lacunae. The mollusc also possesses six longitudinally laid muscle bands on the dorsal surface of the proboscis. The relations of the parts in place from a ventral view are shown in Fig. 3. The visceral nucleus, from this view quite surrounded by the pallial cavity *k* (bounded by the circumscribing line in the diagram), shows at its aboral end, at *z*, a peculiar darkly pigmented ring, which is superficially placed and presents differences in size in different specimens; when the circumference of the ring is large the wall is low, and when contracted it is more prominent and stands out more upon the visceral mass. This limiting wall is made up of the characteristic branched cells, with single and branched muscle fibres (Fig. 27, *m*) cut at different angles, and it carries on the inside a layer of columnar cells which are much elongated in the bend. Pelseneer[1] has also mentioned this structure, and as being like a sucker in form. In Fig. 27, Pl. XXXIX, is represented a vertical section through one side of the ring in a specimen where it is much contracted. The pigment is distributed in the protoplasm of the columnar cells, whose nuclei are also a dark brown.

The pallial cavity of Cymbuliopsis is on the ventral side, and is made by the large fold of the mantle which extends from the dorsal part of the animal around beneath the fin, thickening between its two epithelial layers into the hyaline casque. (This latter appears in sections to be deposited in irregular layers, as it stains with difficulty except in streaks, and shows granules which are doubtless deposits of inorganic salts; it does not contain cells.) Part of the inner layer of the mantle is specialized into the "pallial gland," or "shield" of thecosomatous pteropods. The position of this—seen through from the exterior—is shown in Fig. 3, *p. g.* It is almost symmetrical in this genus, being twisted somewhat to the right, but the asymmetry is not marked, and it is crossed by two transverse bands—an anterior small one and a broader posterior one—somewhat faintly shown in the figure, also one passing along the edges of the structure a part

[1] *Challenger Reports*, Part LXVI, p. 27.

of the way. Sections through this "shield" show that the cells which compose the different areas are quite different in their appearance. Thus in Pl. XXXIX, Fig. 26 shows in section the long club-shaped cells *t*, which cover the general surface of the pallial gland on the side toward the cavity, and stain very deeply, while the transverse bands are made up of the cells *v*, which stain more lightly, and are regularly arranged so as to give the surface an undulatory contour. The outer portion of these closely packed cells *v* is clear, and between the larger cells, near the surface, are found certain smaller nuclei *n*. The transition between the two areas is very abrupt, and the function of the two, whatever it may be, is doubtless as distinct. Behind the pallial gland, which thus forms a widely open pocket, the general pallial cavity is much narrowed down, opening into that part which surrounds the visceral mass by a transverse crescentic slit (below *k*, Fig. 3;—at *y*, Fig. 4). This posterior part of the cavity contains the visceral nucleus suspended in it, but it is asymmetrical in extent on account of the presence of the large nephridium, which extends farther down upon the left side, so that the pallial cavity extends farther dorsalwards on the right side than on the left, while behind it extends quite up on to the dorsal side as far as the large nephridium. Thus in Fig. 4 are shown the relations of the parts in diagram from the right side; *m* the mouth at the proboscis, *t* the rudimentary tentacles, *n* the central nerve ganglia, *k* the casque contained in the mantle, *j* the nephridium with the heart in front of it, *y* the opening from the larger exterior part of the pallial cavity with its pallial gland *p. g.* into the interior part of the same, where open the anus and the genital ducts at *w*. The external features of the mollusc, the extent of the mantle, pallial cavity and shield, the position of the visceral organs, the fin and its musculature have thus been indicated in Pl. XXXVI, Figs. 1–4; the structure of the shield and dark ring or sucker in Pl. XXXIX, Figs. 26 and 27.

In order to show the arrangement of the organs of the visceral mass I have figured on Pl. XXXVII (Figs. 8, 9 and 10) three representative cross-sections at different points through the body of the animal. The outlines of the visceral organs were made with the camera lucida, while the outer epithelium (*k*) of the

mantle and the inner layer (*w*) of the same, and the intervening thickening—the casque—are represented diagramatically in place. Fig. 8 is the most posterior section, the pallial cavity quite surrounds the visceral mass, the nephridium *n* is just cut on the dorsal side as a double cavity at this point. The intestine of Cymbuliopsis, after leaving the stomach, makes a single loop around the visceral nucleus (Fig. 4, *i*) under the genital gland, and opens a little to the *right* of the median line; and here, in Fig. 8, is cut so that the coil is just disappearing at *i* on the left, while the part of the intestine leading directly to the anal opening is cut at *i* on the right. The beginning of the enlargement of the stomach *s* is on the dorsal side, and opens widely into the liver *l*, the opening being to the right of a median line. The liver *l* is quite internal then, and the gland is made up of loose lobules. The genital gland *h* is most exterior, and envelops the liver and intestine. In Fig. 9, farther forward, about the middle of the visceral nucleus, the nephridium is cut in two parts, right and left, *r. n* and *l. n*, while between them appears an irregular part of the pericardial cavity *p. c*, in which the ventricle would appear more anteriorly. This section passes about through the centre of the stomach *s*, with the five thickened plates upon its walls. A very large blood sinus *ao* passes below the stomach into the tissues of the liver *l*, which, with the genital gland *h*, occupies the same relative position as in the other figure. At *a* is seen the terminal portion of the anal opening into the pallial cavity, a little to the right of the median line; although in surface views it is seen to be directed toward the left, yet it does not reach the median vertical line. The pallial cavity itself in this, as in the following sections, is seen to extend farther dorsalwards on the right side than on the left. Fig. 10 is taken far enough forward to pass through the ventricle *v*, just before its union with the posterior blood-vessel *ao*; the nephridium, *r. n* and *l. n*, has almost disappeared on either side, while the pericardial cavity *pc* is becoming more apparent, and would steadily increase in the more anterior sections of the series until it is limited by the general connective-tissue filled space of the body cavity. The stomach *s* is cut through its anterior end, where only two of the thickened plates are developed; the liver has almost disappeared, and the genital gland *h*

is divided into two lateral portions by the ventral position of the accessory glands and the genital ducts, to be described hereafter. In following serial sections farther forward, the liver and the genitalia run out, the stomach runs into the oesophagus, the heart gives off the large aorta, the mantle shows the specialized pallial gland, the nerve ganglia appear around the oesophagus, and the general tissues of the fin and proboscis appear.

The Digestive Organs.

