Structure and Function of the Organs of Feeding and Digestion in the Septibranchs, Cuspidaria and Poromya

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Phil. Trans. R. Soc. Lond. B 1928 **216**, 221-263
doi: 10.1098/rstb.1928.0004

IV. *Structure and Function of the Organs of Feeding and Digestion in the Septibranchs*, Cuspidaria *and* Poromya.*

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Communicated by DR. E. J. ALLEN, *F.R.S.*

(Received May 28,—Read June 30, 1927.)

(PLATES 12, 13, 14.)

CONTENTS.

1. INTRODUCTION.

Previous work on the structure and function of the alimentary system in the Lamellibranchs (YONGE (1923, 1925, 1926A, 1926B)) showed that the many peculiarities which they exhibit appear to be correlated with the highly developed ciliary feeding mechanisms on the gills and palps, as a result of the action of which only the smallest particles are passed into the œsophagus and stomach. This latter organ is concerned chiefly with sorting the particles, the larger ones being passed directly into the mid-gut and the smaller ones entering the ducts of the digestive diverticula ("liver" or "hepatopancreas"), where they are digested intracellularly. The food is largely of a vegetable nature and the digestive processes are concerned especially with the disposal of carbohydrates. There are present, free in the lumen of the gut, in the epithelium and in

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* This paper formed part of a thesis submitted for the degree of Doctor of Science at the University of Edinburgh.

[Published February 7, 1928.

the surrounding tissues, great numbers of phagocytes which actively ingest food particles. Their presence, also, appears to be correlated with the finely divided nature of the food and the fact that, but for the digestive action of these phagocytes, particles of food, unless sufficiently fine to enter the ducts of the digestive diverticula, can only be digested if composed of starch or glycogen. The only extracellular digestive enzymes in the gut of the Lamellibranchs, namely, those set free by the dissolution in the stomach of the head of the crystalline style, act exclusively on these two carbohydrates.

Owing to their deep water habitat, the Septibranchs have been little studied, but PELSENEER (1891, 1911) and PLATE (1897) have reported, on the evidence of the stomach contents, that they are carnivorous, while all investigators who have worked upon them have shown that in structure both the food collecting and digestive organs of the Septibranchs are quite distinct from those of the other Lamellibranchs. Gills are absent, their place being taken by the muscular septum, the labial palps are very small and the gut is provided with a muscular coating of a thickness unknown in the other Lamellibranchs, where the finely divided food is carried through the gut exclusively by ciliary activity, and so muscle for peristalsis is unnecessary.

Clearly, therefore, a study of the structure and function of the organs of feeding and digestion in the Septibranchs would have two valuable results ; not only would it go far towards completing our knowledge of this aspect of the structure and physiology of the Lamellibranchia, but it might be expected—should the carnivorous habit be definitely established—to provide important confirmatory evidence that the peculiar nature of the gut and the digestive processes in those Lamellibranchs which feed by means of ciliary currents *is* due to the size and nature of the food particles.

For the purpose of observing living Septibranchs, carrying out feeding experiments and collecting material for histological examination, a period of four weeks was spent at the Biologiska Station, Trondhjem, Norway, and of one week at the Kristinebergs Zoologiska Station, Sweden. As a result entirely of the kindness and labours of Dr. O. NORDGAARD at Trondhjem and of Dr. M. AURIVILLIUS at Kristineberg, a number of living specimens of these rare animals was obtained, and I wish to record my gratitude to these gentlemen, without whose help this research would have been impossible. I also desire to thank the Council of the Marine Biological Association of the United Kingdom and the Development Commission for granting me the necessary leave of absence from the Plymouth Laboratory.

The work was completed at the Plymouth Laboratory while I was Temporary Assistant Naturalist, and I have to thank the Director, Dr. E. J. ALLEN, F.R.S., for his unfailing interest in it, and other members of the staff for their assistance on many points.

2. MATERIAL.

The Order Septibranchia (PELSENEER) is divided into three families, Poromyidæ (DALL), Cetoconchidæ (RIDEWOOD), and Cuspidariidæ (FISCHER). No representatives of the second of these have ever been examined in the living condition ; they are abyssal and have only been taken on deep-sea expeditions, such as the "Challenger" (see Pelseneer (1888b)) and the "Siboga" (see Pelseneer (1911)). Of the Poromyidæ, I obtained two living specimens of *Poromya granulata* which were dredged in the Trondhjem Fjord at depths of 150 and 200 metres. After returning to Plymouth, I received three further specimens of this species preserved in alcohol which were collected by Dr. M. Aurivillius on an expedition to the Koster Islands in the Skager Rack, and were sent on to me by Dr. N. Hj. Odhner of the Riksmuseum, Stockholm, for whose kindness I am extremely grateful.

Living specimens of three species of Cuspidaria were obtained. Twelve *Cuspidaria obesa* were dredged at depths of between 100 and 300 metres in the Trondhjem Fjord. Unfortunately this species is so small that it is difficult to handle and observe, and most of my observations on living Cuspidaria were made on one specimen of *Cuspidaria rostrata*, which was dredged at a depth of 250 metres at Trondhjem, and three specimens of *Cuspidaria cuspidata*, dredged in the Gullmars Fjord in Sweden at depths of between 40 and 60 metres. I also received from Dr. O. Nordgaard two preserved specimens of *Cuspidaria rostrata*, and since my return Dr. M. Aurivillius has kindly sent me a number of preserved *Cuspidaria rostrata*, and several *C. obesa* and *C. cuspidata*, and one *C. costellata*. This preserved material has proved of great value in the histological and anatomical portions of the research.

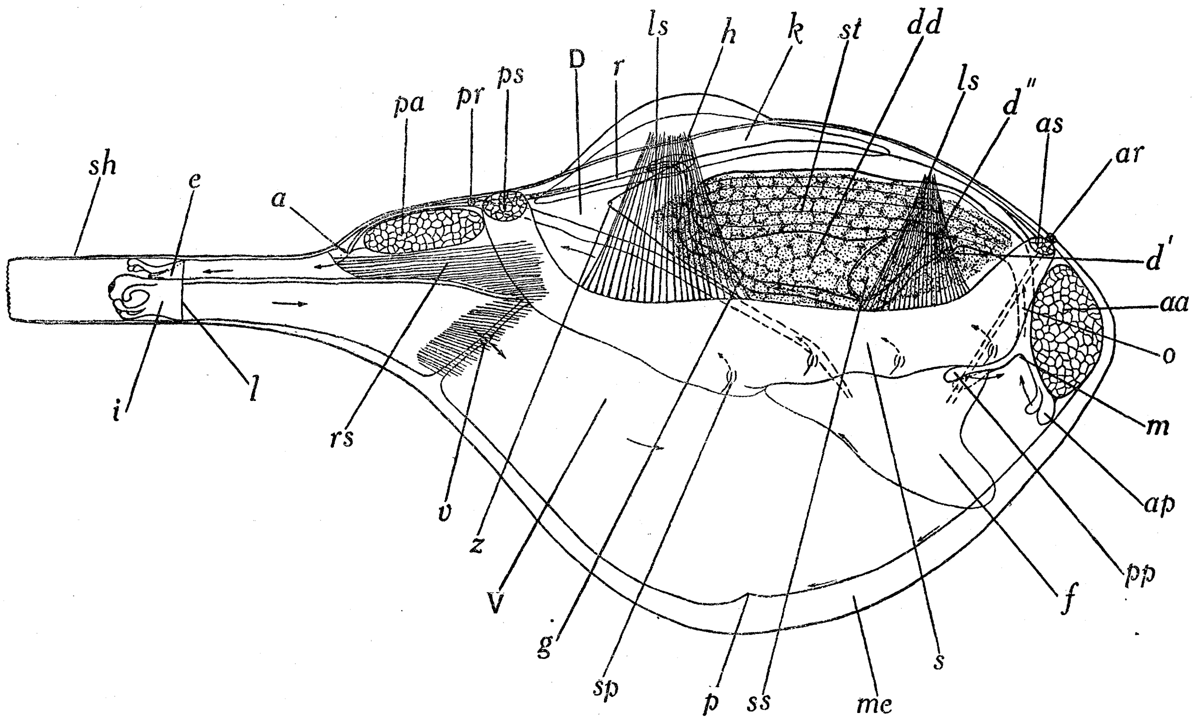
3. Anatomy and Histology of the Organs of Feeding and Digestion.

Throughout this paper, for the sake of convenience, the conditions in the genus Cuspidaria, whose members represent the highest development of the Septibranchs, will be described before those in Poromya. It must not be forgotten, however, that, as shown by Pelseneer (1888a, 1888b, 1891, 1911) and as further emphasised in this paper, Poromya should logically be treated first as it represents a somewhat more primitive condition and shows more affinities to the typical Lamellibranchs—especially to the Anatinacea, from which, according to Pelseneer, the Septibranchs probably sprang—than does the more highly specialised Cuspidaria.

(i) *Anatomy*. A.—*Cuspidaria*.

Literature.—Although the absence of gills in Cuspidaria (Neæra) was first noted by Dall (1886b) and this author has described the shell and external characters of many species of the Cuspidariidæ (1889a, 1889b, 1894), the first adequate description of Cuspidaria was furnished by Pelseneer (1888b), who gave an account of *C. curta*, *C. fragilissima* and *C. platensis* from the "Challenger" material and *C. rostrata* obtained from Naples, later (1891) giving a more detailed description of the last species. He has since (1911) described the Cuspidariidæ taken by the "Siboga" expedition. Grobben (1892) in his memoir on *Cuspidaria cuspidata* has provided the most detailed account of the morphology of the Cuspidariidæ. A short description of the morphology of *Cuspidaria* *obesa* (unfortunately without figures) has been given by Plate (1897). Finally, Ridewood (1903) in his work on the gills of Lamellibranchs gave some account of the septum and palps of *Cuspidaria glacialis*.

General Anatomy.—The observations here recorded on the anatomy of the Cuspidariidæ are based largely on examinations of living and preserved specimens of the comparatively large species, *Cuspidaria rostrata* and *C. cuspidata*. The general anatomy can best be described by reference to text-fig. 1, which represents a lateral view of *Cuspidaria rostrata*.



Text-Fig. 1.—Lateral view of *Cuspidaria rostrata* showing the anatomy of the feeding and digestive organs. × 6. *a.*, anus; *a.a.*, anterior adductor; *a.p.*, anterior labial palps; *a.r.*, anterior retractor of foot; *a.s.*, anterior septal muscle; *d′.*, anterior, right duct of digestive diverticula; *d″.*, posterior, left duct of same; *D.*, dorsal or supra-septal compartment of the mantle cavity; *d.d.*, digestive diverticula; *e.*, exhalant siphon; *f.*, foot; *g.*, mid-gut; *h.*, heart; *i.*, inhalant siphon; *k.*, kidney; *l.*, line of attachment of siphons; *l.s.*, lateral septal muscles; *m.*, mouth; *m.e.*, mantle edge; *o.*, œsophagus; *p.*, point where mantle lobes unite; *p.a.*, posterior adductor; *p.p.*, posterior palps; *p.r.*, posterior retractor of foot; *p.s.*, posterior septal muscle; *r.*, rectum; *r.s.*, retractor muscle of siphons; *s.*, septum; *sh.*, siphonal sheath; *s.p.*, septal pore; *s.s.*, style-sac (style indicated by broken line); *st.*, stomach; *v.*, valve at junction of the inhalant siphon and the mantle cavity; *V.*, ventral or infra-septal cavity; *z.*, posterior end of visceral mass. Arrows indicate direction of water current and food intake.

The animal is flask-shaped, the siphons (*i.* and *e.*) lying in a long posterior extension of the shell. The inhalant siphon (*i.*) is the larger and possesses four club-shaped tentacles which are attached on the ventral side to the base of the siphonal opening, which is large and muscular. The exhalant siphon (*e.*) has a much narrower opening and is shorter, three tentacles, similar in structure to those of the inhalant siphon, are attached to its dorsal surface. In life, the siphons normally project from the shell, but on stimulation, or after fixation, they are withdrawn within the siphonal sheath (*sh.*), as shown in the figure. They are attached to this about half-way along the siphonal extension, along the line marked *l*. Anterior to this the siphons are divided by a stout partition, which terminates at its junction with the muscular septum (*s.*) which divides the mantle cavity into ventral (*V.*) and dorsal (*D.*) chambers. At their base, the siphons are attached to the shell by a widely spreading series of muscle strands (*r.s.*) which, by their contraction, withdraw the siphons. The inhalant siphon is separated from the ventral mantle chamber by a sheet of tissue perforated by a round valve (*v.*) near the centre. The mantle is excessively thin—resembling fine tissue paper in consistency—which is characteristic of the Septibranchs. Ventrally the mantle lobes are bounded by thickened ridges which are united in the posterior half of the mantle cavity, the point of attachment being indicated in the figure by the letter *p*. Projecting in the middle line through the anterior half of the septum is the foot (*f.*), which is long and narrow and possesses a byssus groove on its posterior surface (see text-fig. 6, *b*) associated with a gland in the body of the foot. The foot is capable of great extension and is withdrawn by the action of two retractor muscles which are attached to the mid-dorsal region of the shell, an anterior retractor (*a.r.*) immediately posterior to the large anterior adductor muscle of the shell (*a.a.*), and a posterior retractor (*p.r.*) above the anterior part of the posterior adductor of the shell (*p.a.*). Of the adductor muscles the anterior is the larger and lies in the extreme anterior region of the body with its greatest diameter vertical, while the posterior adductor is situated dorsal to the anterior region of the exhalant siphon, is more oval in cross-section, and is horizontally extended.

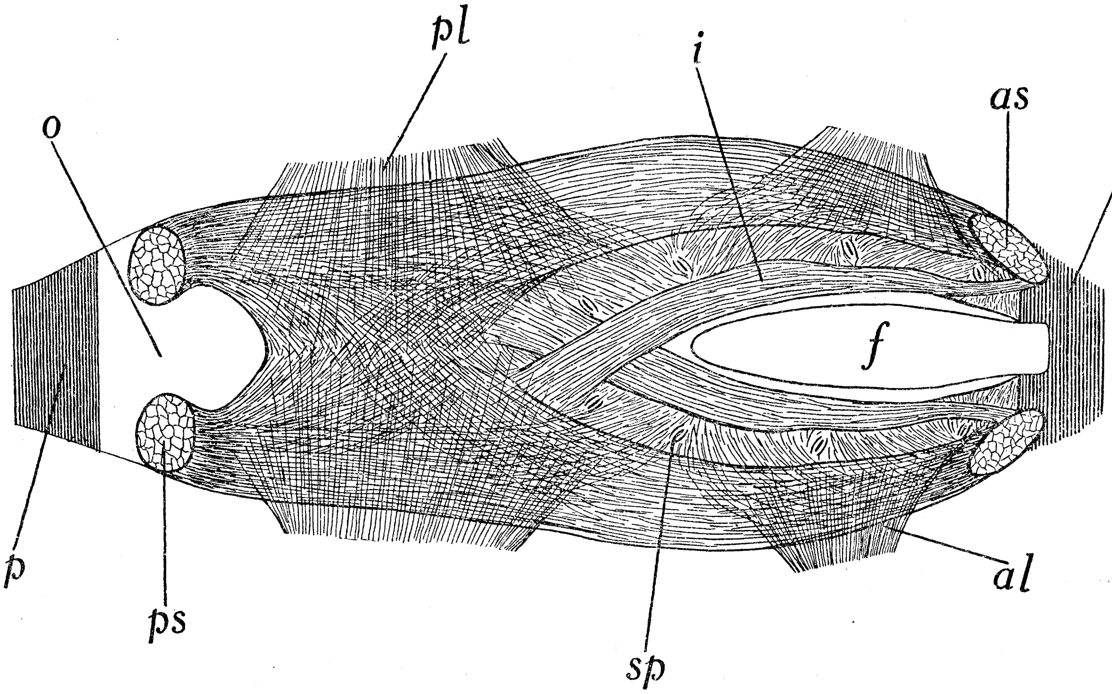
Anterior to the foot and projecting ventrally from the under surface of the septum are the labial palps. These consist of an anterior (*a.p.*) and a posterior (*p.p.*) pair, the latter being slightly the larger. The anterior palps are attached for the greater part of their surface to the posterior ventral surface of the anterior adductor muscle, and form a veil in front of the mouth (*m.*); the posterior pair are wedge-shaped and free, they extend posteriorly on either side of the foot. The palps are not ridged as in the other Lamellibranchs, and this, and especially their small size, has aroused comment from most observers, Dall (1886b) originally stating that they were completely absent, but his material was in bad condition. In later work (1888) he refers to the palps of the Cuspidariidæ as obsolete, and in a further paper (1889b) states that the palps are absent in *Myonera paucistriata* (a member of the Cuspidariidæ). Pelseneer (1888b, 1891) states that the posterior palps of *Cuspidaria curta* and *C. fragilissima* are absent. Grobben noted the small size of the palps in *Cuspidaria cuspidata*, and Plate stated that palps are absent in *C. obesa*. My own observations on this species, however, have shown that, though the posterior palps are reduced to mere ciliated tracts, as described by Plate, the anterior palps, though greatly reduced, are present. In *Myonera dubia*, Pelseneer (1911) states that the posterior palps project very little, but that in *Cuspidaria*

(*Pseudneœra*) *thaumasia* they are large and extend for a considerable distance. I have found both pairs of palps comparatively well developed in *Cuspidaria rostrata* and *C. cuspidata* (see text-fig. 6), but in both they contracted considerably after fixation—probably owing to their possession of relatively powerful muscles—and it is not impossible that they may be present in species in which they have been recorded as absent. That they retain some importance in feeding will be shown in a later section.

Septum.—The septum consists of an extremely thick muscular partition which divides the mantle cavity into two chambers, in the upper of which lies the visceral mass. It is slung longitudinally across the mantle cavity and is attached at either end by a pair of stout muscles to the dorsal region of the shell. The anterior septal muscles (*a.s.*) are attached to the shell immediately posterior to the anterior adductor and on either side of the anterior retractor muscle of the foot, and the posterior pair (*p.s.*) slightly anterior to the posterior adductor. These muscles are called septal retractors by PELSENEER, but both DALL and GROBBEN prefer to call them simply septal muscles, and, in view of the peculiar functioning of the septum, which will be described subsequently, I prefer the latter name. The septum of *C. rostrata* is perforated by four pairs of pores (*s.p.*) which are symmetrically arranged on either side of the middle line in the anterior two-thirds of the exposed septal surface. The most anterior pair are slightly posterior to the mouth, and the hindermost pair a little distance behind the base of the foot. They lie nearer to the base of the foot than to the mantle, as is shown in text-fig. 2. Each consists of a narrow slit-like opening, laterally extended and bounded by low lips. They provide the sole means of communication between the ventral and dorsal chambers of the mantle cavity (or infra- and supra-septal cavities, as they will hereafter be called).

The arrangement of the muscles in the septum has been described by DALL (1889B) and in more detail by GROBBEN, and will most easily be understood by reference to text-fig. 2, which shows the arrangement of the septal muscles as seen from the dorsal aspect after the septum has been dissected out. At the attachment of the septum to the mantle on the outer, and to the sides of the foot on the inner, side, the tissues are thin and somewhat membranous, but the body of the septum consists of thick muscular strands. In the outer regions these run longitudinally, bundles of fibres from the anterior septal muscle (*a.s.*) passing backwards and meeting bundles from the posterior septal muscle (*p.s.*). Smaller bundles of longitudinally directed fibres (*i.*) separate from the anterior septal muscles, pass downwards and then posteriorly along the side of the foot on the inner side of the pores, finally crossing one another posterior to the foot and becoming merged into the general mass of the septum. These fibres have a separate insertion nearer to the middle line than the main anterior septal muscle in *Cuspidaria cuspidata* as described by GROBBEN, and also in *C. modesta*, *C. convexa*, *C.* (*Myonera*) *dubia*, and in two other unidentified species from the "Siboga" collections (PELSENEER (1911)). Besides the longitudinally directed fibres, there are others which pass diagonally across the septum from the main longitudinal bundles, and the somewhat thinner region between the pores is largely composed of such muscles, which have their origin in the anterior septal muscle, while posterior to the foot similar muscles pass across the centre of the septum and meet diagonally directed fibres from the posterior septal muscles. The two sets of muscles from each side unite and, together with the fibres of the inner longitudinal bands from the anterior septal muscle, form a thick muscular sheet composed of closely interwoven fibres, as shown in text-fig. 2. An opening (*o.*) is left between the posterior septal muscles whereby the supra-septal cavity is connected with the cavity of the exhalant siphon.

The septum is also connected with the shell by means of numerous thin muscular strands which extend dorsally through the tissue of the mantle and are attached to the shell near the mid-dorsal line. These lateral septal muscles (text-fig. 1, *l.s.*) are arranged in two pairs in *Cuspidaria rostrata*, a smaller anterior pair (text-fig. 2, *a.l.*) and a larger posterior pair (*p.l.*). The same condition is found in *Cuspidaria mitis*, *C. strictirostris*, *C. corrugata*, and a further unnamed species from the "Siboga" collections (PELSENEER (1911)). In *C. cuspidata*, however, the lateral septal muscles are continuous (see figs. 1 and 2 in GROBBEN) and also in *C. modesta* (PELSENEER (1911)). In other species different conditions are found; there may be one pair of lateral muscles as in an unnamed species from



TEXT-FIG. 2.—Septum of *Cuspidaria rostrata* dissected out and viewed from the dorsal aspect. × 10. *a.*, anterior adductor; *a.l.*, anterior lateral septal muscle; *a.s.*, anterior septal muscle; *f.*, foot; *i.*, inner longitudinal muscles from anterior septal muscle; *o.*, opening leading to exhalant siphon; *p.*, posterior adductor; *p.l.*, posterior lateral septal muscle; *p.s.*, posterior septal muscle; *s.p.*, septal pore.

the "Siboga," four pairs as in *C. fragilissima*, or none as in *C.* (*Myonera*) *dubia* (Pelseneer (1911)). The fine isolated bundles forming these muscles extend down through the mantle until they reach the septum, when they are continued transversely across its dorsal surface, and can be distinguished in sections as a thin layer immediately beneath the epithelium. As will be shown later, their structure is distinct from that of the main septal muscles.