The general position of these has already been described; beginning with a large, loose mouth at the proboscis, from which the long oesophagus leads backward into the stomach, the thickened walls of which bear the triturating plates. At the extreme posterior end of the stomach, at the beginning of the intestine occurs the wide asymmetrical opening into the "liver" (Fig. 8), while the intestine itself takes one bend downward and around over on to the right side and beneath, where it opens nearly upon the median line, although plainly to the right of it, which is contrary to the position described for the other Cymbuliidae. Its latter portion is directed toward the left, as it opens into the pallial cavity. Cymbuliopsis has no buccal armature nor salivary glands; the oesophagus is lined with ciliated epithelium which is raised into secreting folds, Pl. XXXVII, Fig. 11, the whole being contained by longitudinal and circular muscles *m*. In the stomach these folds become brown pigmented villi (seen in diagram around the inside of the cavity *s*, in Figs. 8 and 10) without cilia, the cells of which are thickly distended with drops of secretion, their outer boundaries being blended together, Fig. 12, and the musculature *m* becoming thicker. Of the five thickenings of the stomach walls usual in the thecosomatous pteropods, the fifth, or smallest plate, is in this genus situated on the dorsal side between the pair of larger dorsal plates. All are included in the section from which Fig. 9, Pl. XXXVII, is taken. Besides these five constant ones there are several other irregular spur-like plates of the same structure, placed sometimes in the spaces between the larger plates, or in either end of the stomach. The structure of these thickenings in the walls of the stomach is shown in Fig. 13, Plate XXXVIII, the section being figured from near the edge of one of the ventral plates, at

about the place indicated by x in *s* of Fig. 9. Most exterior are the large nucleated fibres of the circular muscle coat, which control the movements of the stomach; within these is the thickening which carries the large tooth-like plate. This thickening is merely an accumulation of the "gallertgewebe"[1] of the mollusc, as is shown by the branched cells, laid in a matrix which is clear; the network of cell processes is more numerous than is indicated in the drawing (those between the cubical epithelium and the muscle coat), the nuclei of which exist often in pairs and sometimes even in threes, as if growth were taking place. Placed upon this connective tissue thickening of the wall is a single very regular layer of cubical epithelium, which secretes toward the lumen of the stomach the projecting pyramidal "tooth." These latter are of the same general structure as the casque secreted by the mantle, being hyaline, staining with difficulty in streaks, and containing a granular deposit. In Fig. 13 the circular muscles, the connective tissue and the secretory epithelium are tinged with blue, the secretion of the "tooth" at that point being represented in yellow. These plates have been regarded as triturating structures in the pteropods, and the "stomach" has been called a "crop," with reason, doubtless, in this case where there is no radula nor jaws at the mouth. But the lack of this structure (radula) does not prevent the animal from possessing predatory habits, for in one of these specimens an adult heteropod, Firoloidea, was found, having been taken as food; but the stomach is usually full of diatoms, foramenifera, etc., of many kinds.

The digestive gland, the "liver" of the mollusc, constitutes a large part of the visceral nucleus. Its wide asymmetrical opening into the intestine has already been described with Fig. 8, while the character of the cells that compose it is illustrated in Pl. XXXIX, Fig. 20. These are the kind described as "körnerzellen" by Frenzel,[2] and in Cymbuliopsis they are characterized by large greenish-brown masses in various stages of perfection. In some cells there are solid, irregularly spherical, greenish masses; in other cells there is only an irregular central mass in a vacuole-

[1] See also Paneth, *l. c.* p. 255.

[2] *Ueber die Mitteldarmdrüse der Mollusken*, Archiv für mik. Anat., Bd. XXV, p. 52.

like portion of the cell, Fig. 20, *j*. They are all, doubtless, steps in the same process, and sometimes the whole cell is tinged with green without its being aggregated. I have also found these masses outside the cells in the lumen of the alveoli. There are also clumps of very large opaque granules in the peripheral portion of very many of the cells. There are, moreover, rods of cells at various points in the periphery of the liver, the cells of which are smaller than, and very different from the glandular portion of the gland, and in the centres of these rods there are small transparent masses of crystals. I could not make out the exact form of the individual crystals, and appearances favor the assumption that they are derived from the salts in solution in the blood and tissues of the animal, and that the rods may be in reality short ducts with very thick walls, but I cannot describe even their general direction. The blood permeates the "liver" very plentifully, as may be inferred from the large blood-vessel which supplies it, Fig. 9, *ao*, and which is distributed into the blood spaces in the walls of the basement membrane between the alveoli.

In the centre of this digestive gland are large irregular spaces (Pl. XXXVII, Figs. 8–10, in the brownish lobulated mass *l*), into which food products from the stomach may pass in the process of digestion. There are also tracts of ciliated liver cells, situated at various points along the central spaces; they line the passage from the intestine out into the liver, and serve doubtless for transporting food particles, etc., whenever they occur. Thus in Fig. 8 at *y* is seen the relative position of one of the ciliated pads, while the cells represented in Fig. 20 at *i* are taken from a part of the gland which projects into the central space; the cells at *i* are specialized into a ciliated tract, unlike the ordinary cells of an adjoining fold of the liver at *j*. The "liver" of Cymbuliopsis, therefore, is something more than a mere secretory appendage, and comes into direct contact with the food circulated within it. The intestine is quite thin-walled, and lined with simple short columnar ciliated cells, thrown into a few villi in the anterior portion.

The Central Nervous System.

The nerve ganglia of Cymbuliopsis conform to the type of the Cymbuliidae in general, as it has been described in detail for

Cymbulia,[1] with some additions to the descriptions previously given. The general position of the ganglia in the body is shown in Fig. 4, *n*. They are very closely fused, as is shown from ventral view in Fig. 5, which was reconstructed from camera drawings of serial sections. The cerebral ganglia *r. c* and *l. c* (right and left cerebral) lie at the sides of the oesophagus, and are connected to each other around it by the large cerebral commissure *cc*. On the extreme dorsal part of this commissure, *i. e.* in the true morphological position of the cerebral ganglia, there are sometimes a few ganglion cells remaining, but without giving rise to nerve trunks. From the cerebral ganglia two pairs of nerves are given off anteriorly into the proboscis, and one short pair to the otocysts below them, although this pair is much hidden from surface views. The more dorsal pair of cerebral nerves c_1 go to the tentacles and supply the ganglionic swelling at their base. Their other pair c_2 go to the proboscis, supplying the ciliated lips.

The pedal ganglia—connected in Cymbuliopsis, as in Halopsyche and the gymnosomatous pteropods, by a second delicate commissure *s*—give off three pairs of nerve trunks p_1–p_3, which proceed to the fin; p_3 being smaller and supplying the proboscis. There is also a very delicate nerve, *m*, given off from the posterior ventral face of the pedal ganglion, and sinking almost directly to the ventral surface of the base of the fin.

The nerves which pass backward into the body are derived from the visceral and buccal ganglia. Of the former there are three ganglia, giving off the four nerves v_1–v_4, of which v_1 on the right side soon branches, sending one branch back into the mantle above, while the larger branch sinks below and supplies the mantle beneath the fin, and on this side carries the osphradium; v_4 is distributed in a similar way upon the left side of the animal, except that no sense organ is developed on the lower branch; v_2 comes soon to lie close to the oesophagus with the nerves from the buccal ganglia, with which it extends into the visceral nucleus, being laid in the right dorsal region just beneath the nephridium and circulatory organs. The large left branch v_3 bends below, and I have traced it far out into the mantle, along

[1] *Recherches sur le system nerveux des Pteropodes*, par Paul Pelseneer, Archives de Biologie, Tome VII, fasicule 1, p. 115.

the edge and beneath the pallial gland. The fused buccal ganglia are situated in front of the pedal, close to the oesophagus. They give off anteriorly a pair of slender nerves b_2 to the oesophagus, and posteriorly a similar pair, b_1, that run close to the wall of the stomach.

On Pl. XXXVIII, Figs. 14–17, are figured four representative cross-sections through the central ganglia in place. Fig. 14 is the most posterior section, and includes the ring of cerebral and visceral ganglia, the former of which are represented as giving off the cerebral commissure *cc*, above the oesophagus, with the dotted lines; which commissure, however, has been cut in the preceding sections of the series. The cerebral *c*, pass freely into the visceral ganglia *r. v*, *m. v*, *l. v*, and they into each other. Among the nerve cells, located peripherally in the ganglia, there is in the median visceral ganglion *m. v*, situated upon the left side at *k*, a very large bipolar cell, whose processes may be traced to either side into the other ganglia. It is a constant feature of all the specimens examined (four) in the sections through the central ganglia, and in one instance had a diameter of 120μ, while the greatest diameter of the whole ganglion was 225μ. This cell, then, may be taken as presenting the qualities of all the cells of its kind in the periphery of the ganglia. In Fig. 18 I have endeavored to indicate the disposition of the chromatin elements in the large irregular nucleus, which has perhaps taken its present form on account of the shrinkage of the body of the cell, and this is the case with many of the larger cells in section. One of the two or three protoplasmic processes *p* of this large cell is passed through in this section. Fig. 15 is taken ten sections forward. Here the otocysts *o* are cut in section, and the auditory nerve *n* on the right side, the fibres leading upward to a bunch of small cells of the cerebral ganglion; the plane of section being a little oblique, the left auditory nerve was just previously cut in the series. The otocysts in these specimens of Cymbuliopsis contained no traces of otoliths, nor was the internal epithelium at all specialized into ciliated sensory cells, but this may have been caused by the action of acid in the reagents. Although the otocysts lie upon the pedal ganglia, yet they are bound to the visceral ganglion *m. v* by two strands of connective tissue from their investment. In this section also is shown the

origin of the small nerve m, whose fibres are given off from the large cells of the internal posterior face of the pedal ganglion; also the origin of the cerebral nerve c_1 from the dorsal side of the cerebral ganglion $l.\ c$—not apparent in this plane through $r.\ c.$ The buccal ganglia b in the median line just below the oesophagus still show a partial segmentation.

Fig. 16 is four sections in front of Fig. 15, showing, upon the left side, part of the commissure cb which exists between the cerebral ganglia c and the buccal ganglia, and in the same section the point at which a similar connection is to be established with the buccal ganglia from the right side opposite; and also the origin of the pair of buccal nerves b_2 which pass forward from the buccal ganglia, close to the oesophagus; also a part of the elongated origin of the pair c_1. The whole of the central nervous system, including the large nerve trunks, is sheathed in a thin connective tissue envelope, the small cell-nuclei of which are very numerous. Some of this investment cut tangently from the surface of the pedal ganglia is shown in Fig. 16, g; it is likewise seen in all the sections as a limiting membrane of the ganglia.

The pedal ganglia alone exist in the section from which Fig. 17 is taken, the fibres pass from one freely into the other and out into the large trunks of the pedal nerves, the origin of p_1 and p_2 being shown upon the left. The nerves from the cerebral and buccal ganglia are seen above in section, as they pass forward into the proboscis.

The osphradium—Spengel's olfactory organ—of Cymbuliopsis is quite large and long, extending on the right side of the mantle as it narrows to form the opening into the inner part of the pallial cavity. It is composed of ciliated epithelium with ganglion cells beneath, from which fibres of the nerve pass. Fig. 19 shows the arrangement of the epithelium in two patches, a condition which obtains for some distance. There is also a ciliated pad of cells, Fig. 19, a, within the pallial cavity upon the visceral mass, of which mention will be made hereafter; but other than these and the tentacles, the edge of the fin and proboscis also serve as sensory organs, partly as organs of special sense, no doubt.

The Reproductive Organs.

The position of the generative gland has already been shown in Figs. 8–10, *h*. It is distributed over the visceral nucleus as a uniform external layer; is divided up into large follicles by a very thin limiting membrane, brown pigmented in general, of which the internal layer—toward the liver—is more or less free from the general tissues of the gland, so as to form loose spaces in which the genital products may be carried toward the efferent duct and hence to the exterior.

In the specimens of this pteropod examined, the hermaphroditic gland was in the state of female activity; that is to say, the male elements had been matured and shed, while the following development of ova was in process. And so there were no primitive germ cells developing into spermatozoa on the internal side of the gland, while the outer portion of it is filled with ova in all stages of maturity. The changes which take place in the growth of the ovum from the primitive germ cell are shown in the reproductive follicles figured in Pl. XXXIX, Figs. 22 and 23. The germinal cells destined to become ova enlarge—some more rapidly than others, as is shown in the follicle *a*, Fig. 22, and these latter are to complete their development while the other cells contribute only indirectly to the production of ripe ova by furnishing food material for the more vigorous neighboring cells. These latter cells, therefore, increase in size at the expense of the others, and so gradually take on the characters of the ripe ovum in their growth. Thus in the follicle *b* are seen two young ova surrounded by a layer of the other germinal or follicular cells; the nucleus or germinal vesicle is very large and clear, except for chromatin elements scattered about, and in the ovum upon the left of the follicle *b* the nucleolus, or germinal spot, is cut in section, the body of the ovum being granular protoplasmic material. In the follicle *c* a still older stage is shown, the ovum being farther advanced, and evidently using the large irregular cells which it adjoins, while the rest of the follicle is occupied by another ovum which only partially appears in this particular section.

In the further growth of the ovum, food-material is deposited in the protoplasm in the form of large yolk spheres, which have

characteristic forms and markings for different thecosomatous pteropods.[1] The markings upon the yolk spheres of Cymbulioopsis give them the appearance of minute dense cells with a nucleus, but thickened on one border. In follicle *d*, Fig. 23, the protoplasm of the largest ovum is being furnished upon its upper border with the first of these yolk masses. From the beginning these latter are perfectly distinguishable by the manner in which they take the staining used, *i. e.* they remain untouched by the haematoxylin and only take the bright carmine color. Finally, in follicle *e* the ovum has acquired all the characters of ripeness, and in this particular section appears the large nucleus, with the nucleolus *k*, and a great abundance of nutritive material stored up as yolk-spheres *y*. After completing its growth to this stage it is loosened from the follicle and is ready for fertilization.