Although the majority of the known species of the Cuspidariidæ possess, like *C. rostrata*, four pairs of septal pores (see Pelseneer (1911) for details as to species), *C. cuspidata*, *C. convexa* and *C. arctica* var. *glacialis* all have five pairs. If reference be made to text-fig. 6, which represents *C. cuspidata* as seen from the ventral aspect with the mantle lobes drawn apart, the five pairs of pores will be seen. The size of the palps, which were drawn from life, is also clearly shown in the same figure.

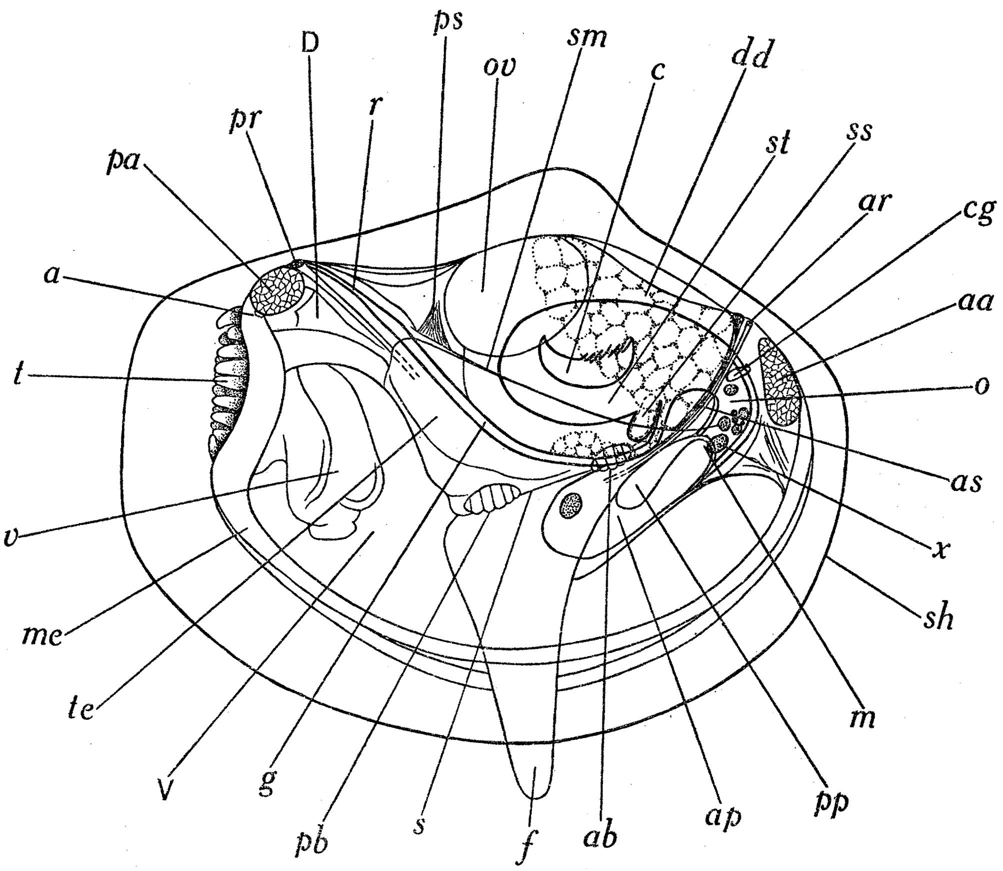
Alimentary System.—Referring again to text-fig. 1, the mouth (*m.*) lies in the middle line between the two pairs of palps and is a laterally extended opening of relatively large size, as is best seen in text-fig. 6. It leads into a short œsophagus (*o.*) with folded walls which extends almost directly dorsally to open into the stomach (*st.*). This latter organ is, for a Lamellibranch, of unusual size and shape. It is long and cylindrical, extending almost from end to end of the visceral mass in a longitudinal direction. Its walls are thrown into a series of prominent folds (see fig. 7), the entire inner surface being covered with a thick cuticular lining. Surrounding it on all sides except the extreme dorsal surface are the brownish, blind-ended tubules of the digestive diverticula (so-called liver or hepatopancreas), the whole consisting of somewhat asymmetrical halves lying on either side of the stomach, into which each opens by a separate duct (*d′.*, *d″.*). Both of these open into the ventral region of the stomach near the anterior end, that on the right (*d′.*) being smaller and slightly anterior to that on the left (*d″.*), which opens on a line with the beginning of the mid-gut.

Both the style-sac (*s.s.*) and the mid-gut (*g.*) open into the stomach near its anterior end and a little to the right of the mid-ventral line, the mid-gut being the more anterior of the two. The style-sac is a short oval cavity and contains a small cylindrical style indicated by the broken line in text-fig. 1. The style removed from a living specimen of *Cuspidaria cuspidata* was only 1·9 mm. long and 0·74 mm. broad, and projected but slightly into the lumen of the stomach. The lumina of the style-sac and the mid-gut are separated by a well-developed fold, but remain connected by a narrow longitudinal slit. The mid-gut is both short and straight; after extending ventrally as far as the base of the style-sac, it is then directed posteriorly, lying among the tubules of the digestive diverticula. Posterior to the stomach it turns abruptly upwards and leaves the visceral mass in the region below the umbo. It becomes merged here into the rectum (*r.*), which at the beginning of its course traverses the heart (*h.*) and later passes between the posterior septal muscles, over the posterior adductor, and then turns downward to open at the anus (*a.*) into the base of the exhalant siphon.

B.—*Poromya*.

Literature.—The anatomy of *Poromya granulata* and *P. tornata* was first described and figured by Pelseneer (1888b), who later (1891) gave a more detailed account of the former species. In 1911 the same author described eight species of Poromya from the "Siboga" collections. Dall (1886a, 1889a, 1889b) has described the shell and external anatomy of the body in a number of species of the Poromyidæ. Ridewood (1903) has provided an account of the structure of the septum and the branchial sieves in *Poromya malespinæ* and *P. oregonensis*.

General Anatomy.—A lateral view of *Poromya granulata* is represented in text-fig. 3. The shell (*sh*.) has no posterior siphonal prolongation as in the Cuspidariidæ, the posterior



Text-Fig. 3.—Lateral view of *Poromya granulata*, showing the anatomy of feeding and digestive organs, × 10. *a*., anus; *a.a*., anterior adductor; *a.b*., anterior branchial sieve; *a.p*., anterior palps; *a.r*., anterior retractor of foot; *a.s*., anterior septal muscle; *c*., crustacean in stomach; *c.g*., cerebral ganglion; *D*., dorsal or supra-septal cavity; *d.d*., digestive diverticula; *f*., foot; *g*., mid-gut; *m*., mouth; *m.e*., mantle edge; *o*., œsophagus; *ov*., ovary; *p.a*., posterior adductor; *p.b*., posterior branchial sieve; *p.p*., posterior palps; *p.r*., posterior retractor of foot; *p.s*., posterior septal muscle; *r*., rectum; *s*., septum; *sh*., outline of shell; *s.m*., line of attachment of septum and mantle; *s.s*., style-sac (style indicated by broken line); *st*., stomach; *t*., tentacles; *te*., testis; *v*., valve between inhalant siphon and infra-septal cavity; *V*., ventral or infra-septal cavity; *x*., sand grains between palps and in œsophagus.

margin being subtruncate and slightly gaping. The siphons are short—almost sessile—and the inhalant opening is much larger than the exhalant (see text-fig. 4, *i.* and *e.*), both being surrounded by a common ring of long, slightly tapering tentacles (text-figs. 3 and 4, *d.* and *t.*) consisting of an unpaired dorsal tentacle (text-fig. 4, *d.*) and seven pairs of tentacles round the lateral and ventral margins of the inhalant siphon. The opening of the inhalant siphon into the infra-septal cavity (*V.*) is guarded by a large muscular valve (*v.*). The surface of the mantle is excessively thin as in the Cuspidariidæ, the ventral margins (*me.*) alone are thick and are free from one another for the entire length of the body from the anterior adductor (*a.a.*) to the siphons. The foot (*f.*) is long and thin and possesses a byssus groove on the posterior surface (see text-fig. 7, *b.*). It has two retractor muscles, an anterior (*a.r.*) and a posterior retractor (*p.r.*) which are attached to the shell in the same relative positions as in *Cuspidaria rostrata*. The palps are broader and larger than those of the Cuspidariidæ, a fact which has been noted by all observers, the anterior pair (*a.p.*) being especially long and, unlike the anterior palps of the Cuspidariidæ, being free from the anterior adductor (see also text-fig. 7). The posterior pair (*p.p.*) are united to one another in the middle line and do not extend back on either side of the foot as in Cuspidaria. The degree to which the mouth (*m.*) is guarded and obscured by the palps is seen best in text-fig. 7 which was drawn from life. The adductor muscles (*a.a.* and *p.a.*) occupy the same relative positions as in *Cuspidaria rostrata* but are smaller, and the posterior adductor is round and not oval in cross-section. The visceral mass occupies the bulk of the supra-septal cavity (*D.*), the dorsally situated ovary (*ov.*) and the more posterior and ventral testis (*te.*) being both well developed (like all the Septibranchs, Poromya is hermaphrodite). Lying above the œsophagus (*o.*) are the cerebral ganglia (*c.g.*).

Septum.—The septum in Poromya is a much smaller and more delicate organ than in the Cuspidariidæ. It is attached to the mantle on its outer sides, the right side being attached along the line marked *s.m.* in text-fig. 3. The two sides are united posterior to the foot, but are closely apposed, and not united, to the base of the foot along the line marked *s.* The septal muscles are very much smaller than those of the Cuspidariidæ and consist of two pairs, one anterior (*a.s.*) and the other posterior (*p.s.*), which are attached to the shell a little distance posterior to the anterior retractor and immediately posterior to the visceral mass respectively. The muscles run through the tissue of the mantle before becoming attached to the shell. There is no indication of lateral septal muscles, but, as will be discussed later, there is evidence that the septal muscles in Poromya may correspond to the *lateral* septal muscles, and not to the septal muscles, of the Cuspidariidæ.

There are no pores like those in the septum of the Cuspidariidæ; instead there are a pair of anterior, and a pair of posterior, branchial sieves (*a.b.*, *p.b.*) which probably represent vestiges of the Lamellibranch gill. Each of these, in the words of RIDEWOOD (p. 272), "has the form of a shallow convex sieve, with the convexity directed downward and outward into the pallial cavity, and is attached all round its edge to the branchial septum by a thickened border." The anterior pair are on a level with the anterior border of the foot and each possesses five filaments, the posterior pair are situated opposite the hind end of the foot and have each six filaments. Both pairs are much nearer to the foot than to the mantle and lie somewhat obliquely. The slit-like openings between the filaments represent the sole means of communication between the infra- and the supra-septal cavities, for the edge of the septum, though not attached to the side of the foot, is too closely applied to it to permit the passage of water. Though all known species of the Poromyidæ possess two pairs of branchial sieves, these vary in size and in the number of filaments in different species. PELSENEER (1911) has tabulated the different conditions found in the eight species collected by the "Siboga" and has shown that the number of filaments in the anterior branchial sieve may vary in number between five and eight, and in the posterior one between five and eleven.

The conditions in the Cetoconchidæ, according to PELSENEER (1888B) and RIDEWOOD, approximate more closely to those found in the Poromyidæ than in the Cuspidariidæ, the septum being thin and possessing three paired sets of openings, consisting, in *Cetoconcha sarsi* (see RIDEWOOD, fig. 60), of an anterior series of five pores, a second series of five pores, and a posterior of three. In cross-section, as shown by RIDEWOOD, the boundaries between the pores appear as shortened gill filaments as in the Poromyidæ. Both the valve guarding the entrance to the infra-septal cavity and the palps of the Cetoconchidæ are large and resemble those of the Poromyidæ, and PELSENEER (1911), apparently with good reason, regards the Cetoconchidæ, though somewhat intermediate between the Poromyidæ and the Cuspidariidæ, as much more nearly related to the former family, concluding (p. 78) "la nécessité d'une famille Cetoconchidæ n'est nullement démontrée."

Alimentary System.—The widely open mouth (*m.*) leads into a short and broad œsophagus (*o.*), which is directed antero-dorsally, turning posteriorly to open into the large cylindrical stomach (*st.*). This is not quite so long nor so regularly cylindrical as the stomach of the Cuspidariidæ, but resembles that in the possession of ridged walls with a thick cuticular lining. It is surrounded except in the posterior region by the brownish tubules of the digestive diverticula (*d.d.*) which extend farther forwards than in Cuspidaria and open by two short, wide ducts near the anterior end of the stomach. There is an even smaller style-sac (*s.s.*) than in Cuspidaria and the contained style does not project far into the lumen of the stomach. The sac is in communication anteriorly with the mid-gut (*g.*) by means of a fine longitudinal slit. The mid-gut is short; after passing beneath the style-sac, it extends posteriorly to the end of the visceral mass and then diagonally upwards, merging into the narrower rectum (*r.*), which passes over the posterior adductor to open at the anus (*a.*) which lies at the base of the exhalant siphon. The cleared specimen of *Poromya granulata* from which text-fig. 3 was drawn contained between its posterior palps and in the œsophagus large sand grains (*x.*), and in the stomach a relatively large crustacean (*c.*), which occupied the centre of the lumen.

(ii) *Histology*. A.—*Cuspidaria*.

Mantle and Foot.—The thin mantle is bounded on both surfaces by a delicate pavement epithelium, as described in detail by Grobben. The thickened ventral edges possess on either side an epithelium of high narrow cells, those on the outer and ventral surfaces being concerned, presumably, with the formation of the shell. The epithelium on the inner side is the only region of the mantle which is ciliated, while there are present beneath the epithelium for the anterior two-thirds of its course large goblet-shaped mucous glands. These glands, which stain darkly with muchæmatein, occur in such numbers as to form a thick layer beneath the epithelium. They discharge their contents by way of fine extensions, which pass between the cells of the epithelium. Grobben has described them in *C. cuspidata*, and Plate in *C. obesa*; in my own sections I have found them in these two species and also in *C. rostrata*. The ciliated regions extend posteriorly to the region of the valve at the posterior end of the mantle cavity.

The surface of the foot is thrown into a series of fine ridges which are bounded by a columnar epithelium which, except near the base of the foot, is ciliated, mucous glands occurring in the tissue beneath. The interior of the foot is composed of plain muscle fibres passing in all directions, amongst which ramify the extensions of the byssus gland, the ciliated duct of which opens on the posterior surface of the foot near the base.

Septum.—Grobben is the only worker who has described the fine histology of the septum in detail, though his findings have been confirmed to some extent by Plate. As shown in fig. 1, both dorsal and ventral surfaces are covered with a low pavement epithelium (*d.e.* and *v.e.*), especially thin on the former; no cilia can be distinguished in sections (though their presence on the dorsal surface was noted in living *C. rostrata* and *C. cuspidata*), but a fine border cuticle is present. Nuclei are infrequent and irregularly distributed. The interior of the septum is composed of a mass of interwoven muscle fibres which, as already noted and figured by Grobben in *C. cuspidata* and confirmed by Plate in *C. obesa*, have a characteristic and unique structure. As shown in fig. 3, they consist of flat fibres which, in the case of fibres from the septum of *C. rostrata*, are about 13 μ wide and less than 2 μ thick. After staining teazed-out fibres with iron hæmatoxylin, cross striations (*sr.*) can be seen, as dark bands somewhat narrower than the intervening lighter portions and about 1·5 μ apart. The fibres are of great length, the nuclei, as shown in fig. 3 (*n.s.*), being situated in the centre of the fibres. They are long and narrow—about 11 μ long and 3 μ wide—and appear to lie in a lightly staining strip (*a.*) in the centre of the fibre, this area extending down the middle of the fibre for some distance beyond the extremities of the nuclei. The fibres are usually wavy and their linear appearance in cross-section is shown in fig. 1 (the cross striations do not appear in this section, which was stained with Delafield's hæmatoxylin and eosin), and in horizontal section, with the striations indicated, in fig. 2. There is an almost complete absence of connective-tissue strands, but there are many wandering cells (*w.c.*) amongst the muscle fibres. This type of muscle appears to be unique in the animal kingdom; it is certainly unique so far as the Lamellibranchs are concerned, and its peculiar structure may be correlated with the remarkable mode of functioning of the septum, particulars of which will be given later.

The lateral muscle fibres which run across the dorsal surface of the septum, immediately beneath the epithelium, consist of plain muscle, roundish in cross-section and are shown (*l.s.m.*) in fig. 1. The striated muscle fibres are not present in the narrow membranous strips which connect the septum to the mantle and to the foot, only a little unstriped muscle—probably derived from the lateral septal muscles—being found between the epithelia in these areas. The septal pores are best studied in cross-section (*i.e.*, in longitudinal sections of the septum). They have been described by PELSENEER (1891) in *C. rostrata*, but not in any histological detail. GROBBEN studied the pores of *C. cuspidata* very carefully and PLATE stated that he found similar conditions in *C. obesa*. RIDEWOOD'S material was too badly preserved for him to determine the structure of the pores. In my own sections I have found essentially similar conditions in all three species examined. The conditions in *C. rostrata* will be described in detail, figs. 1 and 2 respectively, representing longitudinal and horizontal sections through the septum of this species in the neighbourhood of pores. Near the pores the epithelium is raised, becoming columnar with well-defined cells containing regularly arranged and prominent nuclei. As already noted by PELSENEER (1891) and GROBBEN, the inner or dorsal region of the pores is drawn out into the form of a valve (*v.*) with raised dorsally directed lips, the whole being sunk considerably below the dorsal surface of the septum (as shown clearly in fig. 1) in both *C. rostrata* and *C. cuspidata*. In *C. obesa*, however, the valve is relatively larger and its dorsal extremity lies on a level with the upper surface of the septum. In all cases the under surface of the pores is flush with the surface of the septum. The pores are ciliated in two regions on their inner apposed surfaces. There are prominent cilia, at least as long as the cells that bear them, in the extreme dorsal region (*d.c.*), as shown in figs. 1 and 2. Beneath this there is an unciliated area, rather greater in extent than the upper ciliated region, and below this again a second set of cilia (*v.c.*), which extend as far as the central opening of the pores. These cilia are much shorter than those in the dorsal region and are difficult to see, especially in *C. rostrata*. They are more easily distinguished in *C. obesa*, while GROBBEN has noted and figured them in *C. cuspidata*. Around the pores, and particularly in the valvular region, a well-developed sphincter of plain muscle fibres is present beneath the epithelium (figs. 1 and 2, *sp.*), and can easily be identified in both transverse and horizontal sections, the fibres being quite distinct from those of the septal musculature and resembling those of the lateral muscles. The presence of this sphincter has not hitherto been noted but is of some importance, as will be emphasised later.

Palps.—A transverse section through one of the posterior palps of *C. rostrata* is shown in fig. 4. The inner surface (*i.e.*) is lined with a columnar epithelium possessing a uniform coating of cilia, and this is continued for a short distance round either edge of the palp. There are none of the prominent ridges and furrows present on the more complex palps of the typical Lamellibranchs (see Yonge (1926b), which contains references to previous literature). The outer surface (*o.e.*) bears no cilia and is bounded by a thin pavement epithelium with ill-defined cell boundaries and few nuclei. There is a complete absence of mucous glands in both epithelia. Within the palp there is a considerable development of plain muscle (*mu.*) running both transversely and longitudinally, the latter being best shown in longitudinal sections, and being most conspicuous near the base and extending towards the tip of the palp under both epithelia. There are also connective-tissue strands and many wandering cells (*w.c.*), but the latter are never found in the epithelium, as is the case, for example, in Ostrea (Yonge (1926b)).

Mouth and Œsophagus.—The wide mouth is lined with a ciliated epithelium resembling that of the palps of which it forms a continuation. It is surrounded by a moderately thick layer of circular muscle fibres. The œsophagus, as shown in fig. 5, is roughly circular in cross-section, with its walls, especially on the anterior and posterior walls, much folded longitudinally, many of the ridges (*r.o.*) being of considerable height and projecting for some distance into the lumen. The columnar epithelium which lines the lumen is ciliated for the most part. Cilia, however, are not present on the lateral walls in the distal region of the œsophagus, as indicated in fig. 5, the epithelium there being bounded solely by the thin border cuticle, which is also present on the ciliated cells. Surrounding the œsophagus is an extremely thick layer of circular muscle (*c.m.*), as already observed by Pelseneer (1891), Grobben and Plate, a condition never found in the typical Lamellibranchs, where the musculature of the gut throughout is very poorly developed. There are also, here and there, muscle strands (*r.m.*) which radiate out from the interior of the ridges and pass through the circular muscle layer.

Stomach.—Longitudinal and transverse sections of the stomachs of *C. rostrata* and *C. cuspidata* respectively are shown in figs. 6 and 7. The epithelium consists of extremely narrow cells which vary greatly in length so as to form a series of high, longitudinal ridges (*l.r.*). Nuclei are small, and wandering, phagocytic cells are only very rarely found in the epithelium. The cells are filled with fine yellowish-brown granules, especially in the upper regions. There are no cilia in the stomach. At the junction with the œsophagus a thick, lamellated, cuticular layer is formed by the stomach epithelium and this is continued over the surface entire of the stomach, as shown in fig. 6 (*cu.*). The presence of this cuticle has been noted by both Pelseneer (1891) and Grobben, and it appears to be characteristic of the Septibranchs and to represent, very probably, an extension over the whole surface of the stomach of the smaller gastric shield (flèche tricuspide), which is found in all Filibranchs and Eulamellibranchs, where it is situated on the wall of the stomach directly opposite the opening of the style-sac. It provides a firm surface against which the head of the crystalline style can bear as it revolves (see Nelson (1918)). As previously noted (Yonge (1926b)), the gastric shield appears to be formed of the same material as the cilia or the border cuticle; it is certainly not secreted in the usual manner. In Cuspidaria also there is no evidence that the epithelium of the stomach is composed of anything but modified ciliated cells, and there is no evidence of secretion, while, as in Ostrea, there are fine transverse striations having the appearance of cilia extending through the cuticle about its junction with the epithelium. Probably, therefore, the stomach cuticle of the Septibranchs is merely an extension of the gastric shield of the other Lamellibranchs.

Surrounding the epithelium there is a well-developed layer of circular muscle fibres (*c.m.*), and fine fibres also pass between the cells of the epithelium, especially in the centre of the ridges. The presence of these muscles, and the fact that the stomach in Cuspidaria is practically free from the surrounding tissues, provide further important distinctions between the stomach of the Septibranchs and those of the other Lamellibranchs.

Digestive Diverticula.—The opening of the anterior and smaller duct of the digestive diverticula in *C. cuspidata* is shown in fig. 7 (*d.*). The actual duct is, when compared with that of a typical Lamellibranch such as Mytilus (List (1902)), Anodonta (Gutheil (1912)), Mya or Ostrea (Yonge (1923, 1926b)), exceptionally short and wide, approximating most nearly to the conditions found in the Teredinidæ (Sigerfoos (1908), Potts (1923), Yonge (1926a)), where, on account of the elongated shape of the animals, the digestive diverticula are spread out in a thin sheet round the ventral surface of the stomach, and their ducts, as a result, are short and wide. In the Cuspidariidæ, as in the other Lamellibranchs, the ducts are lined by a ciliated epithelium ; but neither phagocytes nor mucous glands are to be seen in this epithelium. The diverticula (*t.*) themselves are notable for their widely open lumina (*l.*) and the extent to which, especially in the regions nearest the ducts, they unite with one another to form a more compact structure than the separate acini characteristic of the majority of the Lamellibranchs. They tend more to the condition found in some of the more highly organised Gastropods, such as Doris, where the digestive "gland" possesses a large central chamber into which secondary cavities open on all sides. In structure, the cells of the tubules of the digestive diverticula do not vary essentially from the conditions found in the other Lamellibranchs (for full details and literature on this subject, see Yonge (1926a)). One kind of cell only is present, groups of large vacuolated cells, which frequently contain brown or yellowish-coloured inclusions of various sizes, being separated from one another by crypts of smaller, less vacuolated and darkly staining, cells (fig. 13, *o.c.* and *cp.*), but the latter, as previously shown (1926a), represent nests of young cells destined to replace the older cells which in time are destroyed and cast into the lumen. As in the digestive diverticula of the other Lamellibranchs, there is no evidence of secretion by any of these cells. The nuclei are of the characteristic shape, namely large, round and with a prominent nucleolus, and are most numerous in the crypts of young cells. No evidence of the presence of cilia was found either in fresh material or in sections, nor any sign of a border cuticle. It is not impossible, however, that, as in other Lamellibranchs, long retractile cilia may be borne on these cells in the living condition (see Potts (*loc. cit.*) and Yonge (1926a)). Around the tubules there is a thin bounding membrane, but no muscle such as surrounds the ducts (see fig. 7). The area between the tubules is conspicuous for the almost complete absence of connective-tissue strands, although there are occasional muscle fibres and a certain number of wandering cells. This is very different from the conditions found in the majority of the Lamellibranchs, where the digestive diverticula are embedded in a firm matrix of connective tissue.

Style-Sac.—The longitudinal section through the stomach of *C. rostrata*, represented in fig. 6, shows the position and relative size of the style-sac (*s.s.*) with its contained style (*c.s.*). The opening of the mid-gut anterior to it is only just indicated in the section (*b.g.*), and, owing to the S-shaped form of the separating ridge, there is the appearance in longitudinal section of three cavities; the narrow cavity (*c.g.*) shown on the left of the style-sac in fig. 6 is in reality a portion of the connecting slit between the style-sac and the gut. The extreme basal region of the style-sac, as shown by horizontal sections, is separate from the mid-gut. The style-sac is lined with an epithelium of large, cubical cells (*e.s.*) with well-defined cell boundaries and large round nuclei which occupy the centre of the cells. The latter are covered by a dense and very even coating of strong, bristle-like cilia; on the edges of this epithelium, where it passes into the typhlosoles which separate the lumina of the style-sac and the mid-gut, there are groups of tall narrow cells. In every particular, therefore, the structure of the style-sac in Cuspidaria resembles that of the other Lamellibranchs, which has been described in detail by NELSON (1918), EDMONDSON (1920) and YONGE (1923, 1926B) and other authors therein quoted. The epithelium of the separating ridge is ciliated and resembles that of the mid-gut.

The style itself is of the usual structure but is exceptionally short. It does not protrude far into the stomach, as is shown clearly in fig. 6, and clearly cannot act against the cuticular lining on the opposite wall of the stomach in the same way that the style in the typical Lamellibranchs acts against the gastric shield. The probable reasons for this will be discussed later; it may be mentioned here, however, that there is strong evidence that the style in the Septibranchs is a vestigial organ.

Mid-Gut and Rectum.—For a short distance after its separation from the style-sac, the mid-gut possesses a prominent typhlosole (fig. 8, *ty.*). The epithelium consists of tall cylindrical cells with long cilia and oval, basally situated, nuclei. Here and there are groups of narrow, darkly staining, and probably young, cells (*y.c.*). Around the epithelium is a thin circular muscle layer (*c.m.*). There is a complete absence of mucous glands in the epithelium, and phagocytic wandering cells are extremely rare. The typhlosole does not extend very far posteriorly and, for the greater part of its course, the mid-gut is a thin-walled oval tube. In the region of the heart, as indicated in text-fig. 1, it merges into the rectum, and the junction between the two is shown in fig. 9. The mid-gut is here much wider and is bounded by a thin ciliated epithelium which contains occasional mucous glands (*m.g.*). The circular muscle layer is extremely thin in this region. The mid-gut (*g.*) is united on its dorsal side to the rectum (*r.*), which has a characteristic structure, being bounded by tall, narrow cells bearing long cilia and interspersed with many mucous glands (*m.g.*), and surrounded by a comparatively thick circular muscle layer. After separating off from the mid-gut, it continues as a straight tube, circular in cross-section and with a narrow lumen.

It is worthy of note that, with the exception of the peculiar mode of union between the mid-gut and rectum, and the absence of phagocytes from the epithelium, both mid-gut and rectum in Cuspidaria have essentially the same structure as in the other Lamellibranchs—*e.g.*, Anodonta (GUTHEIL (1912)), Arca (MATTHIAS (1914)), Mya or Ostrea (YONGE (1923, 1926B)).

The structure of the gut in the three species of Cuspidaria examined is, in all essential details, identical.

B.—*Poromya.*

With the exception of the septum, the structure of the feeding and alimentary organs in *Poromya granulata* is little different from that found in Cuspidaria. The mantle is thin and in structure resembles that of Cuspidaria, the thickened ventral margins are bounded on their inner surfaces by a columnar epithelium which is ciliated but contains few mucous glands beneath it. The surface of the foot is covered with a ciliated epithelium except in the basal area. The septum, a portion of which is shown in longitudinal section in fig. 10, is bounded on either side by well-defined epithelia of cubical cells (*d.e.* and *v.e.*), neither of which show the presence of cilia in sections but possess a border cuticle. The septum is much thinner than in Cuspidaria and the musculature is much slighter. The fibres run mainly longitudinally and are *unstriped* and roundish in cross-section; in no part of the septum is there any indication of the presence of the striped muscle so characteristic of the septum of the Cuspidariidæ. Although it is impossible to be certain without embryological evidence, it may be that the septal muscles in Poromya are homologous with the lateral septal muscles in Cuspidaria, and that the septal muscles in the latter represent a separate development. As noted by RIDEWOOD in *P. malespinæ*, the septum is thicker and more muscular in the region behind the posterior branchial sieve.

The structure of the branchial sieves in *Poromya malespinæ* and *P. oregonensis* has been described by RIDEWOOD, and that of *P. granulata* in less detail by PELSENEER (1891). A transverse section through one of the posterior branchial sieves is shown in fig. 10. The filaments show essentially the same structure as the gill filaments of the other Lamellibranchs. Thick rods of "chitin" (*ch.*) are present beneath the epithelium on the sides of the filaments, the interior of which is filled with strands of "chitin" and also other connective tissue, and wandering cells (*w.c.*) are present both here and in the meshes of the somewhat vacuolated "chitinous" supporting rods. In the dorsal region of the filaments (*i.e.*, morphologically the interlamellar region) there are thick bands of longitudinal muscle (*l.m.*). There is no evidence of any interfilamentar junctions in *Poromya granulata*, nor were they found by RIDEWOOD in *P. oregonensis*, though this author noted their presence in *P. malespinæ*, as did PELSENEER (1888B) in *P. tornata*. Laterally the filaments are bounded by tall epithelial cells which carry long cilia (*l.c.*) which correspond to the lateral cilia of the typical filament. No frontal cilia can be distinguished in *P. granulata*. RIDEWOOD found them in *P. malespinæ* but not in *P. oregonensis*, but small latero-frontal cilia may be present. If so, they are quite different from the large straining latero-frontals found in the typical filament. The reasons for this modification of the ciliation of the filaments composing the branchial sieve will be discussed later.

A longitudinal section through the labial palps, mouth, œsophagus and stomach of *P. granulata* is shown in fig. 11. As will be observed, they do not differ essentially from those of Cuspidaria. The comparatively large palps (*a.p.* and *p.p.*) are ciliated on their inner surfaces only and contain numerous muscle strands; the mouth (*m.*) is large and leads into a wide ciliated œsophagus (*o.*), which is surrounded by a thick layer of muscle (*c.m.*). The stomach (*st.*) is large and its ridged walls are covered with a high columnar epithelium, which contains numerous fine, yellowish, refractile inclusions. A thick cuticular layer (*cu.*) lines all regions of the stomach, which is surrounded by a thick layer of circular muscle fibres. The structure of both ducts and tubules of the digestive diverticula resembles that of Cuspidaria. The style-sac is small and contains a small rounded style which does not project far into the stomach; the mid-gut is connected with the style-sac in the same manner, and has throughout the same structure as in Cuspidaria, being ciliated, round in cross-section in the region of the stomach, and becoming oval before it passes into the rectum. The rectum is narrow, ciliated and contains many mucous glands.

4. THE PROCESS OF FEEDING.

(i) *Mode of Life.*

Both Cuspidaria and Poromya live in mud into which they burrow. This process was followed in the laboratory by placing freshly caught animals in vessels containing sea water beneath which was a layer of mud. All three species of Cuspidaria and *Poromya granulata* behaved in essentially the same manner. No previous observations appear to have been made on *living* Septibranchs, so that the observations recorded in this section probably represent an extension to our knowledge concerning the habits and feeding mechanisms of the Lamellibranchia.

Burrowing is performed largely by means of the foot, which can be protruded from between the shell valves as a thin wedge which, when fully extended, is about the same length as the shorter axis of the shell. It can be directed either ventrally or anteriorly. The burrowing of *C. obesa* was carefully followed at Trondhjem. After being placed on its side on a layer of mud about 1 inch thick, the animal worked its way downwards until the anterior half of the body region (*i.e.*, as apart from the siphonal extension) of the shell was buried. At the same time the siphons with their surrounding tentacles (all tinged red in life) were protruded. About once a minute a violent contraction of the shell valves was observed, a contraction which was apparently connected with movements of the entire animal, whereby it was rotated slightly and at the same time pushed deeper into the mud. This movement was always accompanied by a sudden ejection of water through the *inhalant* siphon—a necessary safeguard if the septum is not to be severely strained or perhaps ruptured. The animals usually burrowed diagonally downwards and with considerable rapidity, though in a series of jerks with appreciable intervals between them. At each movement the posterior end of the animal was raised to an almost vertical position and was then lowered again, the animal at the same time sinking deeper into the mud.

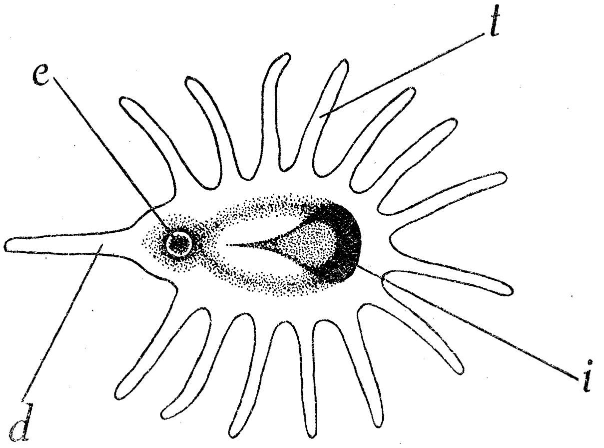
Finally, it burrowed so deeply that the end of the siphonal extension of the shell was flush with the surface of the mud, above which only the siphons projected, and, had not the previous movements of the animal been followed, it would have been difficult to distinguish these. The animals did not usually remain long in this position, but moved about on the surface of the mud, which soon became channelled and pitted as a result of their movements and burrowings. However deeply the animals burrowed the siphons were never covered. Similar habits were observed in the case of *C. cuspidata* at Kristineberg.

Poromya protrudes its siphons and their surrounding tentacles more readily than does Cuspidaria. As already noted, the latter are very long and, when extended, they lie backwardly directed over the posterior region of the shell covering some quarter of its surface; they may, however, erect themselves so that they stand out at right angles to the surface. They were often observed in movement. When placed on mud, Poromya burrows into it in much the same manner as *C. obesa*, using its long, extensile foot. Water appears to be forced out of the shell anteriorly, a procedure which may assist burrowing, as the animal was observed in this manner to force away mud from in front of its shell. During burrowing, the animal was observed to erect itself, posterior end upwards, in the mud and then turn slowly round, sinking into the mud as it did so, finally resuming a horizontal position. It then proceeded to move along and downwards in the channel it had made. All the movements, as in Cuspidaria, were sudden with appreciable intervals between them. As a result of this process, first the anterior end and finally the entire shell became buried beneath the mud. Gradually the animal assumed a vertical position, anterior end downwards, with only the siphons exposed, which lay flush with the surface of the mud, the two siphonal openings pointing directly upwards (text-fig. 4, *i.* and *e.*) and the tentacles (*t.*) lying flat on the surface of the mud, as shown in text-fig. 4.

(ii) *Function of the Septum.*

The movements of the septum were carefully followed with a view to determining the true function of this organ, which has been a matter of dispute.

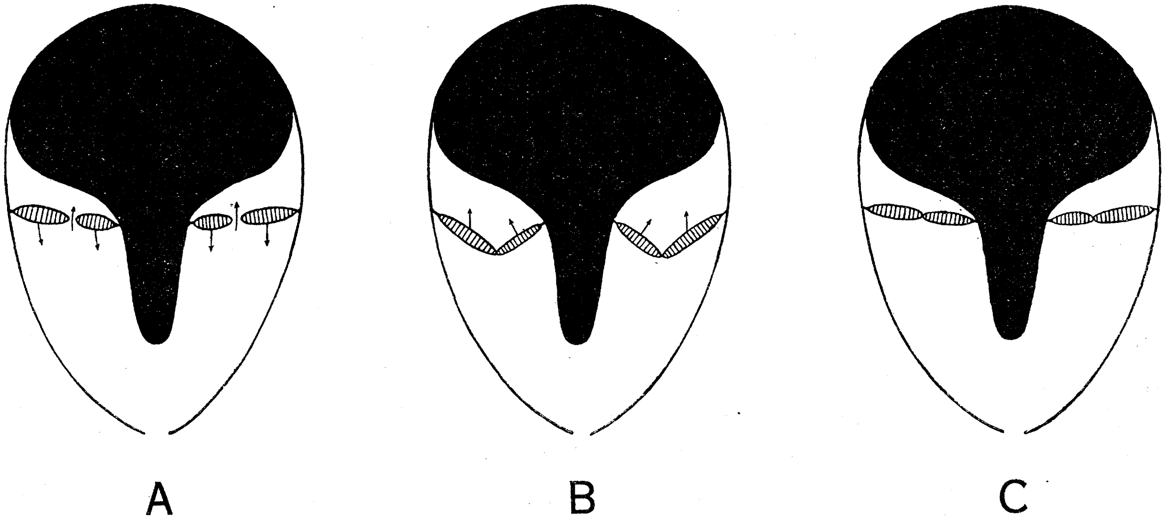
In the Septibranchs, unlike the other Lamellibranchs, there is no continuous current of water passing in through the inhalant, and out by way of the exhalant, siphon, even when these are fully extended and obviously functioning. Instead, there is an occasional widening of the opening of the inhalant siphon followed by a sudden intake of water, while at the same time the exhalant siphon opens to its fullest extent, water being expelled through the opening with considerable force, a fact which can be clearly demonstrated by introducing a suspension of carmine grains into the water around the exhalant siphon. The exhalant siphon in the Septibranchs has an exceptionally narrow opening, the lips of which are normally drawn together—a necessary precaution in view of the danger of small particles entering the siphon in the absence of a steady outflowing current. The inhalant and exhalant movements take place perfectly regularly in animals which are functioning normally with siphons fully extended. In *Cuspidaria obesa* they were observed to take place about six times per minute, and in *C. cuspidata* some four times a minute.



Text-Fig. 4.—*Poromya granulata*, siphons and surrounding tentacles fully extended, drawn from life. × 14. *d.*, dorsal, unpaired tentacle; *e.*, exhalant siphon; *i.*, inhalant siphon; *t.*, one of the fourteen paired tentacles.

By carefully removing the shell valves from the two larger species of Cuspidaria, these sudden movements were found to be caused by the movements of the septum, the action of which did not appear to be interfered with when the shell was removed. Contrary to what has hitherto been assumed from an examination of its anatomy, the septum when at rest, *i.e.*, between the periodic movements, does not lie stretched to its fullest extent ventrally. On the contrary, it is drawn up dorsally to the maximum degree, as shown in text-fig. 5, A. During rest the pores are open and the cilia with which they are lined beat inwards so as to cause a small, but perceptible, current upwards from the infra- into the supra-septal cavity, as indicated by the arrows in the diagram. With the pores still open, the septum is lowered to its fullest extent, when the pores are shut tightly, presumably by means of the sphincter of plain muscle. This condition is indicated diagrammatically in text-fig. 5, B. The valve which guards the entrance to the infra-septal cavity probably prevents water and food from being expelled by way of the inhalant siphon during the downward movement of the septum, while the opening of the exhalant siphon remains shut so that water cannot be drawn through in the wrong direction. As a result, therefore, of the downward movement of the septum, water is transferred from the infra-septal cavity by way of the openings provided by the pores into the supra-septal cavity. The septum is then drawn sharply upwards in the direction indicated by the arrows in text-fig. 5, B, with the pores still tightly shut—the pressure of the water against the dorsally directed valves preventing them from being forced open—until it regains its original position, when it comes to rest, with the pores still shut, as indicated in text-fig. 5, C. Finally, the pores reopen and the slow flow of water through them is renewed. Exactly the same procedure was observed in both *C. rostrata* and *C. cuspidata*.

The movements of the septum are invariably accompanied by the opening and extension of the siphons as already described, this taking place during the upward movement of the septum. The result of the septal movements is clearly to draw water and food matter into the infra-septal cavity, the water being later passed through the pores, slowly when the septum is at rest but quickly and in great quantities during its downward movements, and being expelled through the exhalant siphon. Thus, whatever the origin of the septum, in function it is analogous with the Lamellibranch gill, producing a current of water through the mantle cavity and drawing in food. But, owing to the more powerful, though intermittent, current produced by the septum, the food drawn in need not—and does not—consist solely of fine particles carried in suspension by the water, as in the ciliary feeding Lamellibranchs, but includes comparatively large particles or small animals which may be sucked in unawares as they pass the inconspicuous siphons, which are all that is exposed of the buried Septibranch.



Text-Fig. 5.—Diagram showing movements of septum. A, position of septum when at rest and preliminary to descending, current of water through pores indicated by upward directed arrows, downward movement of septum indicated by arrows; B, position of septum at end of downward movement, pores closed; septum now moves upward as indicated by arrows; C, position at completion of upward movement, pores still shut.

In Poromya the action of the septum does not appear to be so regular. Occasionally—not at perfectly regular intervals and not more than once a minute—a sudden sharp expulsion of water from the exhalant siphon was observed, so powerful, indeed, that if carmine grains were placed in the water they were shot away to a distance of about 4 or 5 cm. Unfortunately, probably owing to the weakness of its musculature, the septum of Poromya did not function after the shell valves had been removed for better observation. It proved impossible, therefore, to determine whether it acts in the same way as the septum of Cuspidaria, a matter of importance in view of the different types of musculature in the septa of the two families. The cilia of the branchial sieves were observed in the living state and seen to beat inwards, like those surrounding the pores of the Cuspidariidæ, and so cause a current of water from the infra- to the supra-septal cavity. The openings of the sieve can probably be closed by the contraction of the longitudinal muscles at the base of the filaments. The septum of Poromya is clearly unfitted for the powerful and frequent movements displayed by that of Cuspidaria; in structure it is too delicate, while the branchial sieves are not adapted to stand the same pressure of water as the pores with their dorsally directed valves.