The genital ducts and the accessory glands are diagramatically represented in Pl. XXXVI, Fig. 6. The common genital duct *d* is quite short, leading from behind down and around to open upward into the uterine portion of the duct *u*, which itself leads backward on one side, into which the seminal receptacle *r. s.* opens, and downward to the exterior on the other side at *h*. The two accessory glands—displaced a little downwards and to the left in the diagram—open very widely into the terminal portion of the duct. The albumeniparous gland is the smaller and exterior, the muciparous is the larger and interior, both being thrown into loose folds. The relative position of these organs in the visceral nucleus is shown in Fig. 4 at *w*, also in the section Fig. 10, the duct and opening being on the right of a median line, the accessory glands occupying nearly a median position in the body. In the specimen here figured the seminal receptacle *r. s.* is filled with spermatozoa, and a portion of the duct which connects it with the duct to the exterior (*e*) is cut at *f* (although it of course soon runs out in the following sections). The walls of this uterine portion are much folded, brown pigmented and ciliated, with a few spermatozoa visible in its upper portion. The genital duct d—d_1, leading from the hermaphrodite gland to the uterus, is cut twice in this section; farther on in the series they unite with each other. Although in this mollusc

[1] See Fol, *Sur le developpement des Pteropodes*, Archives de zoologie exp. et gen., Tome IV, p. 106.

there is but one genital duct common to both sexual elements, yet this is specialized into two portions, as seen in Fig. 24, one portion of a section across the duct being lined with larger ciliated cells than the other portion; a condition which may be analogous to that of those gasteropods where one part of the "oviduct" is specialized into the seminal groove. The duct becomes larger at its lower portion, as seen in Fig. 25, where a few yolk spheres *f*, with the round marking, are included from a passing egg.

The folds of the muciparous gland *m* are much longer than those of the albumeniparous gland *a*. The structure of these is further represented in Pl. XXXIX, Fig. 21, which shows that the cells of the one gland—the muciparous—are larger and clearer than those of the other, both kinds being very regularly arranged upon a thin basement membrane with its occasional nuclei. In addition to the regular basal row of nuclei of the gland cells there is another incomplete row of smaller nuclei *n*, near the lumen of the gland fold, which appear to belong to small cells wedged in between the upper portions of the large gland cells; in some parts of the glands these nuclei are much more numerous than in the figure. It was also shown that analogous small nuclei existed in the pallial gland cells. I do not know their meaning. Cilia are also present in some parts at least of the glands.

Not only is the generative gland, in all these specimens, in a state of female activity, but I have been quite unable to find any penis to indicate that they ever function as males, or at least so as to effect a copulation among themselves. In the case here described and figured the seminal receptacle is filled with spermatozoa (in other instances it was empty) and ova are passing through the genital duct, but it is not probable that both the sexual elements were derived from the same individual gland, and a penis therefore probably exists in some other individuals functioning as males. This organ is described for the other Cymbuliidae as a protrusible tube lying upon the dorsal side of the animal, with its exterior opening a greater or less distance behind the tentacles; and connected with the external opening of the genital glands by a ciliated groove for the conveyance of the male element. There is indeed in Cymbuliopsis a narrow band of ciliated cells (Fig. 19, *a*) leading away from the external

opening of the genital organs, but it becomes less and less conspicuous in its anterior course until it is lost near the opening into the inner pallial cavity; but it does not lead into any groove or cavity, nor is there any indication of its relation to any penis, nor does the latter appear at all in the serial sections. This element of the structure of a functionally male pteropod is therefore only rudimentary, and it is possible that the germ cells never produce functional spermatozoa, but always ova, thus effecting a true separation of the sexes in many cases, at least, in this genus. Or perhaps the lack of a penis is only another one of the peculiar modifications of the mollusc, such as the want of a buccal armature, or the occasional lack of tentacles.

The Nephridium and Heart.

The general position of these organs in the body has already been indicated in Fig. 4 at *j*; their relations to each other are shown in diagram in Fig. 7, seen from the dorsal surface, the anterior direction being toward the bottom of the page. The nephridium of Cymbuliopsis is a single large loose sac lying above the visceral nucleus, across the pallial cavity, and bent in a horseshoe shape around the heart and pericardium which lie in front of it. Its position is quite superficial, and parts of its cavity are separated from the visceral mass. It is also asymmetrically disposed (the right lobe *r. n* being smaller than the left *l. n*); extending farther down upon the left side of the body than upon the right, Fig. 9 *r. n*, *l. n*, and extending out above the pallial cavity upon the right side, while the pallial cavity lies above it upon the left. Posteriorly its cavity extends out above and also beneath the pallial cavity, so it is cut twice in the section Fig. 8, *n*. It communicates upon the right side with the pallial cavity by a large ciliated opening *o* surrounded by a muscle, but this is the only opening that appears in the sections; and a second communication—with the pericardium as is the rule in the Mollusca—has doubtless been lost. It is also stated by Bronn and Keferstein that this opening into the pericardium has never been observed in Tiedmannia, so that in these points also these two genera seem to be similar.

[1] Klassen und Ordnungen des Thierreichs—Malacozoa, p. 609.

In front of and above the cavity of the nephridium, lying between its two large horns, is the pericardium, within which is the large ventricle. The pericardium begins as a recess lying above the nephridium, Fig. 9, *pc*, and broadens out anteriorly. It is shut off from the other parts of the body cavity by a layer of the connective tissue network. I have indicated in diagram, Fig. 7, the position of the two large blood-vessels connecting with the ventricle, and have called the anterior one, with a spacious sinus just in front of the ventricle, the auricle *t*; the other thicker-walled vessel *ao* passing backward over the visceral nucleus is evidently an aorta leading from the ventricle to the liver (in section Fig. 9, *ao*) and the other organs (Fig. 8, *ao*). The vessel *t* passes far forward into the fin, becoming rather smaller in its course and opening out into a very loose network of large lacunae just anterior to the central nerve ganglia; in none of all the tissues indeed do the characters of the molluscan branched connective tissue cells appear so clearly in sections as in this region just anterior to the pedal ganglia. There are large loose spaces in the body cavity in front of and beneath the ventricle, and I had expected to find in one of these the auricle of the circulatory system as it has been described in pteropod anatomy—*i. e.* as being an incompletely closed sinus into which the blood from the tissues is collected and from which it passes into the ventricle; but the sections of the material at hand were insufficient to warrant such conclusions. Furthermore, these spaces before mentioned contain certain lateral and dorsal areas of closely aggregated cells that do not differ much, except in greater size and abundance, from the other cells about the visceral organs, but which present a peculiar appearance in section through their mass. Their significance I cannot determine by a study of this form alone.

The lack of material is my only plea for the insufficient way in which the circulatory system of Cymbuliopsis has been followed up, and for the incomplete nature of the sexual differences. But in other respects it is hoped that the general pteropod structures have been indicated; and this genus seems to be generally typical of the whole family.

Explanation of Plates.

Fig. 1. Surface view of Cymbuliopsis from dorsal side; *p* proboscis, *t* tentacles, 1—3 muscle bands.

Fig. 2. Casque, from dorsal position when in place.

Fig. 3. Diagram of the parts in place, from ventral view, twice the natural size; *p.g* pallial gland with the bands across it, *k* the pallial cavity entered by a narrowed opening behind the pallial gland from this view, *z* the dark aboral ring.

Fig. 4. Diagram of the organs in place in optical section from the right side; *m* mouth, *t* tentacles, *n* central nerve ganglia, *j* nephridium with heart in front of it, *k* casque within the layers of the mantle, *i* intestine, *w* accessory genital glands, *y* opening from large to the interior pallial cavity, *p.g* pallial gland.