The peculiar state of affairs in the Cuspidariidæ, whereby the septum between its periods of activity is in its shortest condition, *may* be connected with the peculiar type of muscle of which it is composed. The flat fibres are very long and wavy, and it may be that on stimulation they straighten out and so extend the septum. This appears a more probable explanation than that the septum is in a state of tonus for the greater part of its existence. Physiological experiments—unfortunately impossible with the limited material and apparatus at my disposal—are needed to determine in what state the septum of Cuspidaria is actually relaxed, while the physiology of the septal muscle would undoubtedly repay further investigation. One thing only is clear, that the development of striped muscle is correlated with the need for a continuous series of comparatively sudden movements—a state of affairs which has led to the development of striped muscle in the adductors of members of the Pectinacea and the Ostræacea, which constantly close the shell valves for the rejection of foreign particles or for swimming.

From morphological considerations, PELSENEER (1891) came to a conclusion as to the function of the septum which agrees fairly closely with my observations on the living animal. He states (p. 225), " Cette cloison, avec ses orifices, entretient assurément une active circulation d'eau sur la paroi intérieure du manteau (dorsalement au septum, comme chez *Poromya*): la cloison, en se contractant, ferme ses orifices et chasse l'eau par le siphon anal; lorsqu'elle se relâche, le siphon anal étant fermé, les orifices du septum s'ouvrent et l'eau entre dans la chambre supraseptale, la valvule du siphon branchial pouvant empêcher qu'elle sorte par ce dernier."

GROBBEN agreed in the main with the above statement, considering that so muscular an organ as the septum could not be concerned with respiration, but would be of great importance in changing the water in the mantle cavity, as it is clearly adapted for powerful movements, while in view of the cross striation of the muscle he thought it probable that very strong contractions could be accomplished. He goes on to state (p. 113) that, " Doch möchte ich glauben, dass nur von Zeit zu Zeit ein solch ausgiebiger, durch Contraction des Septums bewirkter Wasserwechsel stattfindet, dass im Uebrigen, wenn sich das Thier in Ruhe befindet, die wenngleich geringe Verbreitung von Wimpern an den Spalten, sowie im Mantel und am Fuss für einen langsamen Wasserwechsel sich als ausreichend erweist. Anderseits wird aber die geringe Ausdehnung von Wimperepithelien an den die Mantelhöhle begrenzenden Flächen wieder auf einen zeitweilig nothwendigen ausgiebigeren Wasserwechsel durch Contraction des Septums hinweisen." In view of his lack of observations on living animals this statement is remarkably accurate.

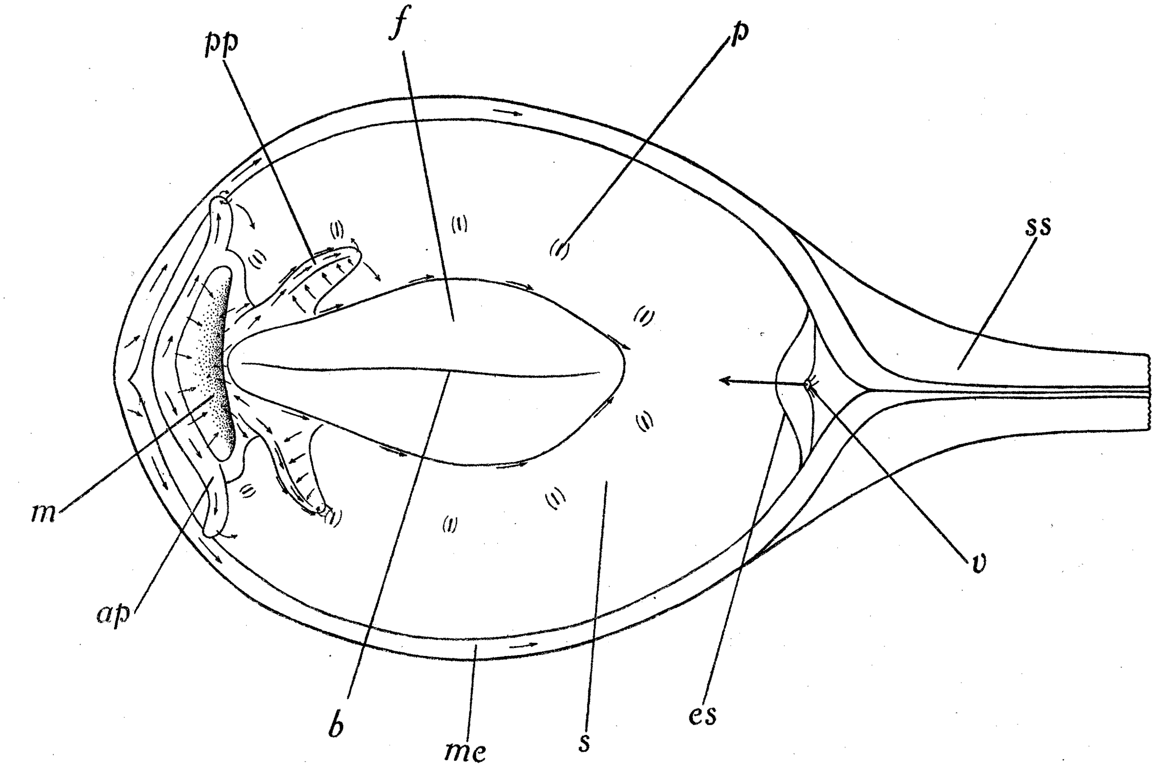
PLATE did not think it probable that the movements of the septum could be intermittent, with a musculature so enormously developed and histologically so highly differentiated. He thought, moreover, that the cilia on the pores did not serve to pass water through, but merely acted as a sieving apparatus preventing the passage of food particles into the upper cavity. These opinions have not stood the test of experimental verification.

DALL had a very different opinion as to the function of the septum. He considered (1889B, p. 443) that the septal muscles, "if not homologous with, at least perform the functions of, the siphonal retractors of ordinary Pelecypods, and in forms like *Poromya mactroides*, where the usual retractors are present, the siphonal septum is destitute of muscularity, or possesses it only to an inferior degree." Later (p. 445), referring to the septal pores in Cuspidaria, he stated, "I suppose that they serve to admit fresh water to the upper chamber, which I believe to be utilised in some, if not all, instances as a marsupium. It is probable that, by suitable muscular contractions, the septum will operate somewhat like the washer of a pump-valve, and that the upper chamber can be filled or emptied of its contained water at will. . . . I do not regard it (the septum) as in any way homologous with the normal ctenidia." He supports his theory that the supra-septal cavity is a marsupium where the ova develop (as quite possibly—though quite incidentally—they do, for the eggs are large and yolky and the developing embryo will not require food for some time after hatching) by stating that in young specimens of various species of Cuspidaria and Poromya the septal pores or sieves are partially or completely shut, only opening completely when the animals attain sexual maturity. It is clear, however, that if they were completely shut the animals could neither feed nor respire, since a through current of water could not be maintained. There appears to be no justification for DALL's views as to the function of the septum; his views with regard to its origin will be discussed later. RIDEWOOD makes no comment on the function of the septum.

(iii) *The Intake of Food.*

In the Cuspidariidæ, particles or small animals are drawn in through the inhalant siphon as a result of the water current caused by the sudden upward movement of the septum. The four club-shaped tentacles which surround the inhalant siphon may perhaps assist in this, for they are freely movable and bend inwards, in a claw-like fashion, around the opening of the siphon beyond which they extend; but this was never experimentally proved. Food passes through the valve leading into the infra-septal cavity, as indicated by the large arrow in text-fig. 6, and, as the animals always lie with the anterior end downwards, it will then fall down towards the mouth region. There are no cilia to guide it there such as are present on the gills of the ciliary feeding Lamellibranchs.

The palps probably serve to push the food into the mouth (though this was never experimentally demonstrated as it was in Poromya). Though they are small, especially the posterior pair which are absent in *C. obesa*, frequent movements were observed, as would be expected in view of their relatively well-developed musculature. In the majority of the Lamellibranchs, the two pairs of palps are closely applied to one another so that the mouth is obscured, but in Cuspidaria the large mouth is fully exposed and may extend considerably when food is swallowed and passed into the muscular œsophagus.



Text-Fig. 6.—Ventral view of *Cuspidaria cuspidata* with mantle lobes drawn back to expose septum, drawn from life. × 15. *a.p.*, anterior palps; *b*, byssus groove; *e.s.*, posterior end of septum; *f.*, foot; *m.*, mouth; *m.e.*, mantle edge; *p.*, septal pore; *p.p.*, posterior palps; *s.*, ventral surface of septum; *s.s.*, siphonal sheath; *v.*, valve between inhalant siphon and infra-septal cavity. Large arrow indicates direction of main food and respiratory current, smaller arrows indicate direction of ciliary currents.

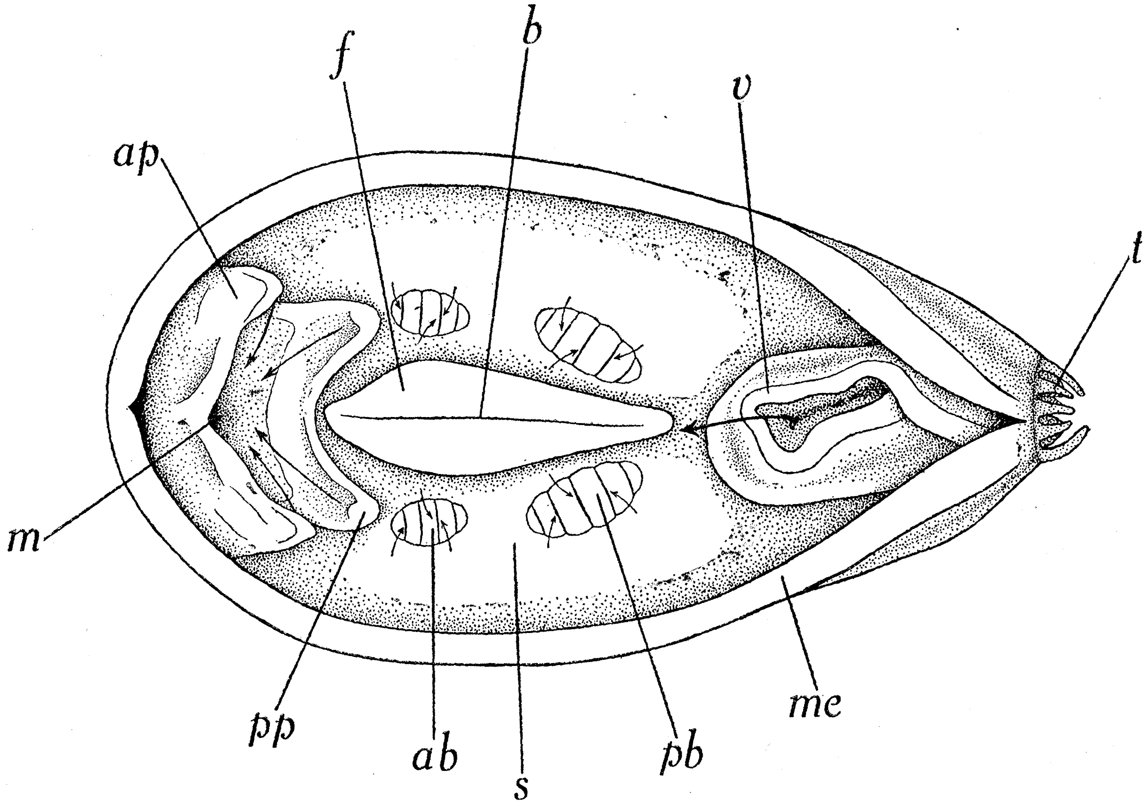
The cilia on the inner surfaces of the posterior palps (*p.p.*) beat in the directions indicated by the arrows in text-fig. 6. There is an outer lateral area on which the cilia beat towards the tip of the palp, the cilia on the remainder of the surface beating across it and carrying particles into this backwardly directed stream. On the anterior palps (*a.p.*), the cilia on the inner surfaces beat towards the tips of the palps. The cilia on the basal region of the palps, perhaps better described as the lips of the mouth, beat inwards, as do those within the mouth and lining the œsophagus. As a result of the action of the cilia on the palps, small particles are carried *away* from the mouth, being passed from the palps through the septal pores (as shown in text-fig. 6) or else in the case of the posterior palps, posteriorly by way of the foot. The cilia on the foot beat posteriorly and particles are carried to the hinder end, where they appear to be drawn through the posterior pair of pores. As we have seen, cilia are absent on the greater part of the surface of the mantle, only the thickened marginal ridges (*m.e.*) possessing them. These cilia beat posteriorly and carry fine particles to the hind end of the mantle cavity in the region beneath the valve. This ciliary current corresponds to the "untere Rückströmung" originally described by STENTA (1903) and which has been shown invariably to be present in the ventral region of the mantle in all Lamellibranchs (see especially KELLOGG (1915)). This current is always concerned with the cleansing of the mantle cavity and the rejection of useless particles, and it is noteworthy that it is the only ciliary current in the mantle cavity of the Septibranchs which clearly corresponds to a current found in the other Lamellibranchs. Particles are massed together at the posterior end of the mantle cavity as the result of its action and, as in other siphonate Lamellibranchs, are probably disposed of by sudden contractions of the shell valves, which force out water and suspended matter through the *inhalant* siphon.

Such cilia as are present in the infra-septal cavity, *i.e.*, on the mantle edges, on the foot, on the palps and round the pores, are therefore all concerned, not with feeding, but with the removal of fine particles from the mantle cavity. This cleansing is obviously of great importance to animals which live in mud and are consequently in constant danger of being clogged with fine particles. Feeding is the result, exclusively, of the *muscular* action of the siphons, the septum, the palps and the anterior region of the gut (aided perhaps by cilia to a slight degree in the last instance).

In the supra-septal cavity there are, on the surface of the visceral mass, cilia which beat posteriorly and carry particles towards the exhalant siphon. In living specimens of *Cuspidaria rostrata* and *C. cuspidata*, moreover, a sparse ciliation was observed on the dorsal surface of the septum (never on the ventral surface), as a result of the action of which particles were carried backwards. There are no cilia on the mantle surface. All cilia in the supra-septal cavity, therefore, serve to carry away particles and also, no doubt, assist the cilia of the septal pores in maintaining a slight circulation through the mantle cavity when the septum is at rest.

In Poromya, as shown in text-fig. 7, conditions are essentially the same. Owing to the fact that the inhalant siphon (see text-fig. 4) has a wider opening, larger particles are drawn in than in Cuspidaria. When the animal is sunk in the mud and the siphons are functioning, the inhalant siphon does not project above the surface and its dorso-ventrally compressed aperture is normally shut, owing to the coming together of the rounded lips. The exhalant siphon is much smaller, is round and protrudes slightly as a roundish papilla, about 1 mm. in diameter. Pieces of the gonad of Pecten about a millimetre across were placed on the inhalant siphon of a living Poromya. At first they were refused and pushed away by the surrounding tentacles, but on the second attempt they were drawn in slowly through the siphonal opening, being seized by the lips and slowly passed into the infra-septal cavity. A few moments later the inhalant siphon opened to its fullest extent and no sign of the food could be seen. A piece of coagulated blood, some 2 to 3 mm. long and 1 mm. wide, from Myxine was later fed to the same animal and was similarly taken in.

It was observed that food was taken into the inhalant siphon by a series of movements clearly related to the movements of the septum, or, if the food was not too large, by one sudden inrush. Both siphons were opened to their fullest extent, there was a sudden ejection of water through the exhalant siphon (showing that the septum had contracted) and at the same time matter was pulled into the inhalant siphon. After a series of these movements the larger food masses were finally taken completely into the mantle cavity. During the process of food intake, the lips of the inhalant siphonal opening were fully expanded and raised to a height of some 2 or 3 mm., *i.e.*, above the exhalant siphon.



TEXT-FIG. 7.—Ventral view of *Poromya granulata* with mantle lobes drawn back to expose septum, drawn from life. × 20. *a.b.*, anterior branchial sieve; *a.p.*, anterior palps; *b.*, byssus groove; *f.*, foot; *m.*, mouth; *m.e.*, mantle edge; *p.b.*, posterior branchial sieve; *p.p.*, posterior palps; *s.*, septum; *t.*, tentacles surrounding siphonal openings; *v.*, valve between inhalant siphon and infra-septal cavity. Large arrows indicate direction of food intake, small arrows the passage of the water current through the branchial sieves.

If too much food was taken in, then the surplus was frequently ejected—as a result of sudden contractions of the shell valves—but only if the food was still, at any rate partially, in the inhalant siphon and had not passed the valve leading into the infra-septal cavity.

As in the Cuspidariidæ, the food falls down towards the mouth. There it is at once pushed into the mouth by the palps, which are both larger and more active than those of Cuspidaria. After placing pieces of the gonad of Pecten upon them, both pairs of palps immediately curled inward, as indicated by the arrows in text-fig. 7, and quickly pushed the food into the large mouth, which opened wide to receive and swallow it. There is thus not the slightest doubt concerning the muscular function of the palps in Poromya.

The only cilia whose presence could be identified in the *living* animal were those on the branchial sieves, and it is significant that the frontal cilia, concerned with food collection in the other Lamellibranchs, have been lost, while the lateral cilia, concerned with the creation of the water current, are alone retained. Sections show the presence of cilia on the palps, on the mantle edges and on the foot, but these are evidently too small and their action too feeble to be easily identified by placing carmine upon them. The observations, moreover, had to be made on one specimen only and without the aid of a binocular microscope. In view of the similarity in the feeding habits and the structure of the feeding organs in the two genera, there can be little reason to doubt that the cilia in the mantle cavity of Poromya serve the same function as those of Cuspidaria, namely, to clear the mantle cavity of small particles, and to maintain a slight water current when the septum is at rest.

(iv) *Passage of Food through the Gut.*

Food is carried through the œsophagus largely by the peristaltic movements of its thick muscular layer. In Poromya, food was occasionally rejected through the mouth, apparently by antiperistaltic movements.

In the stomach the food is broken up into small fragments. The stomach in the Septibranchs is a crushing gizzard, as its structure (see figs. 6 and 7) plainly indicates. The powerful musculature serves to contract its walls violently so that the ridges with their thick cuticle come together and crush up the large food masses which lie between them. It often proved difficult to section the stomach of both Poromya and Cuspidaria owing to the mass of chitinous fragments and sometimes sand grains which filled the lumen. Occasionally, as shown in text-fig. 3, whole Crustacea were found in the stomach. The crushed-up fragments must either be pushed into the wide ciliated ducts of the digestive diverticula (fig. 7) or into the opening of the mid-gut. It is necessary that particles having food value should be passed into the former opening, for in the digestive diverticula alone can they be digested, whereas the useless fragments of chitin, sand, and the like will need to be passed into the mid-gut. In the stomach of the ciliary feeding Lamellibranchs there is a highly efficient sorting mechanism (see Nelson (1918), Yonge (1923, 1926b)), but in the stomach of the Septibranchs there is no such mechanism, and it is not easy to see how such a separation takes place and exactly how food is separated from fæcal matter. Within the tubules of the digestive diverticula it is quite possible that, as in other Lamellibranchs, a circulation is maintained by the action of long, retractile cilia which cannot be distinguished after fixation and may be withdrawn when fresh material is pressed out under a coverslip for examination. The presence of these cilia is rendered the more probable owing to the lack of a muscular network round the tubules, such as is found in the Crustacea (see YONGE (1924) for details and literature), and serves, by its alternate contractions and relaxations, to produce a circulation through the tubules of the " hepatopancreas."

Material is probably passed through the short mid-gut chiefly by ciliary action, for there is very little muscle and cilia are abundant (see fig. 8); the same is probably true for the rectum, though the more powerful encircling muscles in this region may aid in defæcation. Both of these regions of the gut, therefore, possess a similar function, as well as a similar structure, to that found in the other Lamellibranchs. The fæces are discharged into the posterior region of the supra-septal cavity and will be quickly ejected through the exhalant siphon.

5. THE NATURE OF THE FOOD.

Alone amongst the Lamellibranchia, the Septibranchia are carnivorous. PELSENEER (1891) originally came to this conclusion, stating (p. 219) that " *Poromya* est carnivore; la longueur de l'ouverture palléale antérieure, la largeur de la bouche et de l'œsophage, et la brieveté de l'intestin s'accordent avec ce régime." Later (p. 224) he writes, " *Cuspidaria* est franchement *carnivore*. Dans l'estomac de *C. rostrata*, j'ai trouvé seulement un animal d'aspect déjà un peu défiguré, mais oculé et à revêtement de spicules. C'est là, avec *Poromya*, une exception parmi les Lamellibranches; ce régime s'explique par l'habitat de ces deux genres dans des eaux profondes où ne s'étend pas la vie végétale. Les mouvements du septum musculaire aident probablement à attirer la proie *morte* dans le manteau (qui est assex ouvert), et la largeur de l'œsophage en facilite l'ingestion."

PLATE found the remains of Copepods and Annelids in the stomach of *C. obesa*, but continues by stating " Ich . . . glaube aber nicht, dass die Cuspidarien sich hinsichtlich der Ernährung irgendwie von den übrigen Muscheln, die kurz als Planktonfresser bezeichnet werden können, unterscheiden." Neither the extent of PLATE's investigations (sections through a single specimen of *C. obesa*) nor his knowledge of the feeding of the Cuspidariidæ are of sufficient significance for much weight to be attached to the above statement.

PELSENEER (1911) in his account of the Cetoconcha (Silenia) in the " Siboga " collections —the only complete specimens of this rare genus as yet examined—states (p. 79) that the stomach contains " des débris de Crustacés " adding that Cetoconcha is thus, like the other Septibranchs, a carnivore.

My own investigations bear out fully PELSENEER's conclusions. The stomach contents of two living specimens of *C. cuspidata* were examined at Kristineberg. One consisted of a Crustacean (probably, in the opinion of Dr. M. V. Lebour, an early stage of a parasitic Copepod) in almost perfect condition, 2·2 mm. long and with a carapace 1 mm. wide, and also of the empty shell of an Ostracod 1 mm. long and 0·36 mm. broad. The other consisted chiefly of the remains of a Crustacean embedded in a mass of sand grains, the whole measuring some 0·9 mm. in length and 0·45 mm. in breadth. In neither stomach was there the slightest indication of that suspension of fine particles and plankton which invariably constitute the stomach contents of the ciliary feeding Lamellibranchs (see Hunt (1925) and Savage (1925) for accounts of the stomach contents of *Pecten opercularis* and *Ostrea edulis* respectively).

The manner in which the sand grains were embedded in the food indicates the power of the gizzard and also suggests that the presence of sand grains may assist in the breaking up of the food. A similar suggestion has been made in the case of the ciliary feeding Lamellibranchs, which take in sand grains, but the almost complete absence of muscle in the gut, and the high development of the ciliary sorting mechanism in the stomach, of these animals provide conclusive evidence against this theory. The welding together of the food and the sand grains *may* be assisted by the substance of the style (for there are no mucous glands in the œsophagus or stomach)—indeed, in view of the almost total absence of finely divided or starchy foods, this appears to be the only function which the style can perform.

In Poromya also, as shown in text-fig. 3, Crustacea are taken whole into the stomach. In sections of both Poromya and the three species of Cuspidaria, the stomach was frequently found packed with fragments of animals, usually Crustacea, while the mid-gut contained fragments of chitin, spines, limbs, etc., all clearly of either Crustacean or Annelid origin. There was never any evidence of the presence of vegetable matter or fine plankton organisms in any part of the alimentary canal.

To what extent the Septibranchs depend on living or dead prey must remain uncertain. Pelseneer, as quoted above, suggests that the latter form the principal food, and, in view of the sluggish habits of the Septibranchs, this is quite possible. An active animal could doubtless easily escape them, especially since the Septibranchs have no means of actively seizing their prey, unless it chanced to swim too near to the aperture of the inhalant siphon and so was drawn in by the sudden and unexpected current. For the most part we can imagine the Septibranchs moving about slowly through the mud and sucking in the small dead or dying animals which they encounter. In deeper waters they will not have the opportunity, and neither there nor in shallower waters the power, of swallowing the diatoms, peridinians and other fine phytoplankton organisms which form the food of the great majority of the Lamellibranchs.

6. Assimilation.

A number of feeding experiments were carried out, specimens of Cuspidaria being placed in water containing, in suspension, iron saccharate (some of which passes into colloidal solution), Indian ink or the coagulated blood of various fish. Poromya was fed directly with pieces of the coagulated blood of Myxine and with pieces of the gonad of Pecten, a second specimen being placed in a suspension of iron saccharate in sea water. After suitable periods the animals were fixed in appropriate ways.

After feeding *C. obesa* with iron saccharate and treating in the usual manner (for details see YONGE (1926A)) after periods of 6, 9 and 12 hours and one day, and subsequent sectioning, iron was found to be present in the mantle cavity, where it was attached to all the ciliated areas, especially the foot and the margins of the mantle, *i.e.*, clearly in process of being removed from the mantle cavity. It was also present in the lumen of the stomach, the mid-gut and the rectum, but it was never found in the epithelial cells of these regions. It was absorbed solely by the cells lining the tubules of the digestive diverticula, in the manner shown in fig. 12, which represents the condition found subsequent to feeding for 6 hours. The iron saccharate is taken into large vacuoles (*f.*) within the cells and never appears in a diffuse or finely granular condition. Precisely the same state of affairs was found in Nucula, Mya, Teredo (YONGE (1926A)) and in Ostrea (YONGE (1926B)), and, as was pointed out in the former paper, there is reason to suppose that this method of ingestion in large vacuoles is an indication of the presence of *intracellular* digestion. Iron saccharate is absorbed in a diffuse or finely granular condition in animals—Annelida or Arthropoda, for example—in which digestion is exclusively *extracellular*.

The same conditions were found in Poromya, an animal fixed 9 hours after it had been placed in a suspension of iron saccharate showing the presence of iron lying on the cilia, on the mantle edges, on the foot, on the palps, and passing through the branchial sieves into the supra-septal cavity (evidence that these cilia serve the same function as those in Cuspidaria). It was also found free in the lumen of the stomach and of the gut, but it was absorbed *exclusively* in the cells of the tubules of the digestive diverticula, and there only in large vacuoles.

Specimens of *C. obesa* which had been placed in a suspension of Indian ink and later fixed in Bouin, showed, in sections, the presence of small quantities of Indian ink lying on the cilia in the mantle cavity, and also being passed into the supra-septal cavity by way of the pores. A few particles were found in the stomach lying against the cuticle, but none in the digestive diverticula.

Previous feeding experiments using the blood corpuscles of fish (YONGE (1926A, 1926B)) have shown that these are taken in freely by Lamellibranchs and are ingested. With the exception of Teredo, however, in all the Lamellibranchs studied they were ingested by the phagocytes which abound in the epithelium, the surrounding tissue and the lumen of the gut; especially were they so ingested in the stomach, the ducts of the digestive diverticula and the mid-gut. They were seized while still in the lumen by these phagocytes, which ingested them and then carried them through the epithelium and into the connective tissue. Within the phagocytes they are slowly digested. Only in the case of Teredo, where, as we have seen, the ducts of the digestive diverticula are exceptionally short and wide, did the blood corpuscles succeed in passing into the tubules of the digestive diverticula, where they are ingested by the cells.

In the Septibranchs, histological examination revealed the almost complete absence of these wandering phagocytic cells, and the fate of the coagulated blood corpuscles with which they were fed was, therefore, of the greatest interest. Specimens of all three species of Cuspidaria were treated in this manner. *C. obesa* removed and fixed in Bouin after 12 hours of such feeding showed the presence, after sectioning and staining with iron hæmatoxylin and acid fuchsin, of blood corpuscles ingested in the cells of the tubules of the digestive diverticula and in no other region. The same conditions were found in *C. rostrata* after similar treatment. In both of these experiments the blood of cod was used.

Fig. 13 shows the appearance in cross-section of a single tubule from the digestive diverticula of a *C. cuspidata* which had been in a suspension in sea water of the coagulated blood of a wrasse for 10 hours. The animal was fixed in Bouin and the section figured was stained with Mann's methyl-blue eosin combination. The effect is very striking, the ingested blood corpuscles staining a bright red while the cytoplasm colours blue; the nuclei (*n.t.*) are blue except for the prominent nucleoli, which stain red. Great numbers of the blood corpuscles are ingested, the great majority (*b.c.i.*) having already been carried towards the base of the cells; one, however, remains free in the lumen (*b.c.l.*) while several others are in process of ingestion (*b.c.p.*), apparently sinking into the protoplasm of the cells rather than being actively enclosed by it. Ingestion takes place in the older, vacuolated cells (*o.c.*) and not in the crypts of young, darkly staining cells (*cp.*). In many cases the ingested blood corpuscles can be seen lying within clearly defined vacuoles. Although some of the ingested corpuscles lay against the basement membrane (*b.m.*) of the tubules, in none of the sections was there any evidence of their being carried away by wandering phagocytic cells, as was observed in Teredo (YONGE (1926A)). Perhaps this occurs later in digestion, but lack of material and the danger of the animals dying if they were left for too long a period after feeding, prevented any more prolonged feeding experiments from being undertaken.

Blood corpuscles were found in small numbers in the lumina of different regions of the gut, but *never* ingested in phagocytes.

Similar results were obtained in Poromya, blood corpuscles from the blood of Myxine being ingested exclusively in the tubules of the digestive diverticula. In this case, moreover, swallowed blood corpuscles were obtained from the stomach 4 hours after feeding, as a result of antiperistaltic regurgitations from the stomach. They were examined and found to be undamaged—showing the lack of proteases and lipases in the stomach—and were in no case being ingested by phagocytes, as was found to occur in the stomach lumen of *Ostrea edulis* 3 hours after the beginning of feeding (YONGE (1926B)). There were no phagocytes in the regurgitated fluid.

It will be observed that, while matter in colloidal solution, such as iron saccharate, or in coagulated masses, such as blood, is taken within the alimentary canal, the finely divided particles of Indian ink, or of iron saccharate in suspension, though they are drawn into the mantle cavity by the action of the septum, are almost entirely removed from it by the cleansing cilia and very little enters the gut.

As a result of these feeding experiments—though it is to be regretted that more could not be carried out—it can be stated definitely that the only absorptive surface in the gut of the Septibranchs, as in the other Lamellibranchs, is provided by the tubules of the digestive diverticula. There both soluble matter, such as iron saccharate, is absorbed, and comparatively large particles, like blood corpuscles, are ingested, the latter being, presumably, digested intracellularly. In the ciliary feeding Lamellibranchs this localisation of the absorptive surface is compensated for by the presence of the phagocytes in the lumen and epithelium of all regions of the gut, but this is not the case in the Septibranchs.

The reason why such comparatively large particles as blood corpuscles pass into the digestive diverticula of the Septibranchs but not into those of the other Lamellibranchs (with the exception of Teredo) is clearly due to the absence of phagocytes in the gut and in the ducts of the diverticula, which could ingest them prior to their entrance into the tubules, and to the exceptionally short and wide ducts which lead from the stomach into the digestive diverticula.

As is well known, the tissues of the Lamellibranchs are normally exceptionally rich in glycogen, a fact which has been recorded by many investigators (see especially RUSSELL (1923)), and there is no doubt as to the primary importance of this reserve food substance in the metabolism of these animals. In previous work on Ostrea (1926B) attention was drawn to this fact and to the striking degree to which the digestive processes are specialised for dealing with carbohydrate food. In the Septibranchs, however, the food is not predominantly carbohydrate ; on the contrary, it must be largely protein, and the special digestive mechanism for dealing with carbohydrates provided in the style is much reduced. It would, therefore, appear probable that glycogen is not stored to any great extent in the Septibranchs. In order to obtain some evidence on this point, one freshly caught specimen of *C. obesa* was fixed in Carnoy's fluid and sections prepared which were treated with the Langhan's iodine method. No indication of the presence of glycogen was found in any of the sections. Thus we have evidence of an alteration in the metabolism of the Septibranchs consequent on their assumption of a carnivorous diet.

7. GENERAL DISCUSSION OF RESULTS.

This research is particularly interesting in its bearings on the general problems of feeding and digestion in the Lamellibranchia. This class of the Mollusca possesses, on the gills and the palps and in the stomach, the most elaborate and most efficient ciliary feeding mechanism found in the entire animal kingdom. Associated with this are the many peculiarities, both morphological and physiological, of the gut, to which reference was made in the introductory section. It has been shown, I think conclusively, in the foregoing account that the Septibranchs are carnivorous and that feeding mechanisms, an alimentary system and digestive processes, have been evolved for dealing with large food masses, thus providing a striking example of the evolution of function.

In place of the gills has evolved the muscular septum. This performs the same function in maintaining a circulation of water through the mantle cavity, being assisted in this by the vestiges of the gill ciliation in the lateral cilia, on the filaments of the branchial sieve in Poromya, and in the cilia around the pores in Cuspidaria. But it also, by its sudden movements, draws in large masses of food, which the continuous, but slowly moving, current created by the gill cilia could never do. The large food masses introduced into the infra-septal cavity in this manner are pushed into the mouth by the small, but very muscular, labial palps. The exceptionally highly developed ciliary mechanism on the ridged palps of the other Lamellibranchs, which acts by rigorously sorting the particles passed on to it from the gills, rejecting the larger particles and passing the smaller ones into the mouth (for details see WALLENGREN (1905) and YONGE (1923, 1926B)), has been lost, the few remaining cilia being concerned exclusively with the rejection of fine particles which might impede the working of the gut. That this ciliation is of importance is shown by the fact that these ciliated tracts are retained, even though the palps, as in the case of the posterior pair in *C. obesa*, have been lost. A similar rôle is played by the remaining cilia in the mantle cavity, on the foot and on the ventral margins of the mantle. The survival of these cilia and no others is clearly correlated with the danger which both the Septibranchs and the other Lamellibranchs face in common, that of being silted up by fine particles of mud or sand. Mucous glands, as universal as cilia in the other Lamellibranchs, are confined to the ciliated regions in the Septibranchs.

The foregut of the Septibranchs is *totally unlike* that of the Lamellibranchs which feed on fine particles. Although the œsophagus possesses cilia, these are clearly of little importance, food being carried along by the peristaltic movements of the thick surrounding muscle, so conspicuously absent in the other Lamellibranchs. The stomach is even more highly specialised and acts as a crushing gizzard, for which function its ridged walls, cuticular lining, surrounding muscles and freedom from the surrounding tissues, all combine to fit it—clearly a very different structure from the complex ciliated organ of the other Lamellibranchs, which is almost devoid of muscle.

The crystalline style in the Septibranchs has no longer the great importance that it possesses in the other Lamellibranchs. In the latter, by its rotation it assists in the movement of the fine particles through the gut, and by the dissolution of the head in the stomach it sets free carbohydate-splitting enzymes (NELSON (1918, 1925)), and also maintains the fluid in the stomach near the optimum hydrogen-ion concentration for the action of the enzymes (YONGE (1925, 1926B)). In the Septibranchs, owing to the contractions of the gizzard-like stomach, the style can no longer project freely across the stomach and bear against the gastric shield on the opposite wall; on the contrary, it barely projects out of the short style-sac in which it is secreted; it would clearly be worn away by the contraction of the stomach were it to project any farther. The cuticular lining of the stomach probably represents an extension over the entire stomach of the gastric shield, which covers only a small area in the stomachs of the other Lamellibranchs.

The shortness and exceptional width of the ducts leading into the tubules of the digestive diverticula are correlated, no doubt, with the comparatively large fragments forced into them by the squeezing action of the stomach. The wide lumina of the tubules, especially in the neighbourhood of the ducts, are to be attributed to the same cause.

The only regions of the gut which perform essentially the same function as in the other Lamellibranchs, the mid-gut and the rectum, show no structural modifications.

The absence of the wandering phagocytes which form so conspicuous a feature in the gut of the ciliary feeding Lamellibranchs is very striking, and there can be no doubt that these have developed owing to the necessity of dealing with food particles too large to enter the ducts of the digestive diverticula, and which cannot, owing to their nature, be digested by the amylase or the glycogenase from the style, which represent the only extracellular enzymes present in the gut of the Lamellibranchs. In the Septibranchs, where there are no particles of this size to be dealt with (the blood corpuscles were swallowed in the form of coagulated masses, and not individually), and, moreover, where the epithelium of the stomach is covered with a thick layer of cuticle, there is clearly no scope for the action of these phagocytes. Furthermore, the widely open ducts of the digestive diverticula allow food particles of the order of magnitude normally seized by phagocytes (*e.g.*, red blood corpuscles) to enter the tubules where they are ingested.

There is no evidence of any elaboration of extracellular enzymes other than those in the style, and these, on account of the carnivorous habit, must be of very little use to the animal. Indeed, there is a close correlation, borne out still further by the conditions found in the Septibranchs, between the degree of development of the style and a finely divided and largely vegetable food. Thus in the Gastropods the style is best developed in such animals as Crepidula (Mackintosh (1925)), which feed by ciliary mechanisms (Orton (1912)), and is lost in the carnivorous species, to be regained in the Thecosomatous Pteropods which, descending from carnivorous ancestors, have taken to a pelagic life and developed ciliary feeding mechanisms (Yonge (1926c)).

The tubules of the digestive diverticula, like those of the other Lamellibranchs (Yonge (1926a)), show no histological evidence of secretion, nor did the examination of blood corpuscles which had been in the stomach for four hours indicate any action by digestive enzymes. It appears, therefore, that, though capable of modifying their feeding mechanisms and the structure of their alimentary canal, *the Septibranchs have been incapable of modifying their digestive processes.* The Lamellibranchs have retained the power of intracellular digestion to a far greater extent than the other large groups of the Mollusca, which is clearly correlated with the fact that in the Lamellibranchs alone are fulfilled the two essential conditions of intracellular digestion, namely, the maximum of ingesting surface (in the ramifications of the tubules of the digestive diverticula) and the presentation to this of fine particles which can be directly ingested, the latter being ensured by the rigorous sorting action of the ciliary mechanisms on the gills and the palps and in the stomach. In the Septibranchs the second of these conditions is absent, and it is only by the crude method of breaking up the large prey in the stomach that small particles for passage into the diverticula can be obtained. In no other metazoan carnivore, with the exception of certain of the Turbellarians (see WESTBLAD (1923), WILLIER, etc. (1925)), where the gut cells are amœboid and unite to form syncytia during absorption, when they take in water and swell out so that they surround the soft food which they ingest intracellularly, is there this complete lack of a preliminary protein digestion. In the Cœlenterates, though digestion is largely intracellular, there is invariably a preliminary breaking down of the prey by means of an extracellular protease. In the Septibranchs, there are no modifications other than the crushing action of the stomach, and they must still rely upon exactly the same methods of digestion (less the digestive action of the phagocytes) which have served the Lamellibranchs, which possess highly developed ciliary feeding mechanisms. It seems probable that they must, at least, have developed a more powerful intracellular protease in the digestive diverticula than is found, for example, in Ostrea, in which, as in probably all similar Lamellibranchs, digestion is primarily concerned with carbohydrates.

The Septibranchs are a small group. It seems probable that this is due to their failure to develop methods of digestion suitable to a carnivore, and to the comparative failure of their extremely interesting feeding mechanism. They have achieved the remarkable feat of transforming a feeding mechanism and correlated alimentary system and digestive processes, which together represent the highest developments of their kind in the animal kingdom for dealing with finely divided food, largely of a vegetable nature, into mechanisms for dealing with large food masses of animal origin. It is not surprising, therefore, that the result has been largely in the nature of a makeshift.

The question of the origin of the Septibranchs is one of the greatest interest. It follows from the preceding statements that they cannot have evolved in the face of keen competition. The evidence we possess points to their having evolved in deep water. All the known Septibranchs are marine and inhabit considerable depths, the Cetoconchidæ, in particular, being abyssal animals. The two specimens of *Cetoconcha* (*Silenia*) *sarsi* taken by the "Challenger" came from depths of 1,950 and 2,650 fathoms, and the single specimen of *Poromya* (*Verticordia*) *tornata* from 1,850 fathoms. It seems not improbable that in the greatest depths the ciliary feeding Lamellibranchs cannot exist owing to the lack of phytoplankton. Animals which happened to pass into these deep waters would die, unless it chanced that feeding mechanisms capable of dealing with comparatively large animal prey, either living or dead, were evolved. In the case of the Septibranchs this happened, and, as a result, they spread downwards into the abyssal regions where the sparseness of the animal population and the consequent lack of serious competition allowed them to survive in spite of the inadequate nature of their organs of feeding and digestion. As they became more specialised and so more capable of surviving the keen competition for food which exists in the shallower seas, they worked their way back into shallower water. It is noteworthy that the most highly specialised of the three families of the Septibranchia, the Cuspidariidæ, are found in the shallowest waters. The three specimens of *C. cuspidata* obtained in the Gullmars Fjord were all taken in depths of about 50 metres along with many other Lamellibranchs.

The supposition that the Septibranchs are a comparatively recent group is borne out by the paleontological evidence; thus in ZITTEL's text-book (1913) it is stated that the Cuspidariidæ range back to the Jurassic and the Poromyacidæ only to the Cretaceous. The smallness of the group at the present time points to their comparative failure.

The origin of the septum has been a matter of dispute, DALL (1888, 1889B, 1894, 1895) maintaining that it is pallial in origin or else an anterior prolongation of the septum dividing the inhalant and exhalant siphons, while PELSENEER (1888A, 1889, 1891, 1911) considers it to be branchial. In support of this view he states that the nervous supply comes from the branchial nerve and not from the siphonal or pallial nerve, and concludes that the septum represents the inner demibranch only. PELSENEER has received the support of GROBBEN, who regards the anterior part of the septum, at least, as of branchial origin; but PLATE agrees with DALL, since he found that the septum of *C. obesa* was innervated by a nerve leaving the cerebral ganglion side by side with the visceral commissure and not by a branchial branch of the visceral nerve. PELSENEER (1911) thinks he is mistaken in this. RIDEWOOD does not agree with DALL that the muscularity of the septum is evidence against its being of branchial origin, but finds it difficult to understand how it could have developed such important attachments to the shell. I do not intend to engage in this controversy, which is not likely to be definitely settled until the embryology of the Septibranchs has been studied. There do, however, appear to be substantial reasons for agreeing with PELSENEER rather than with DALL; the septum certainly performs the same function in creating a current of water through the mantle cavity as do the gills—a fact which DALL failed to realise—and it is difficult to see how it could have evolved except as a direct development from the gills.

The validity of the separate order Septibranchia formed by PELSENEER has been questioned by DALL, GROBBEN and RIDEWOOD, the last-named summarising the conflicting evidence and adding (p. 183), "The reduction of the branchial organs is certainly very remarkable, but there are greater differences between the three genera included in the Septibranchia than between a form like *Poromya malespinæ*, on the one hand, and *Verticordia* on the other. The conditions found in *Poromya*, *Cetoconcha*, and *Cuspidaria* may be considered to have evolved independently, although following the same general trend. The relations between these forms and the Verticordiidæ being obvious, it is proposed, in the absence of more accurate information as to general anatomy, to place the three families, Poromyidæ, Cetoconchidæ and Cuspidariidæ after the Verticordiidæ, in a terminal sub-order (Poromyacea) of the Synaptorhabda."