Fig. 5. Central nervous system: p_1—p_3 pedal nerves, c_1—c_2 cerebral nerves, b_1—b_2 buccal nerves, v_1—v_4 visceral nerves, *m* small posterior pedal nerve, *s* small pedal commissure, *o* otocysts, *r. c*, *l. c* right and left cerebral ganglia, *cc* cerebral commissure.

Fig. 6. Diagram of genital duct and accessory glands, *d* genital duct, *r. s* seminal receptacle, *u* uterine portion of the duct, *h* external opening.

Fig. 7. Diagram of nephridium and heart from dorsal side; *t* auricle, *v* ventricle, *pc* pericardium, *ao* aorta, *o* opening into pallial cavity, *r. n*, *l. n* right and left lobes of nephridium.

Fig. 8. Section across the more posterior part of the visceral nucleus; mantle and pallial cavity put in in diagram; *k* external layer of mantle, *w* internal layer of same, lining the pallial cavity, *s* stomach, *i* intestine, *h* hermaphroditic gland, *ao* aorta, *n* nephridium cut in two parts at this point, *l* liver—the letter itself being placed in one of the spaces of the same; *y* one of the ciliated projections of liver cells.

Fig. 9. Section through about the middle of the visceral nucleus; *r. n*, *l. n* right and left portions of the nephridium, *pc* pericardium, *a* anus, other letters as in the previous figure.

Fig. 10. Section across a more anterior portion of the visceral nucleus; *v* ventricle, *m* folds of the muciparous gland, *a* of the albumeniparous gland, dd_1 genital duct cut in two places, *r. s* seminal receptacle, *f* fragment of uterus, *e* leading to the external opening, other letters as before.

Fig. 11. Folds of lining of oesophagus; *m* muscle fibres, circular and longitudinal.

Fig. 12. Villi of beginning of stomach; *m* muscles.

FIG. 13. Portion of a thickened part of stomach wall, with secretion.

FIG. 14. Section through posterior part of central ganglia; *c* cerebral ganglia, *r. v*, *l. v* right and left visceral, *m. v* median visceral with the large ganglion cell *k*, b_1 buccal nerves, *cc* cerebral commissure, *oe* oesophagus in outline.

FIG. 15. Section through about the middle of the central ganglia; *r. c*, *l. c* right and left cerebral ganglia, c_1 origin of the pair of nerves c_1, *b* buccal ganglia, *l. p* left pedal ganglion, *m. v* median visceral, *o* otocysts, *n* auditory nerve.

FIG. 16. Section taken four sections anterior to that of the last figure; *c* cerebral ganglia, *r. p*, *l. p* right and left pedal, c_1 origin of the nerves c_1, b_2 origin of the nerves b_2 from buccal ganglia, *cb* cerebrobuccal connective, *g* connective tissue sheath of ganglia.

FIG. 17. Section through the pedal ganglia (*r. p*, *l. p*) with origin of large nerves cut upon the left side, c_1c_2 cerebral nerves, b_2 buccal nerves.

FIG. 18. Large ganglion cell; *p* protoplasmic process.

FIG. 19. The osphradium with nerve.

FIG. 19*a*. Ciliated band on the visceral nucleus.

FIG. 20. "Liver" cells; *i* with specialized ciliated cells, *j* ordinary secreting cells, with various cell contents.

FIG. 21. Section across the folds of the accessory genital glands; *m* muciparous, *a* albumeniparous gland, *n* the smaller exterior nuclei.

FIG. 22. Growth of ovum; *a*, *b*, *c* successive stages in a series of follicles.

FIG. 23. *d*, *e* older stages in the same series, *y* yolk spheres, *k* nucleolus.

FIG. 24. Section across the genital duct; large muciparous gland cells in outline.

FIG. 25. Through lower portion of the genital duct; *f* yolk spheres of a passing egg.

FIG. 26. Section in pallial gland; *t* the cells of the dark areas, *v* those of the lighter transverse bands, *n* small exterior nuclei.

FIG. 27. Vertical section through one rim of the aboral ring, *m* muscle fibres.