As PELSENEER (1911) points out, the taxonomic divisions we establish are of relative value only, since continuity is the law of nature, and in his opinion the establishment of the order Septibranchia is justified, for they represent, "le stade final d'une longue évolution dans un sens déterminé."

On the other hand, the very different structure of the septum in Poromya and Cuspidaria, particularly the development of the striated musculature in the latter, does rather support the opinion of Ridewood that they may have evolved independently and that the structural resemblances may therefore be due to convergence, the result of similar habitats and the necessity for dealing with similar food. Like the Teredinidæ, the Septibranchs appear to be highly specialised animals, adapted to peculiar conditions, rather than the apex of the evolution of the Lamellibranchs. But we need further evidence, especially embryological, before these questions can be satisfactorily answered. For the time being, however, the order Septibranchia may be conveniently employed to denote the three families (or two, if, as Pelseneer suggests, the Cetoconchidæ are to be included under the Poromyidæ) of carnivorous Lamellibranchs which draw in water and food by means of a muscular septum, and whose alimentary system has been greatly modified as a result of their change of habits and food.

8. Summary.

1. Living and preserved specimens of the Septibranchs, *Cuspidaria rostrata*, *C. cuspidata*, and *C. obesa*, and *Poromya granulata*, have been studied for the purpose of investigating the structure and functions of the organs of feeding and digestion.

2. In Cuspidaria the septum is extremely thick, and is attached to the shell by large anterior and posterior septal muscles and by delicate lateral muscles the arrangement of which varies in the different species. The mass of the septum consists of longitudinal bundles of flat, striated, muscle fibres which cross over one another posterior to the foot. The lateral muscles are smooth and pass transversely across the dorsal surface of the septum. The septum is perforated by narrow, slit-like pores, either four or five according to the species, which have dorsally directed valves. They are bounded by a columnar epithelium which is ciliated in two regions, and are surrounded by a sphincter of plain muscle.

3. The septum of Poromya is more delicate. It is attached to the shell by a pair of anterior and a pair of posterior septal muscles, and is composed of plain muscle fibres. It is perforated by a pair of anterior, and a pair of posterior, branchial sieves. In *P. granulata* the former possess five and the latter six filaments. These resemble ordinary gill filaments, lateral, but not frontal, cilia being present in *P. granulata*; longitudinal muscles occur at their bases.

4. The palps are small in Cuspidaria, the posterior pair being absent in *C. obesa*, but are larger in Poromya. They are ciliated on their inner surfaces, are smooth and very muscular.

5. The mouth and the œsophagus are large, both are ciliated and surrounded by a thick layer of muscle.

6. The stomach is large and cylindrical, the walls are ridged and covered throughout

with a thick cuticle which probably represents an extension of the gastric shield. It is surrounded by a thick layer of muscle and is free from the surrounding tissues.

7. The ciliated ducts of the digestive diverticula are exceptionally short and wide. The tubules have the same structure as in the digestive diverticula of the other Lamellibranchs. The style-sac is short and contains a small oval style which does not project far into the stomach.

8. The short mid-gut is ciliated and possesses little muscle. The rectum is narrow, ciliated, contains mucous glands and is surrounded by muscle. The anus opens at the base of the exhalant siphon.

9. There is an almost complete absence of the wandering phagocytic cells found in the gut of the ciliary feeding Lamellibranchs.

10. Both Cuspidaria and Poromya live in mud into which they burrow.

11. The septum in Cuspidaria makes regular movements, first descending and then drawing sharply upwards. Between movements it is in its shortest condition. As a result of the movements, water and food are drawn into the mantle cavity. In Poromya the septum appears to act in a similar manner, though less frequently.

12. The cilia on the septal pores and branchial sieves and in the supra-septal cavity serve to maintain a slow current of water through the mantle cavity when the septum is at rest. The cilia in the infra-septal cavity—on the palps, the foot and on the mantle edges—remove fine particles from the mantle cavity.

13. Food is pushed into the mouth by the muscular palps, being then passed through the œsophagus, largely by peristalsis, and crushed up in the gizzard-like stomach, the fragments being passed either into the ducts of the digestive diverticula or into the mid-gut, through which they are passed by ciliary action.

14. The Septibranchs are carnivorous, feeding on small animals either dead or alive, usually Crustacea or Annelida.

15. The tubules of the digestive diverticula provide the only absorbing surface in the gut, they are organs of absorption and intracellular digestion. There is no evidence that they secrete.

16. Fine particles, such as Indian ink, if taken into the mantle cavity are almost all removed by the cleansing action of the cilia and few enter the gut.

17. There is no evidence of any storage of glycogen in *C. obesa*.

18. The Septibranchs have converted feeding mechanisms, and an alimentary system specialised for dealing with fine particles, into an apparatus for the disposal of large food masses.

19. The crystalline style in the Septibranchs is small and, since in the other Lamellibranchs it is concerned essentially with the movement through the gut of fine particles and with the digestion of carbohydrates, is probably vestigial.

20. The absence of wandering phagocytic cells is to be attributed to the absence in the food of particles small enough for them to ingest, and also to the ease with which particles can enter the digestive diverticula.

21. The digestive processes do not otherwise appear to differ from those of the remaining Lamellibranchs. Although carnivores, the Septibranchs have not developed a preliminary extracellular digestion of protein.

22. The Septibranchs are a small and unsuccessful group, which probably evolved in deep water where the majority of them still live. The origin of the septum is disputed, but the balance of the evidence is in favour of its being branchial.

23. The order Septibranchia, established by Pelseneer, is probably valid, though Cuspidaria and Poromya may resemble each other as the result of convergence and not of a common origin.

24. The conditions found in the carnivorous Septibranchs provide valuable confirmatory evidence that the peculiar nature of the gut and of the digestive processes in the other Lamellibranchs is due to the finely divided food collected by their elaborate ciliary feeding mechanisms.

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10. DESCRIPTION OF PLATES.

List of Reference Letters.

a. = clear area in which lies nucleus of striated fibre.
a.p. = anterior palp.
b.c.i. = ingested blood corpuscles.
b.c.l. = blood corpuscle in lumen.
b.c.p. = blood corpuscle in process of being ingested.
b.g. = beginning of mid-gut.
b.m. = basement membrane.
c.g. = connecting groove between style-sac and mid-gut.
c.m. = circular muscle.
c.s. = crystalline style.
ch. = "chitinous" supporting rod in filament of branchial sieve.
cp. = crypts of young cells in tubules of digestive diverticula.
cu. = cuticle.
d. = duct of digestive diverticula.
d.c. = dorsal ciliated tract round septal pore.
d.e. = dorsal epithelium of septum.
e.s. = epithelium of style-sac.
f. = iron in vacuoles in tubule cells.
g. = mid-gut.
I. = infra-septal cavity.

i.e. = epithelium of inner surface of palps.
l. = wide lumina of digestive diverticula.
l.c. = lateral cilia.
l.m. = longitudinal muscles.
l.r. = longitudinal ridges in stomach.
l.s.m. = lateral septal muscles.
m. = mouth.
m.g. = mucous gland.
mu. = muscle strands.
n.b.c. = nucleus of ingested blood corpuscle.
n.s. = nucleus of striated fibre.
n.t. = nucleus of tubule cell.
o. = œsophagus.
o.c. = older, vacuolated cells of tubules.
o.e. = epithelium of outer surface of palps.
p.p. = posterior palp.
r. = rectum.
r.m. = radiating muscle fibres.
r.o. = longitudinal ridges in œsophagus.
S. = supra-septal cavity.
s.m. = septal muscle.
s.s. = style-sac.
sp. = sphincter of plain muscle round septal pore.
sr. = striation in muscle fibre.
st. = stomach.
t. = tubule of digestive diverticula.
ty. = typhlosole.
v. = valve on dorsal side of septal pore.
v.c. = ventral ciliated tract round septal pore.
v.e. = ventral epithelium of septum.
va. = vacuole in tubule cell.
w.c. = wandering cell.
y.c. = young, darkly staining cells in mid-gut.

PLATE 12.

FIG. 1. *Cuspidaria rostrata.*—Longitudinal section through the septum cutting a septal pore transversely, Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.

FIG. 2. *Cuspidaria rostrata.*—Horizontal section through the septum passing somewhat obliquely through a septal pore in the dorsal region. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 200.

FIG. 3. *Cuspidaria rostrata.*—Portion of a teazed-out muscle fibre from the septum. Fixed alcohol. stained iron hæmatoxylin. × 666.

FIG. 4. *Cuspidaria rostrata.*—Transverse section through a posterior palp, about the middle. Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.

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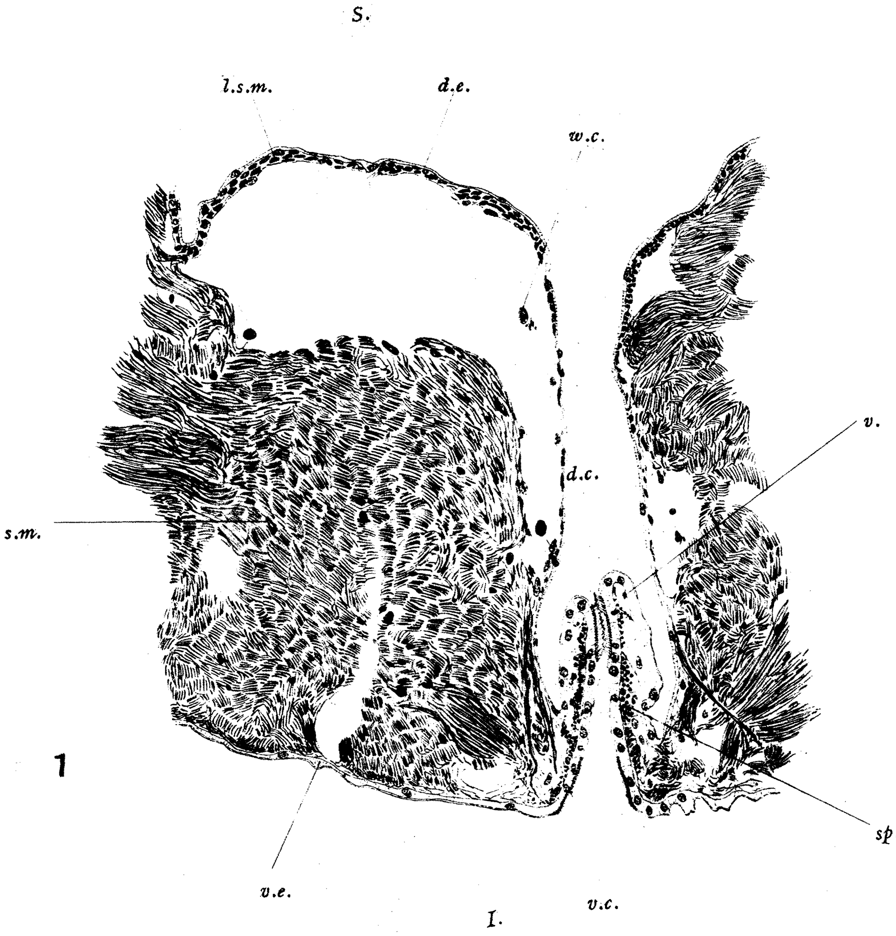
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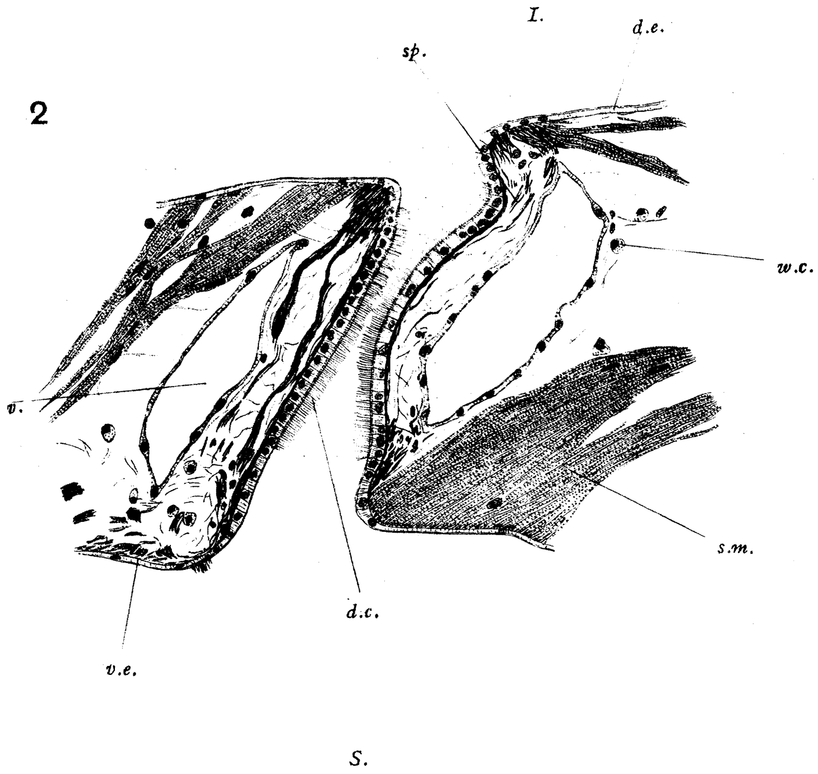
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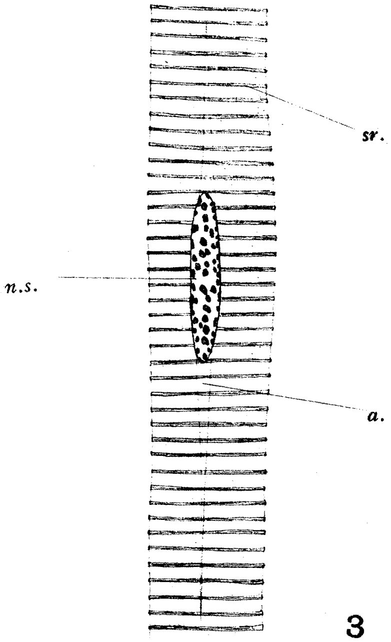
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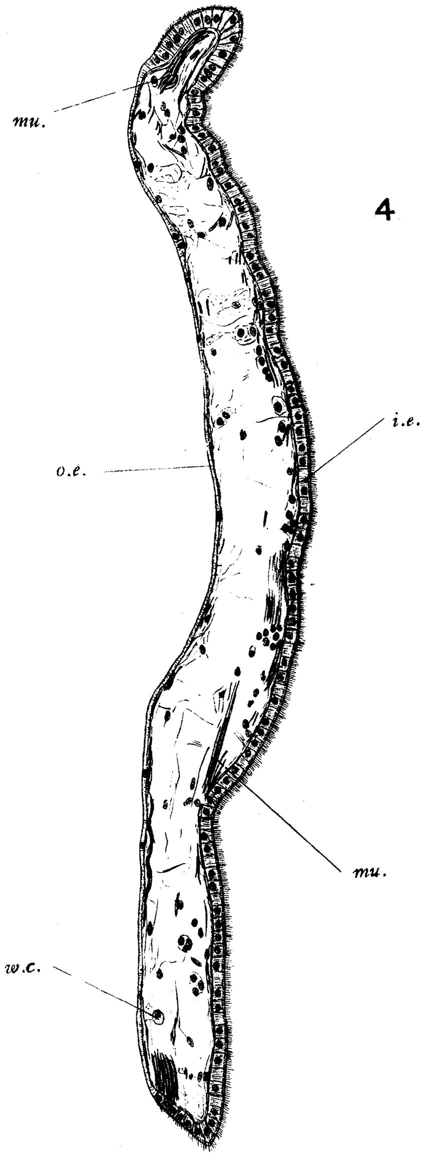
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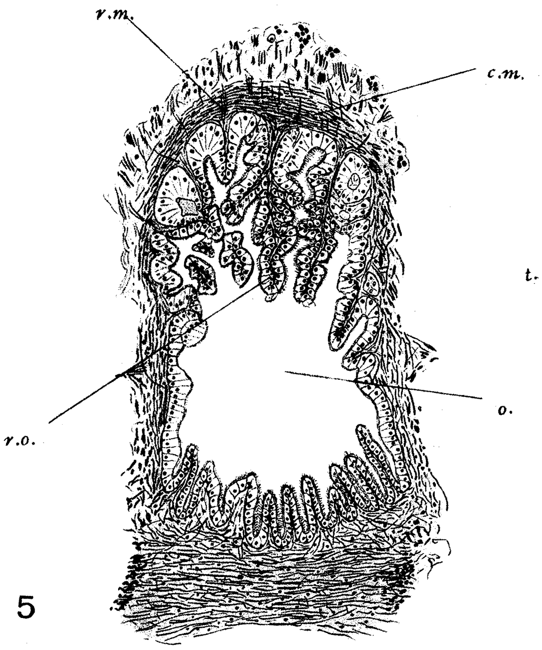
PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES



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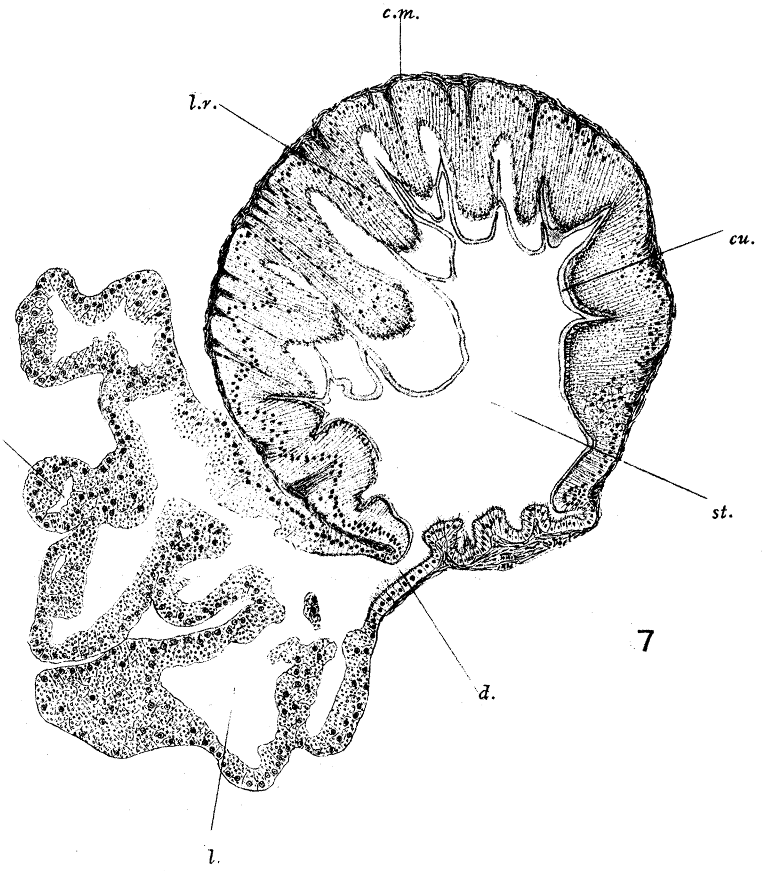

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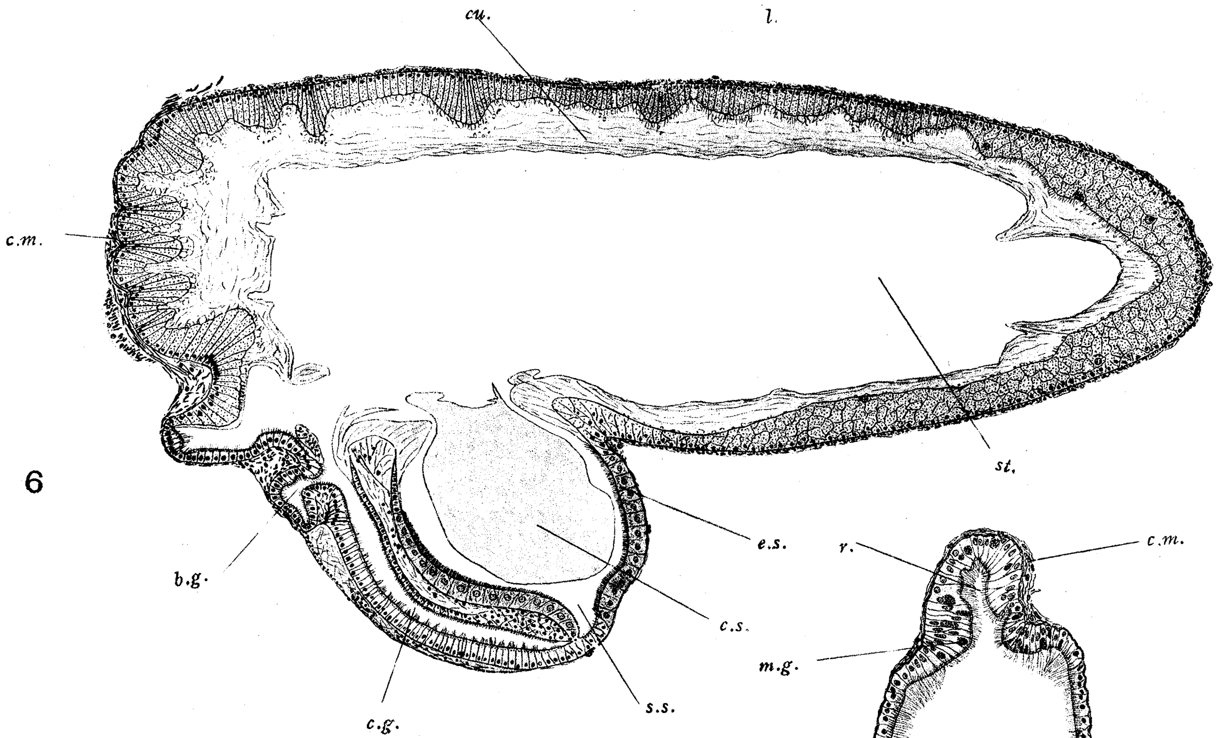