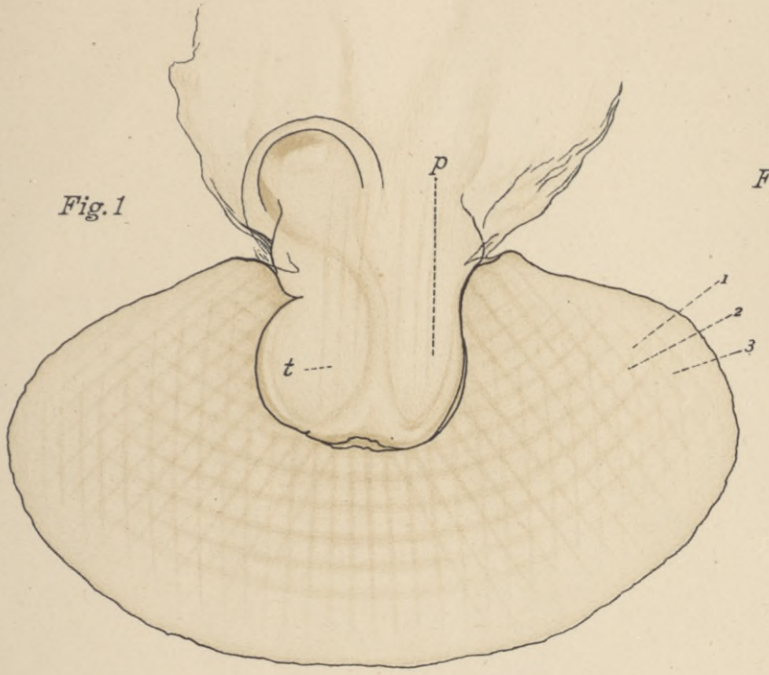


Fig. 1

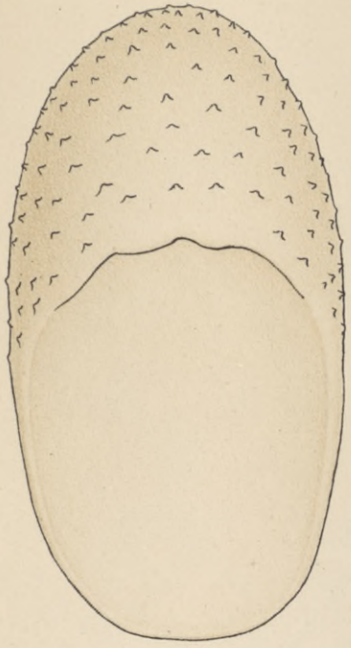


Fig. 2

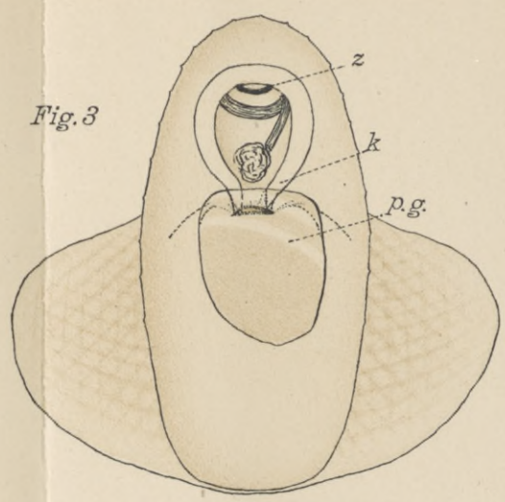


Fig. 3

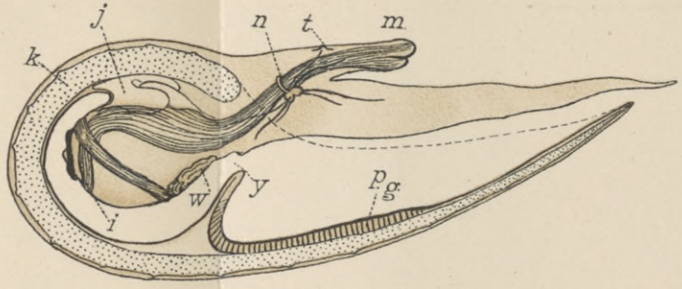


Fig. 4

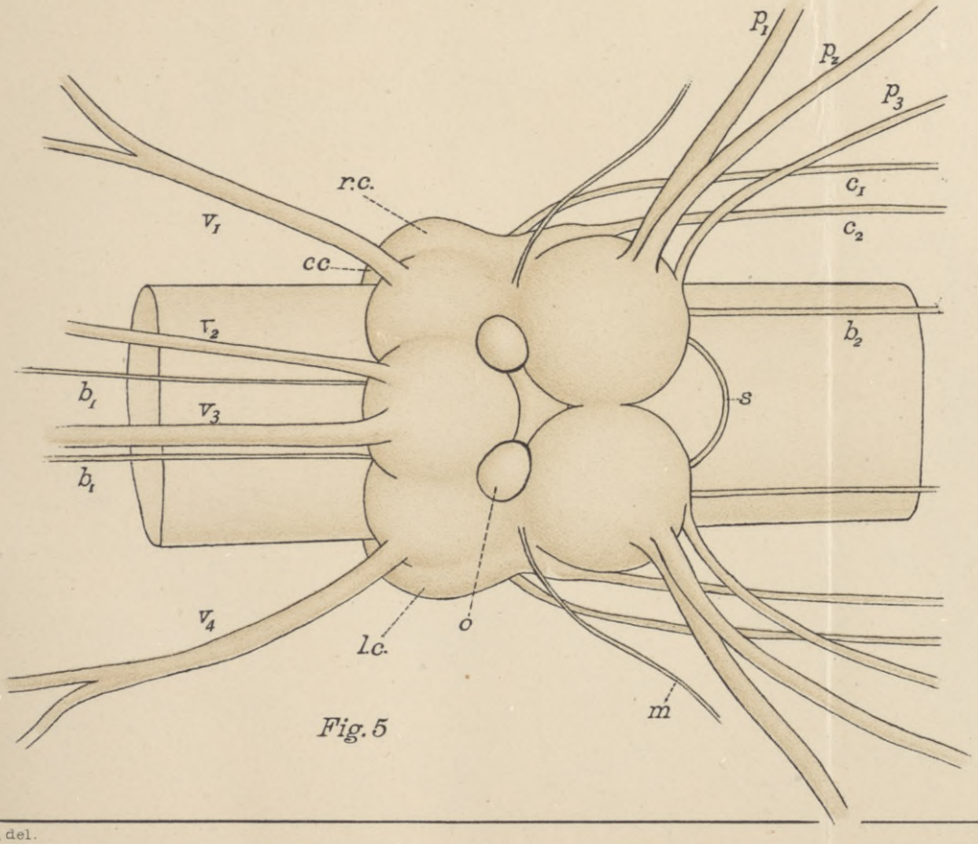


Fig. 5

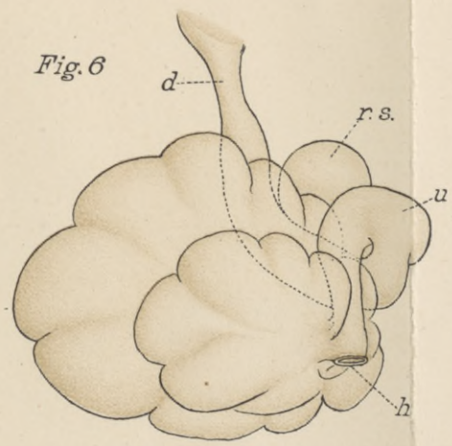


Fig. 6

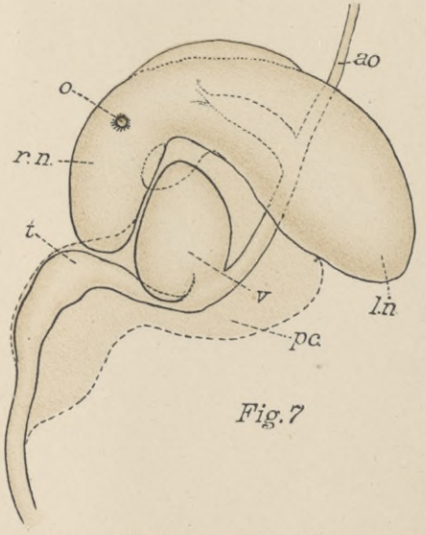


Fig. 7

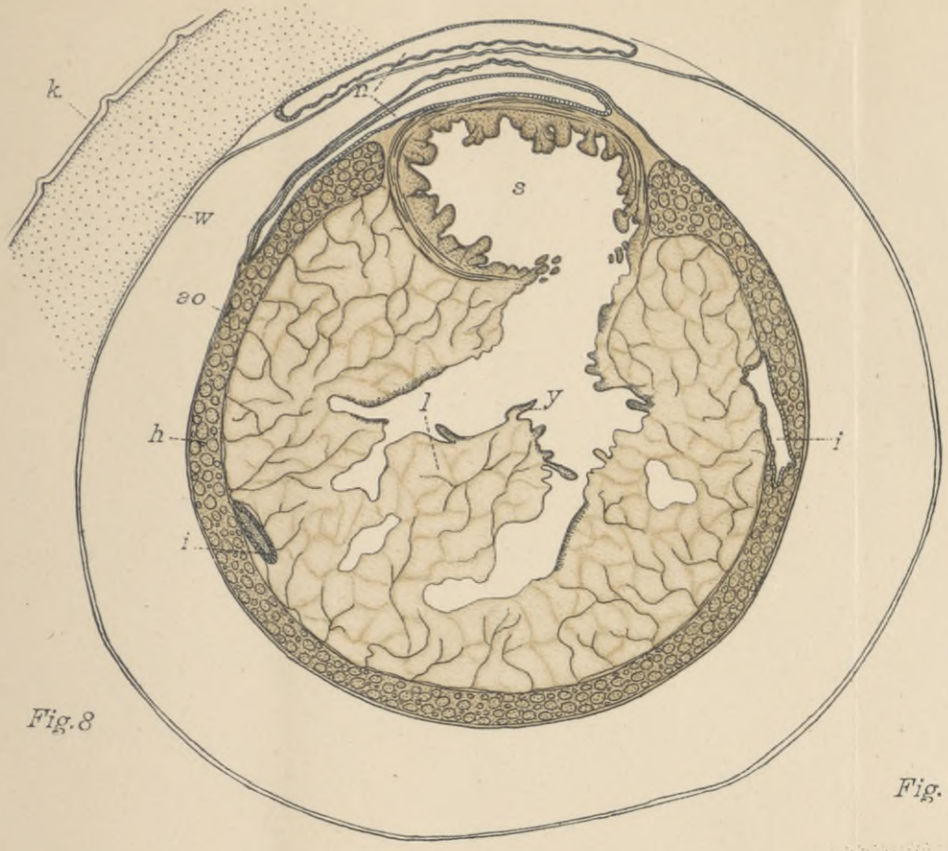


Fig. 8

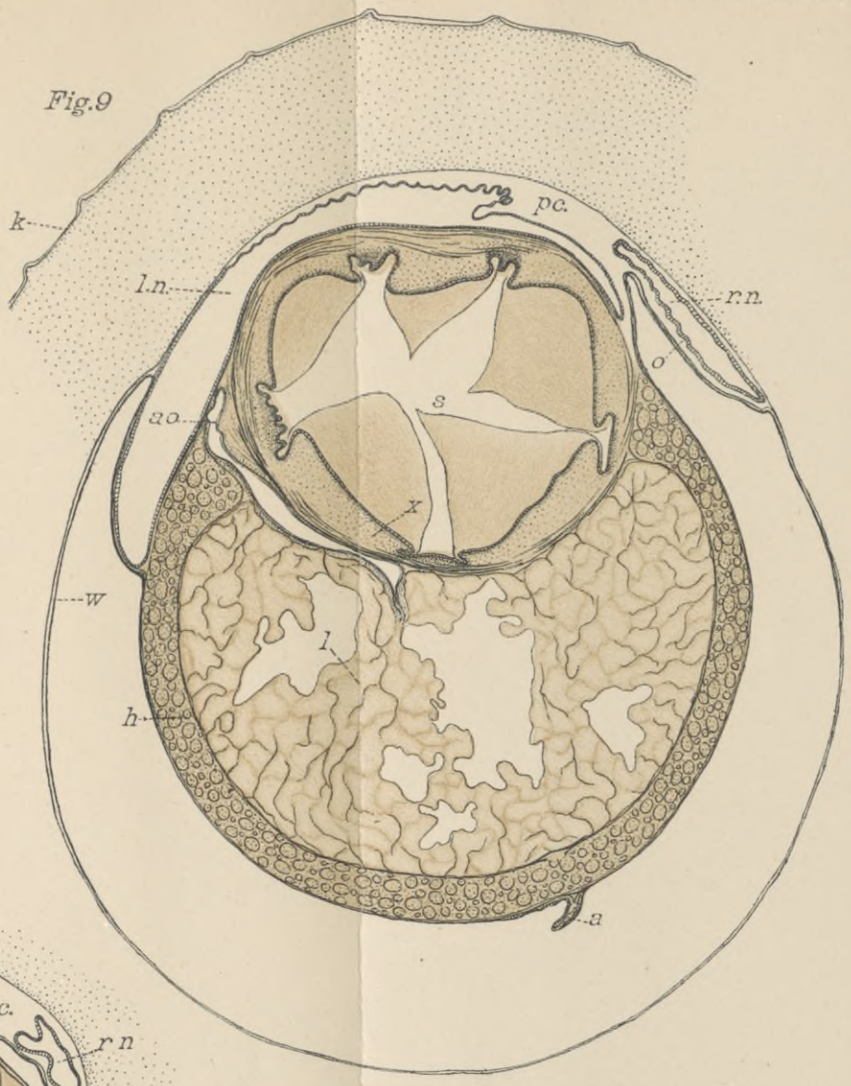


Fig. 9

Fig. 10

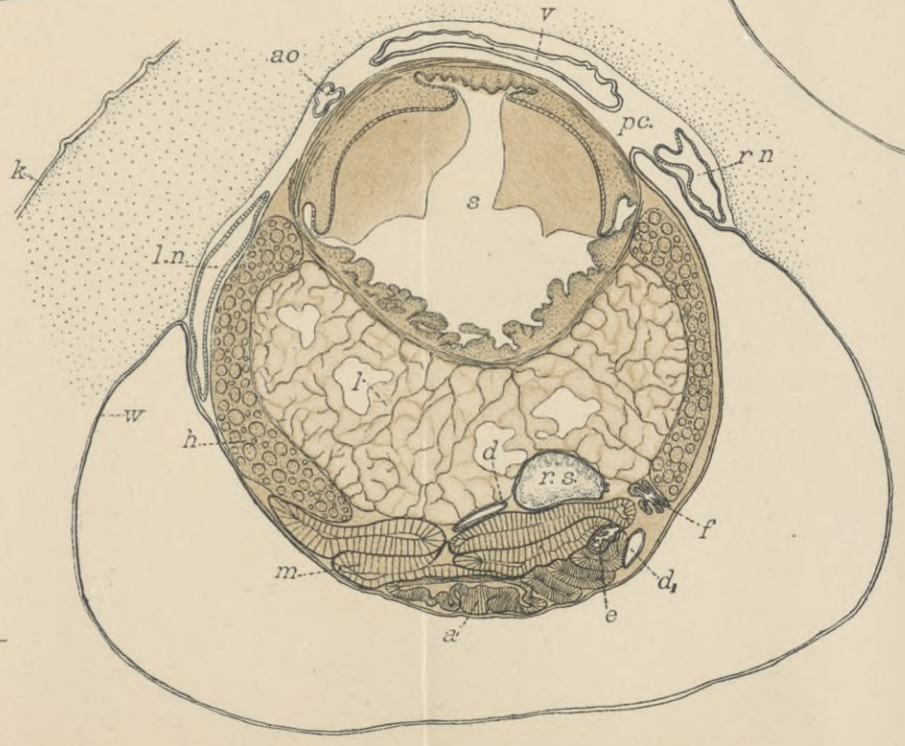


Fig. 11

Fig. 12

Fig. 13

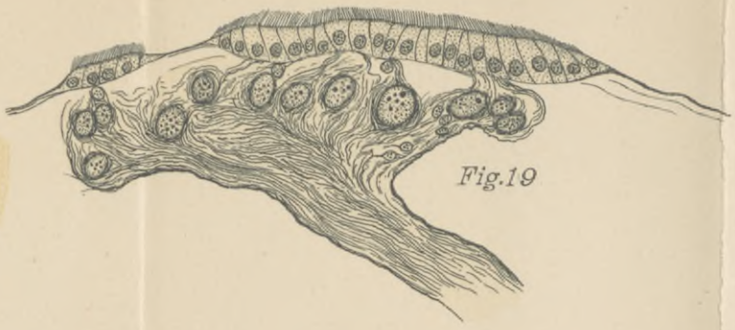