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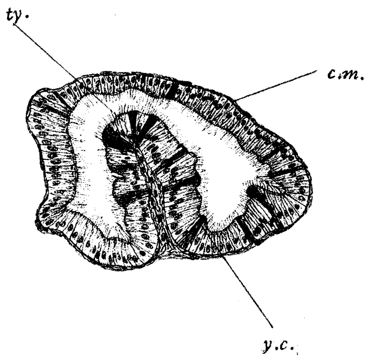

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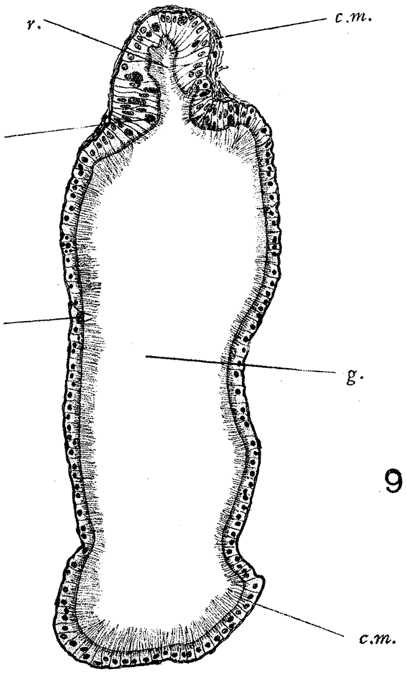

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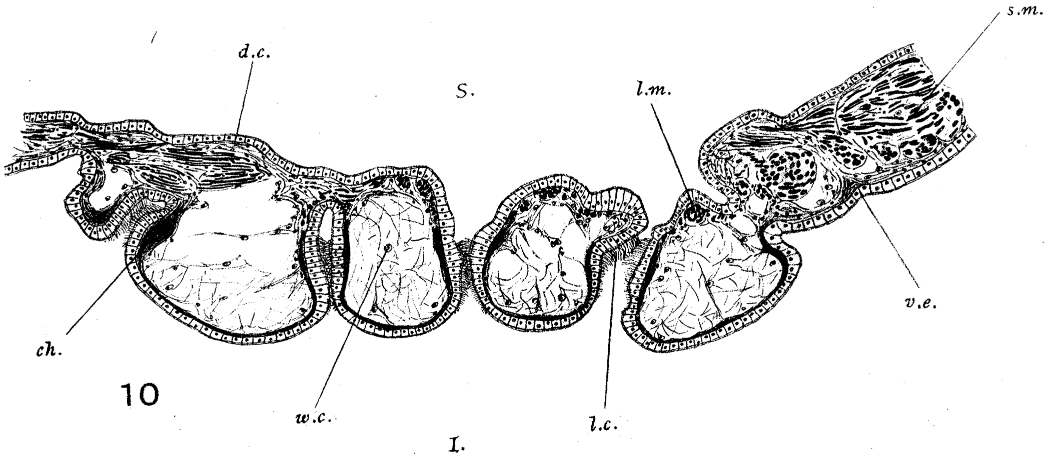
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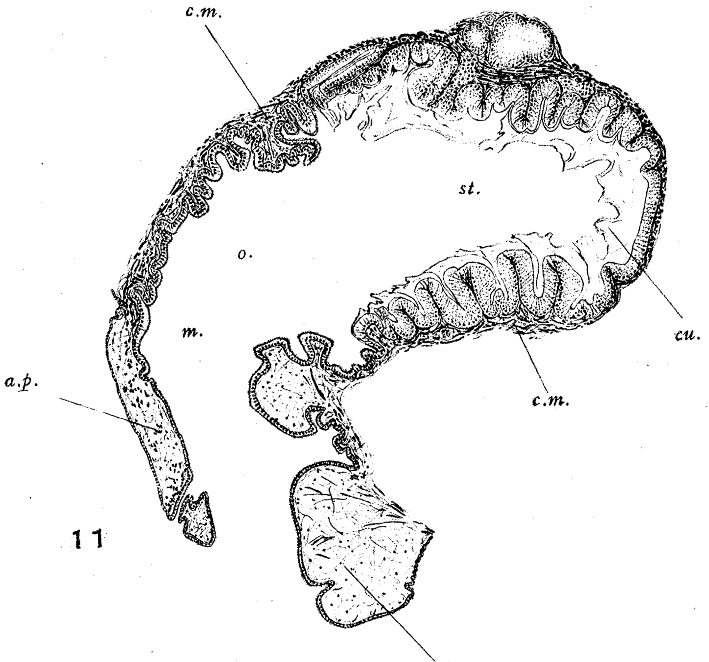
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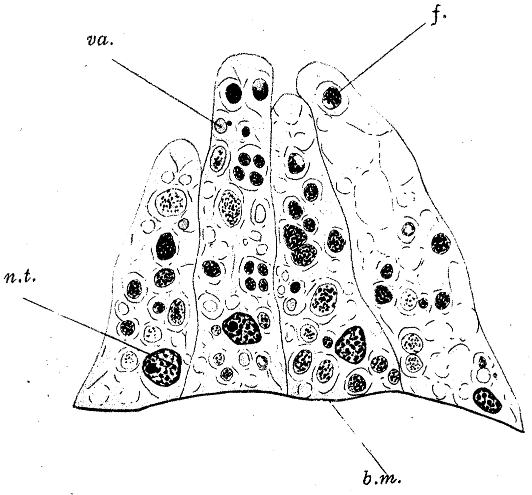
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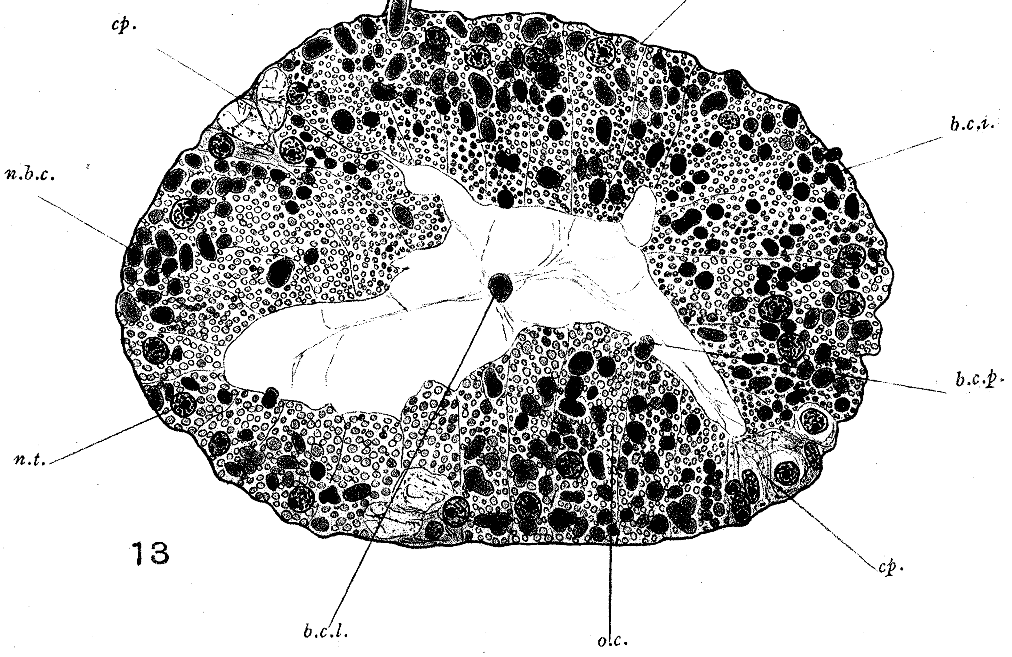
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cp.
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PLATE 13.

FIG. 5. *Cuspidaria cuspidata*.—Transverse section through the œsophagus immediately anterior to the stomach. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 76.

FIG. 6. *Cuspidaria rostrata*.—Longitudinal section through the stomach and style-sac, showing also the beginning of the mid-gut and the connecting groove between it and the style-sac. Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 76.

FIG. 7.—*Cuspidaria cuspidata*.—Transverse section through the stomach passing through the opening of the anterior and smaller duct of the digestive diverticula. The shortness of the duct and the wide lumina of the tubules into which it opens are both shown. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 76.

FIG. 8. *Cuspidaria cuspidata*.—Transverse section through the mid-gut immediately posterior to its separation from the style-sac, showing the presence of the typhlosole. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 112.

FIG. 9. *Cuspidaria cuspidata*.—Transverse section through the mid-gut in the region of its junction with the rectum to which it is united dorsally. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 112.

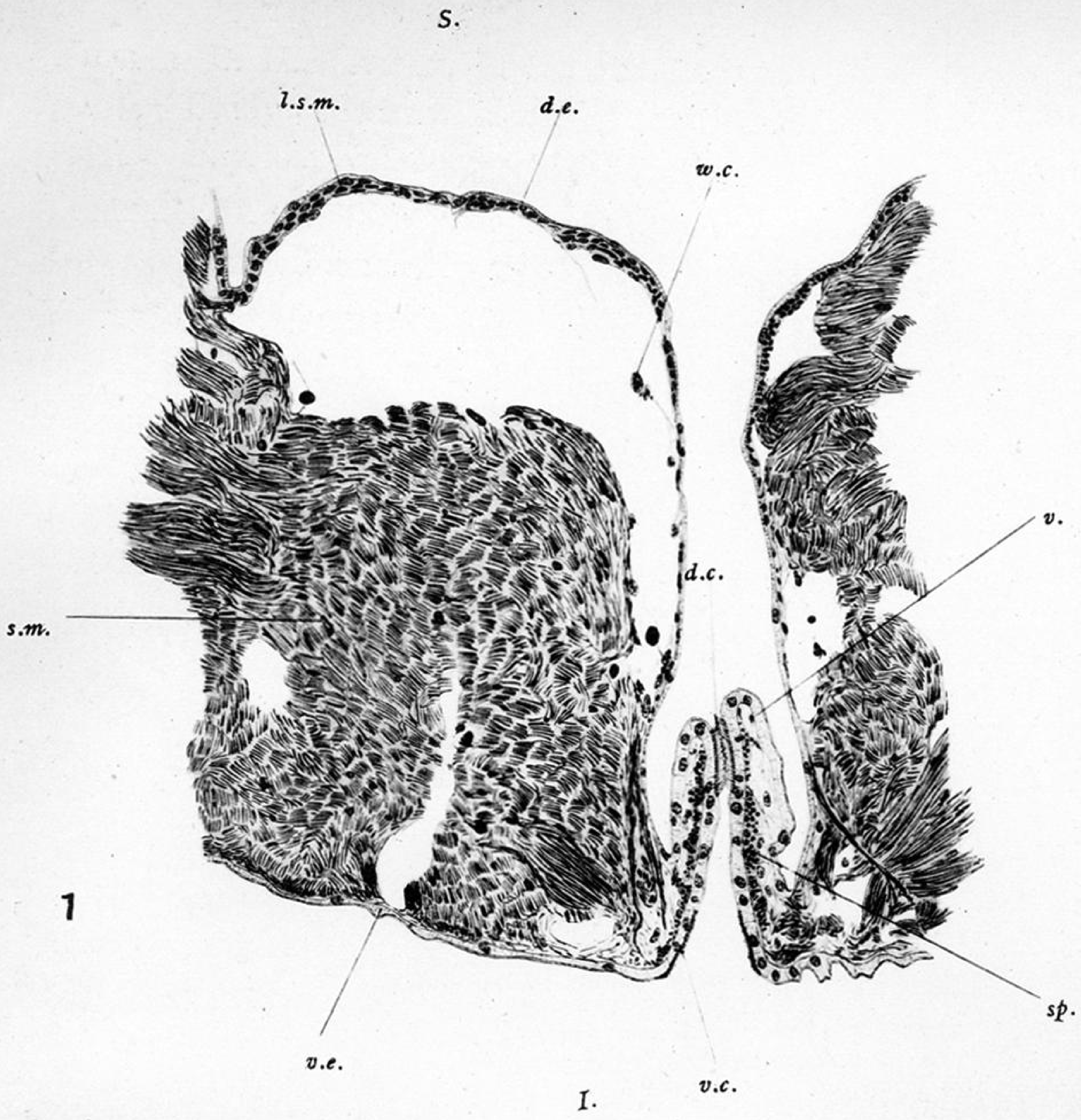
PLATE 14.

FIG. 10. *Poromya granulata*.—Longitudinal section through the septum cutting one of the posterior branchial sieves at right angles. The filaments are shown in transverse section and their resemblance to the gill filaments of the other Lamellibranchs is shown. Fixed alcohol, stained Delafield's hæmatoxylin and eosin. 6 μ × 100.

FIG. 11. *Poromya granulata*.—Longitudinal section through the palps, mouth, œsophagus and stomach, showing their mutual relationships and the wide lumen of the œsophagus and stomach. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 34.

FIG. 12. *Cuspidaria obesa*.—Section through four cells from a tubule of the digestive diverticula fixed after 12 hours of feeding with a suspension of iron saccharate. Fixed equal parts Bouin and 5 per cent. ammonium sulphide in absolute alcohol, iron treated with the Prussian blue method, sections stained with alum carmine. 6 μ × 865.

FIG. 13. *Cuspidaria cuspidata*.—Transverse section through a single tubule of the digestive diverticula fixed after 10 hours of feeding with blood from a Wrasse. The structure of the tubule is shown, also the presence of blood corpuscles, free in the lumen, in process of ingestion and actually ingested within the cells. Fixed Bouin, stained Mann's methyl blue and eosin. 6 μ × 572.



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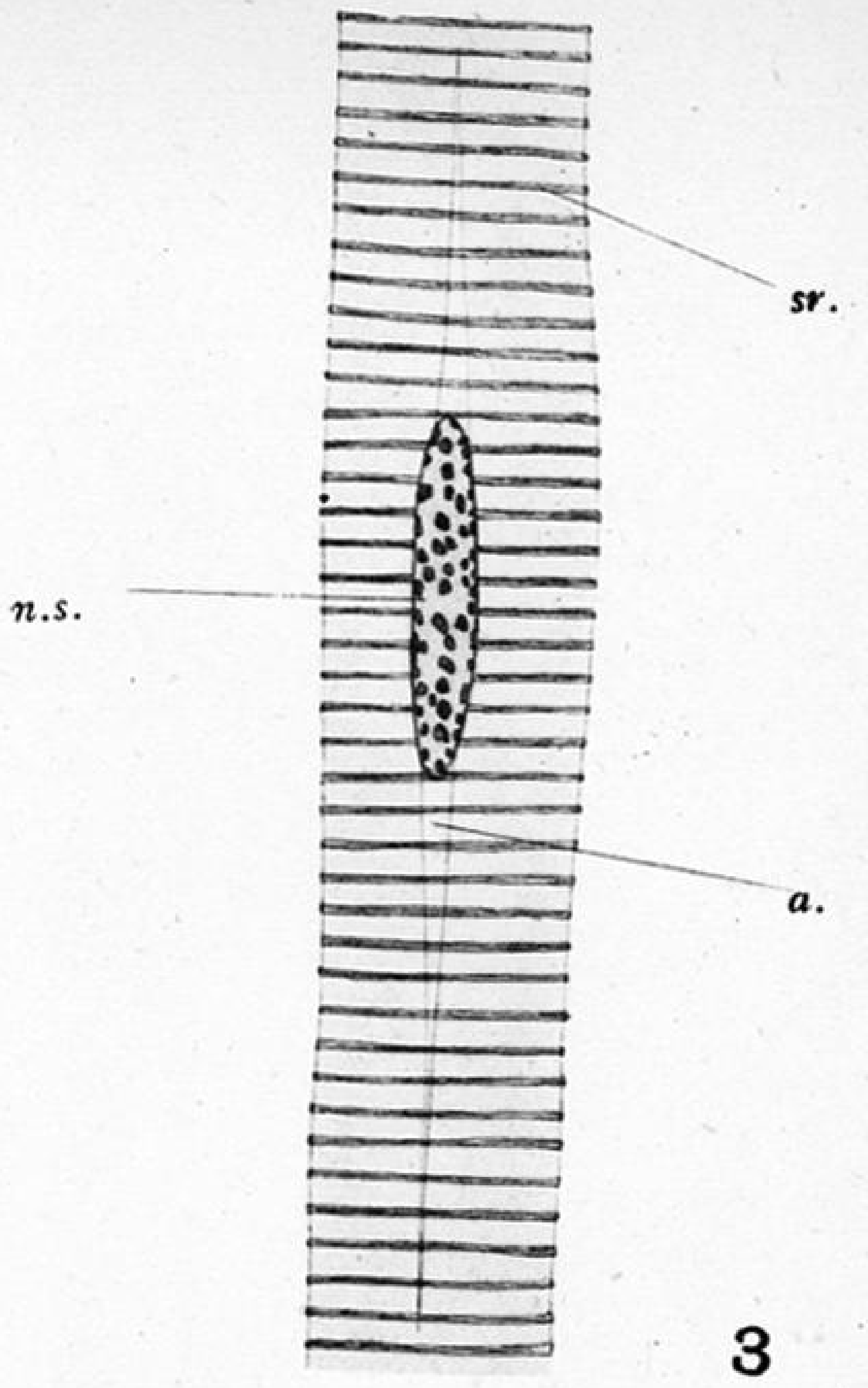

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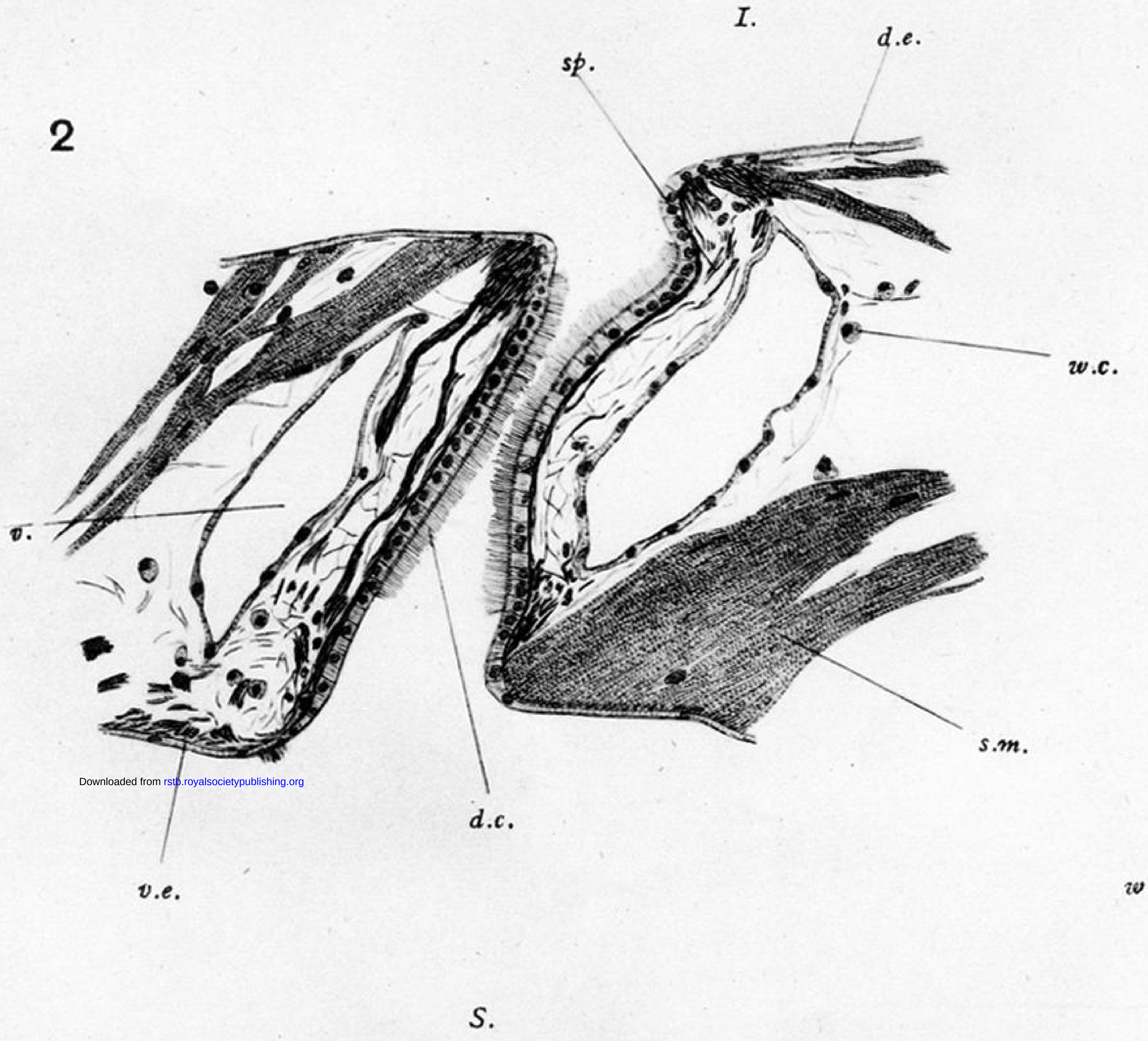

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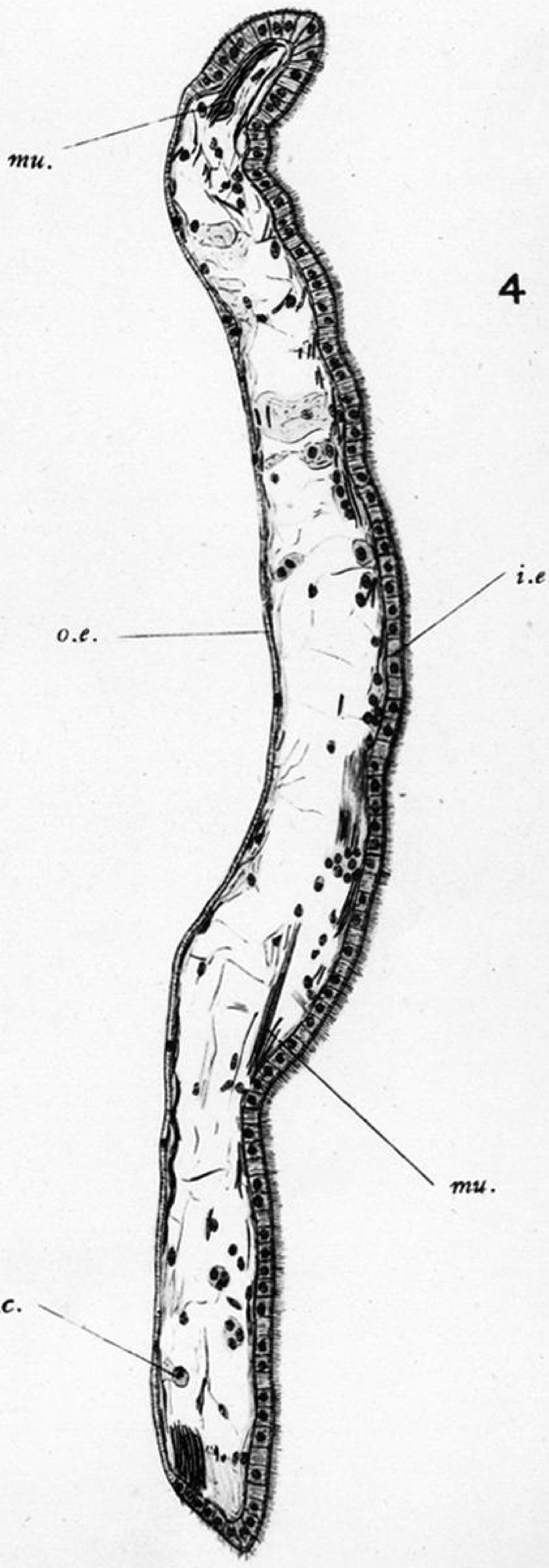

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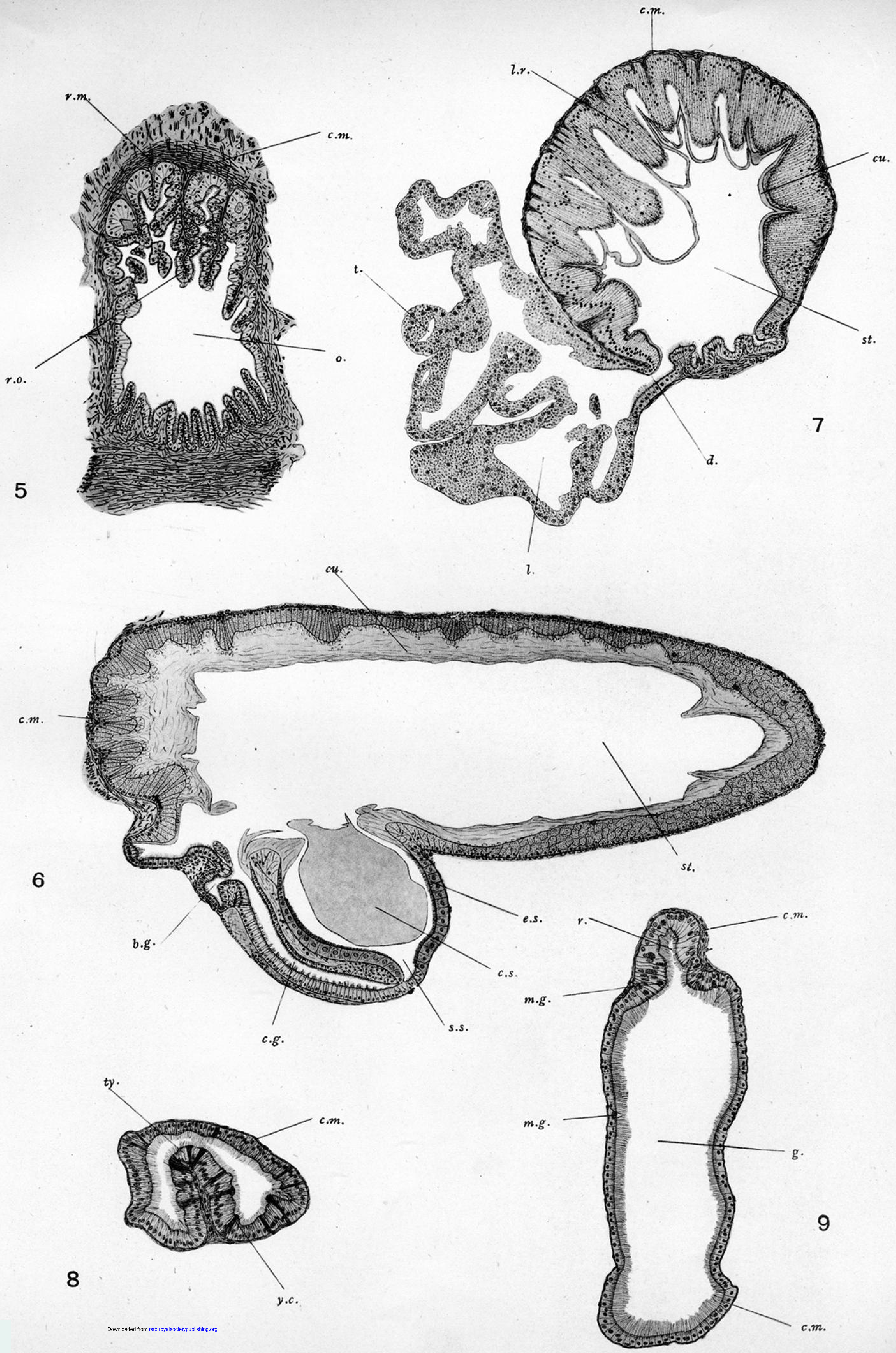
PLATE 12.

FIG. 1. *Cuspidaria rostrata.*—Longitudinal section through the septum cutting a septal pore transversely, Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.

FIG. 2. *Cuspidaria rostrata.*—Horizontal section through the septum passing somewhat obliquely through a septal pore in the dorsal region. Fixed Bouin, stained iron hæmatoxylin and acid fuchsin. 6 μ × 200.

FIG. 3. *Cuspidaria rostrata.*—Portion of a teazed-out muscle fibre from the septum. Fixed alcohol. stained iron hæmatoxylin. × 666.

FIG. 4. *Cuspidaria rostrata.*—Transverse section through a posterior palp, about the middle. Fixed Bouin, stained Delafield's hæmatoxylin and eosin. 6 μ × 200.



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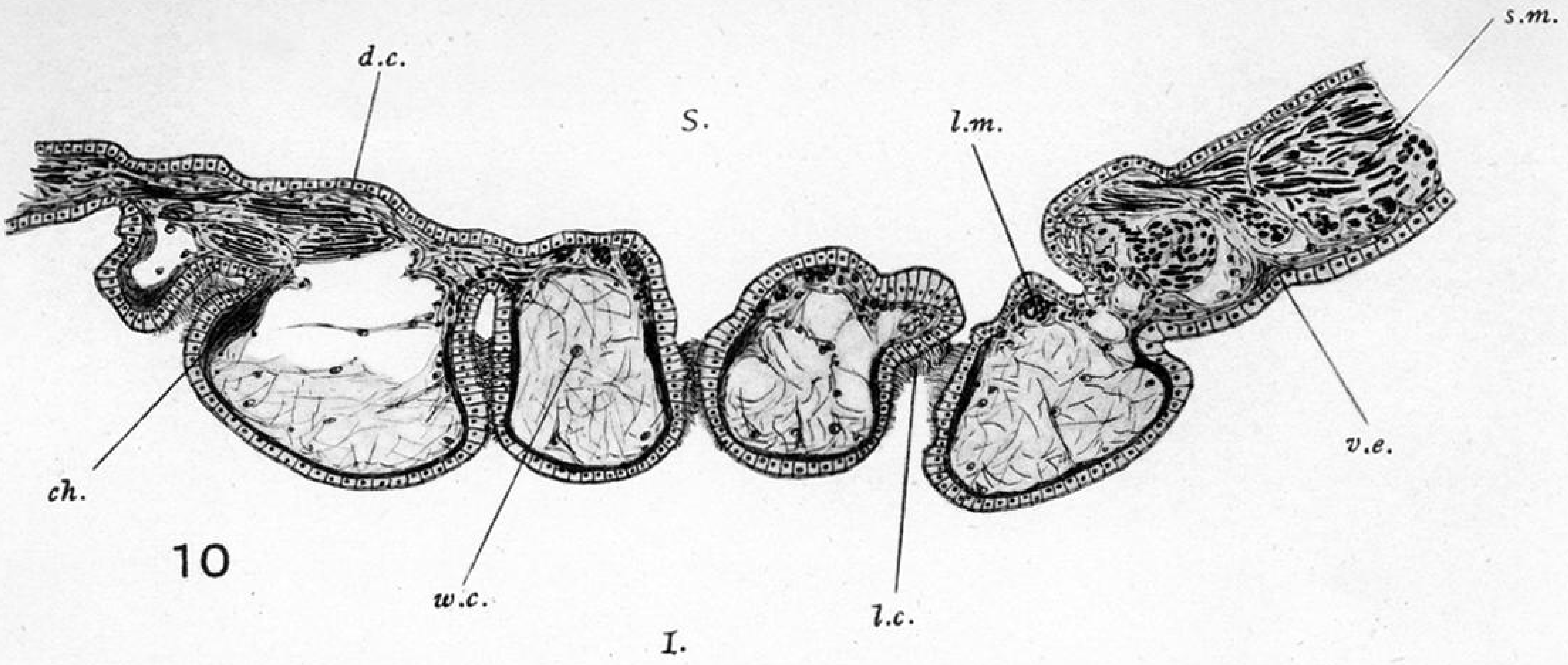

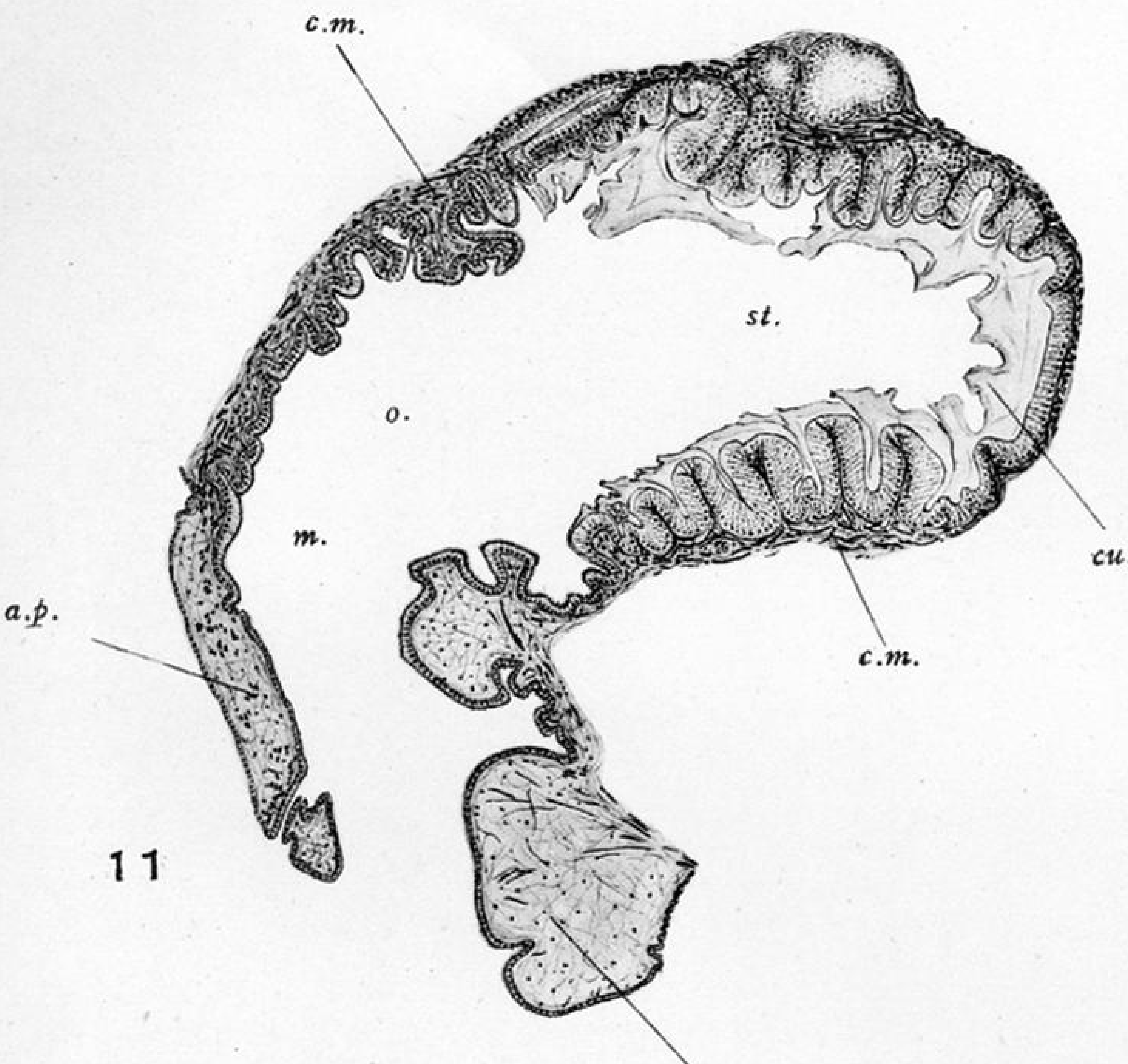

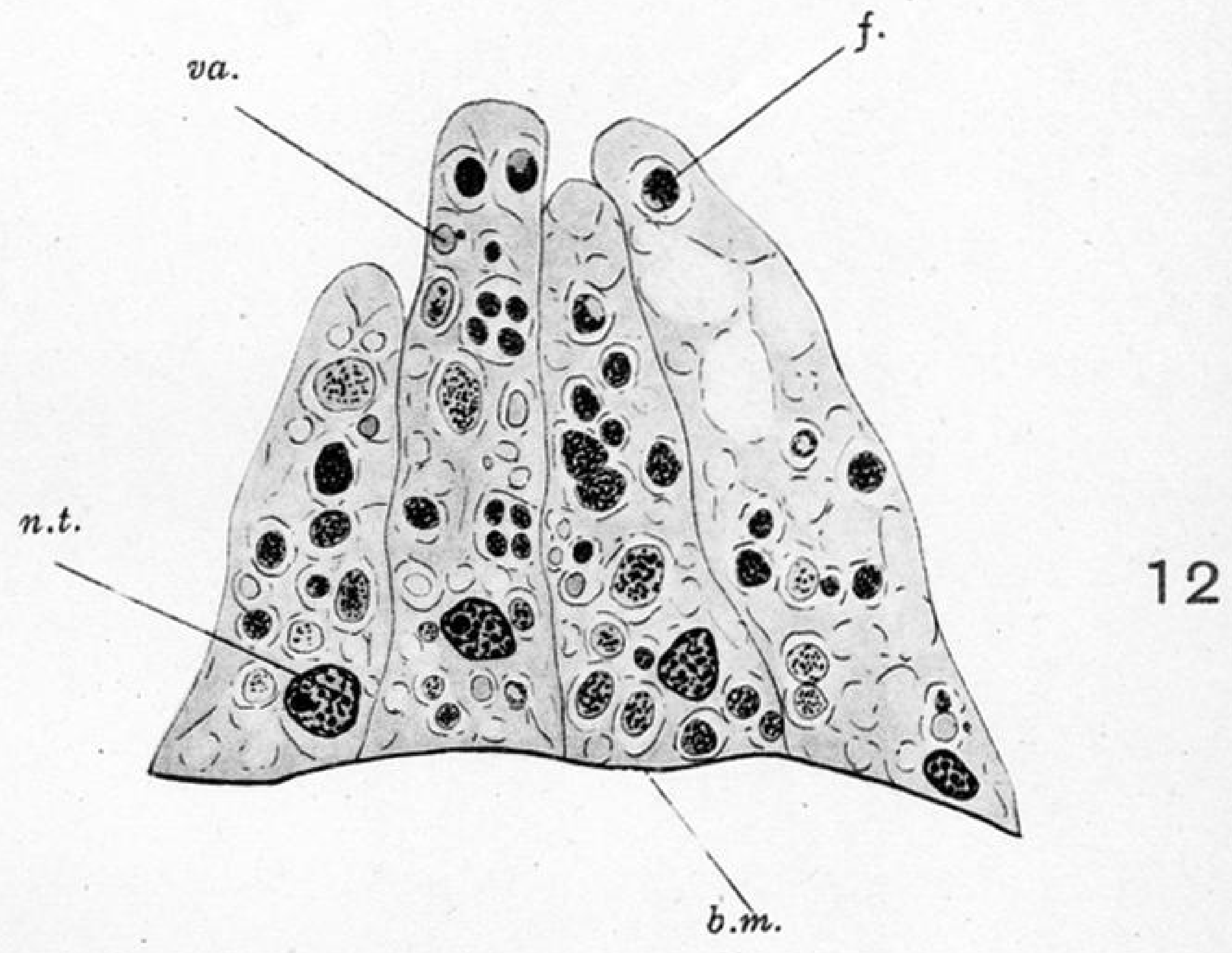

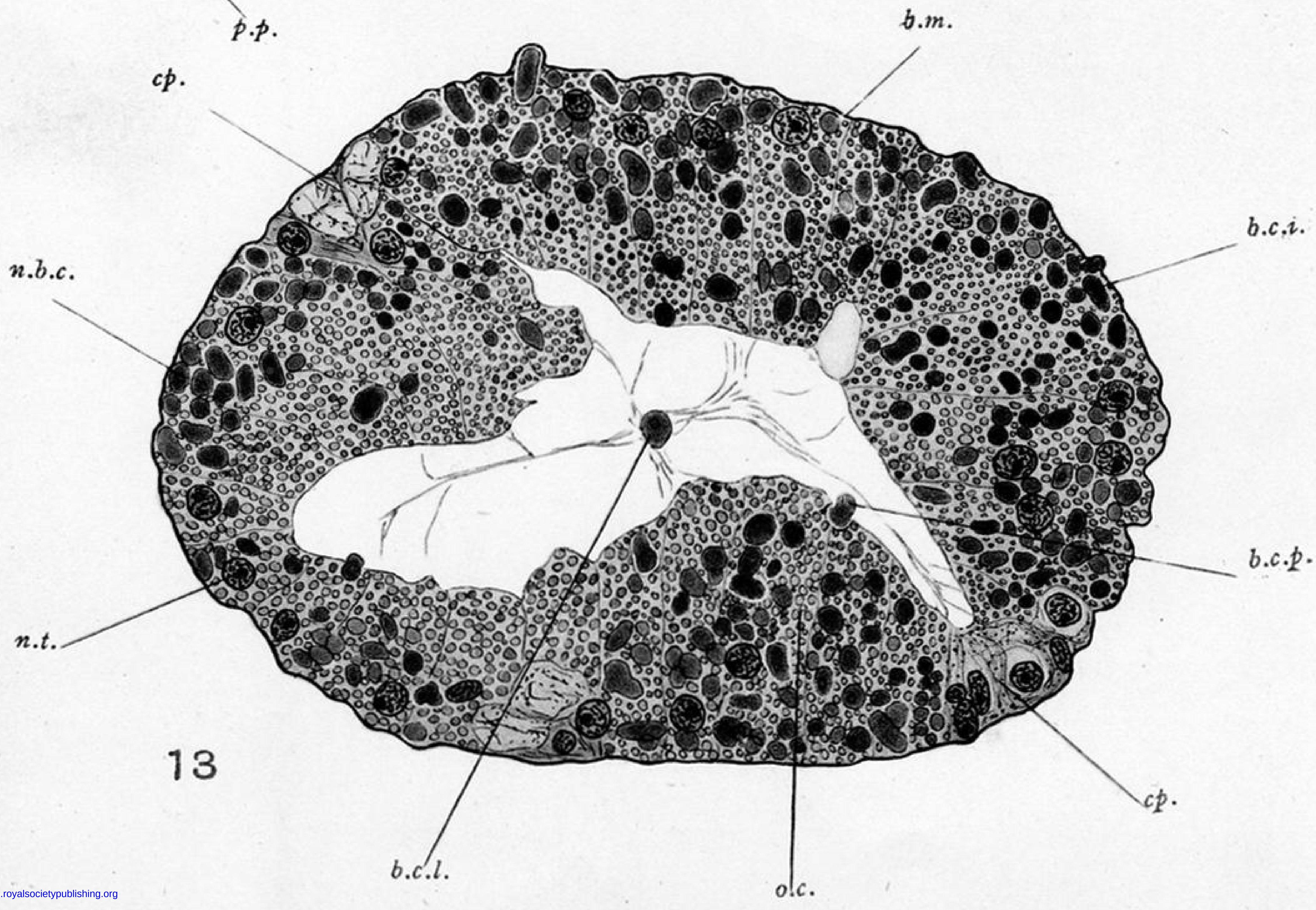

Plate 14.

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