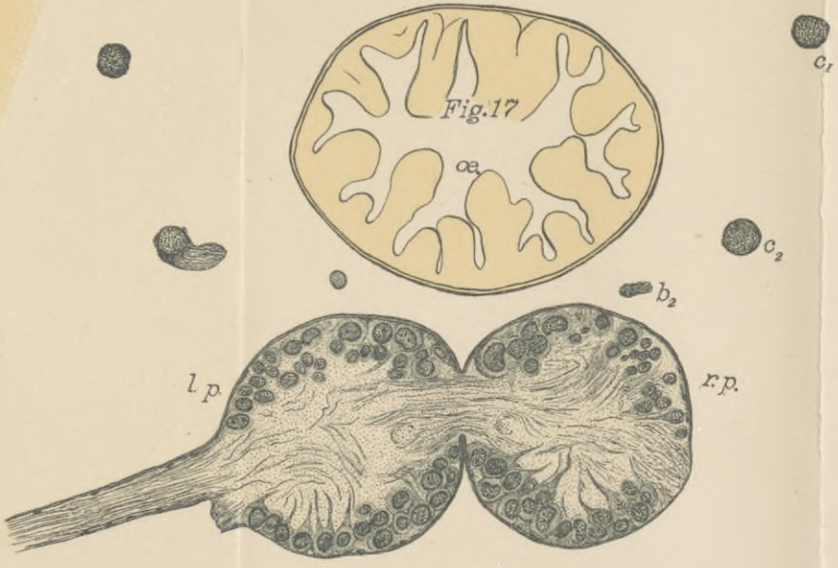


Fig. 19

Fig. 19 a



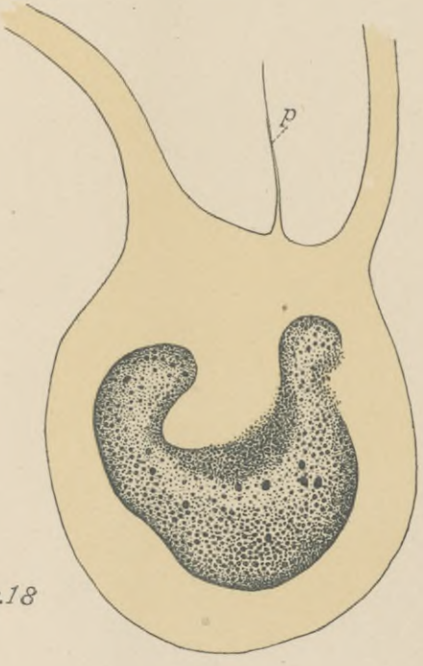
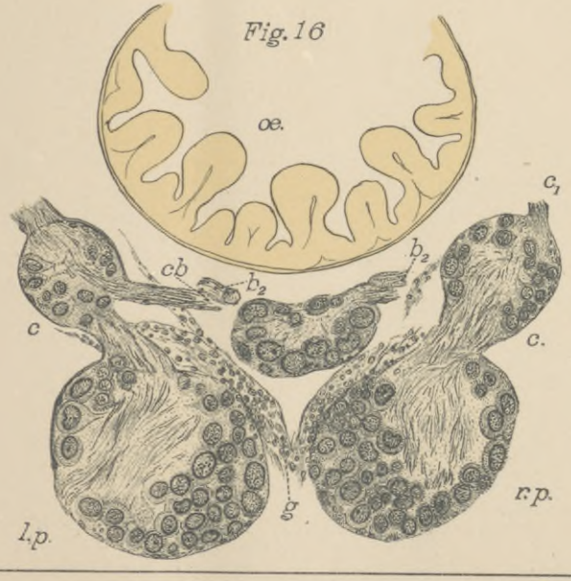
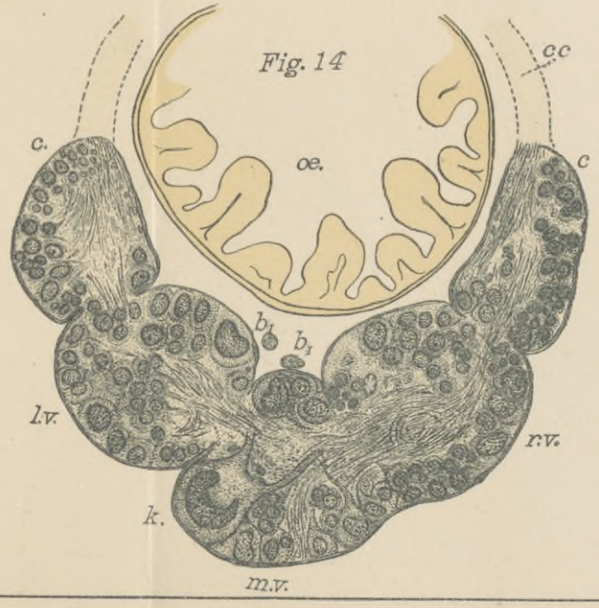


Fig. 18





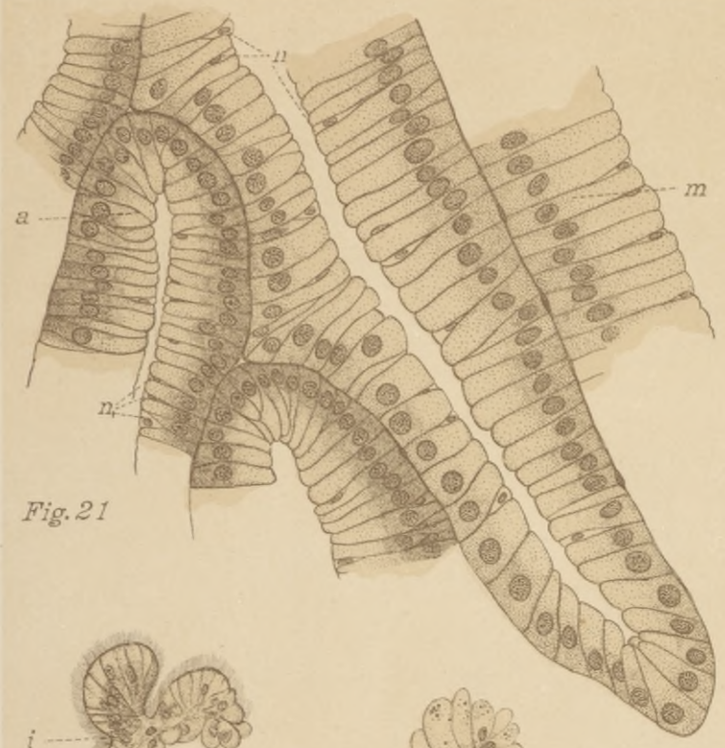


Fig. 21

Fig. 22

Fig. 26

Fig. 20

Fig. 23

Fig. 25

Fig. 24

Fig. 27