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fused propterygium and metapterygium*. The articulation with the pectoral girdle was normal, and there were 17 complete and 1 incomplete radials (text-fig. 60). The fin on the right side was typical, the epiphyses only being united; it had 17 radials.

Budgett † has described and illustrated a small flange of cartilage on the external side of the metapterygium in the larval *Polypterus*, which suggests traces of a biserial arrangement of radials on the metapterygium. He says, "On the free edge of the metapterygium, at its distal end, is a slight flange of cartilage, seemingly forming a rudimentary continuation round the distal end of the radial cartilage." I saw no traces of this cartilaginous flange, but on removing the dermal skeleton from the fins I found a flange in the position described, and it was apparently a continuation of the small distal cartilages. But on examining sections it proved to be connective tissue without any cartilage.

24. A Descriptive Study of an Oligochæte Worm of the Family Enchytræidæ; with an Appendix on certain Commensal Protozoa. By H. H. STIRRUP, B.Sc. (Birm.), Lecturer in Agricultural Biology, East Anglian Institute of Agriculture, Chelmsford ‡.

[Received March 10, 1913: Read March 18, 1913.]

(Plates XLVI.-XLIX. § and Text-figures 61-67.)

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INTRODUCTION.

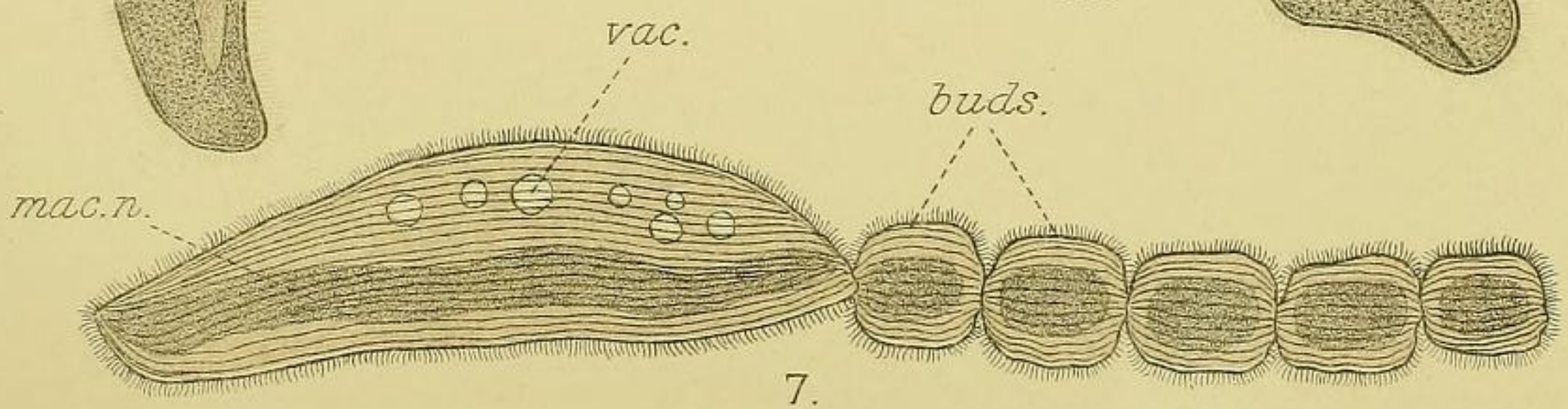
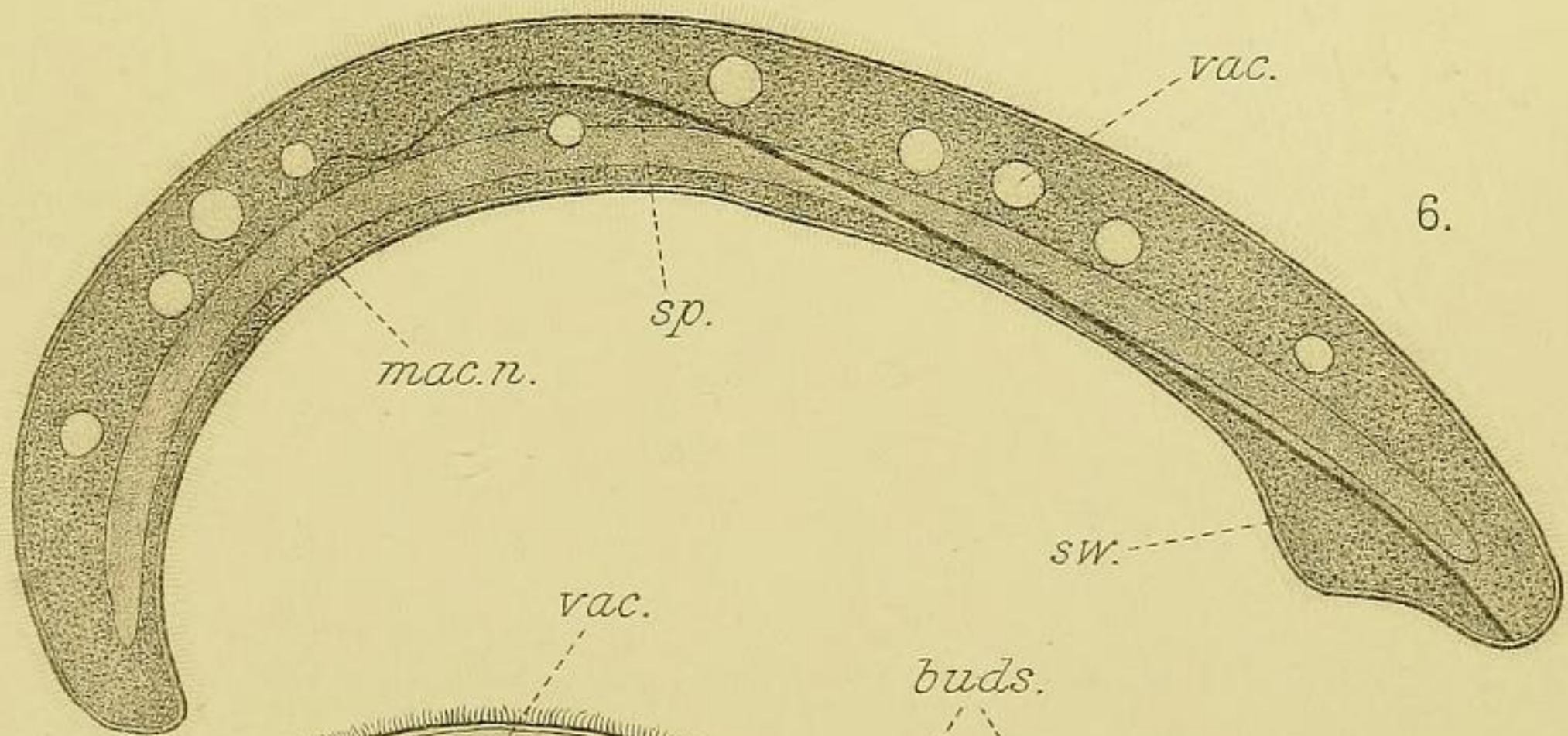
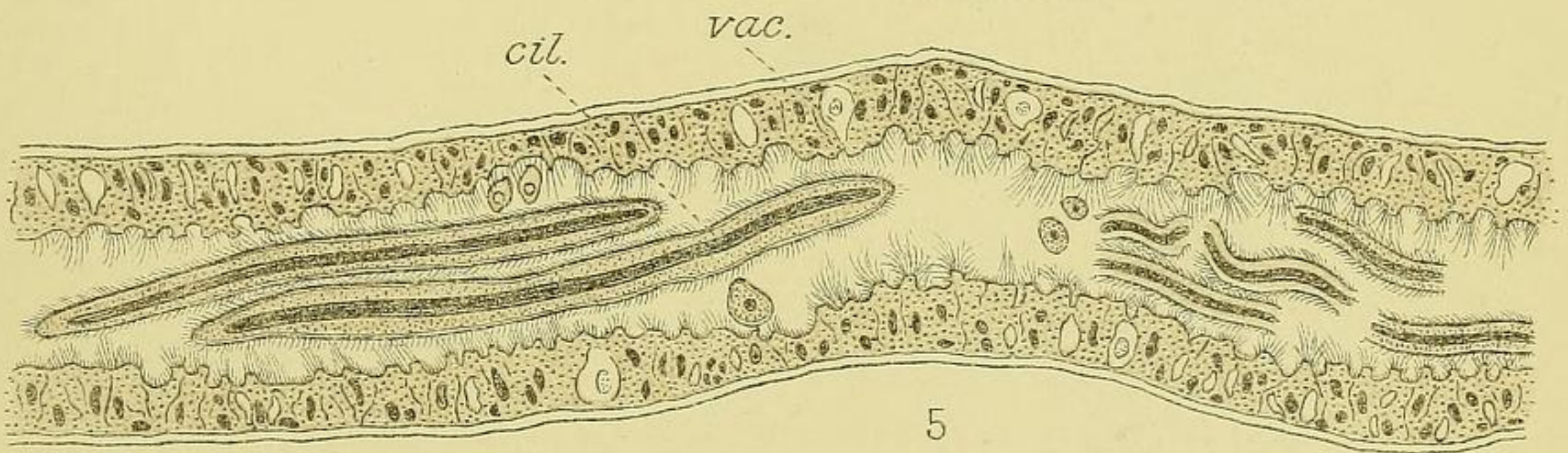
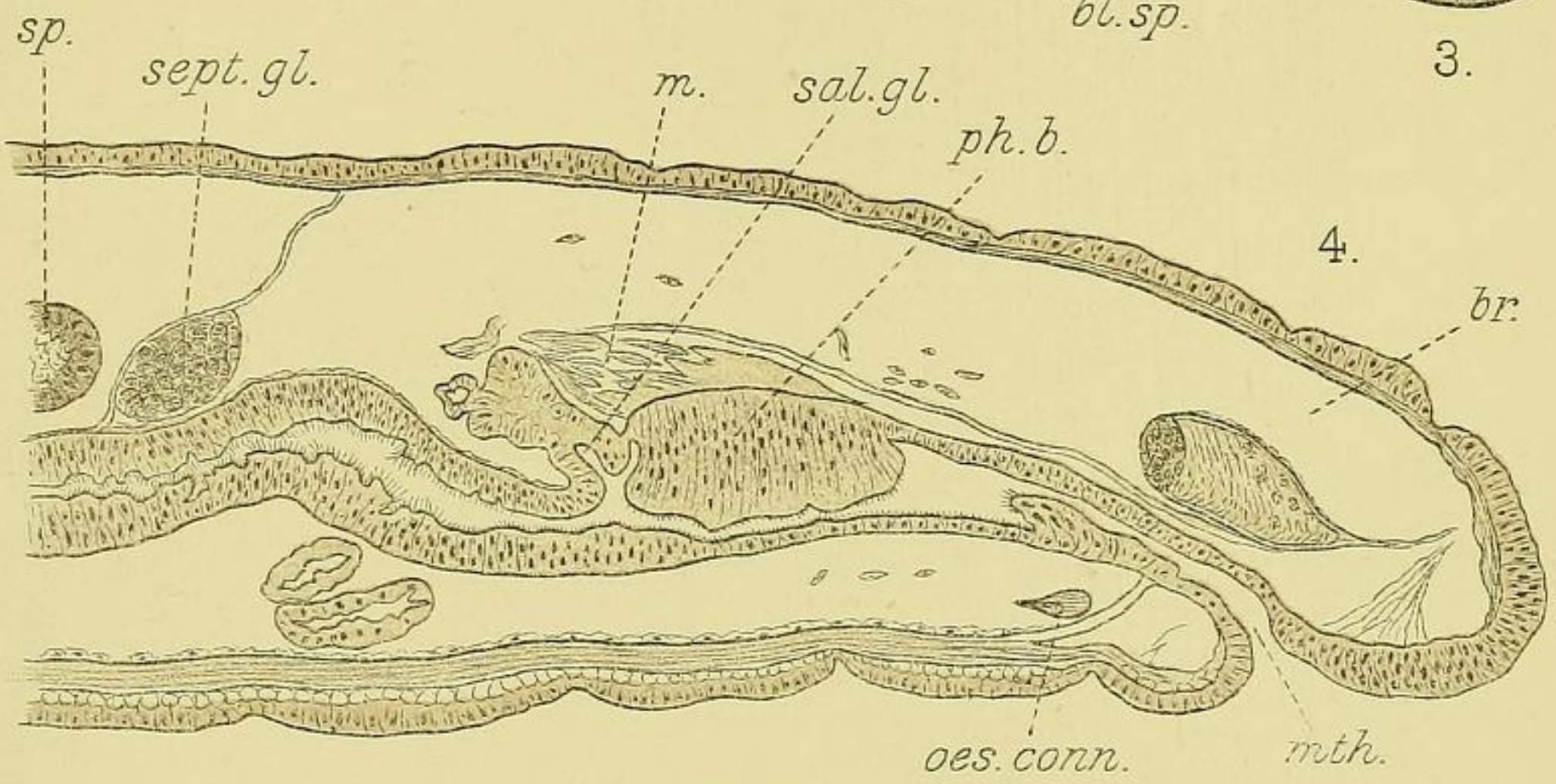
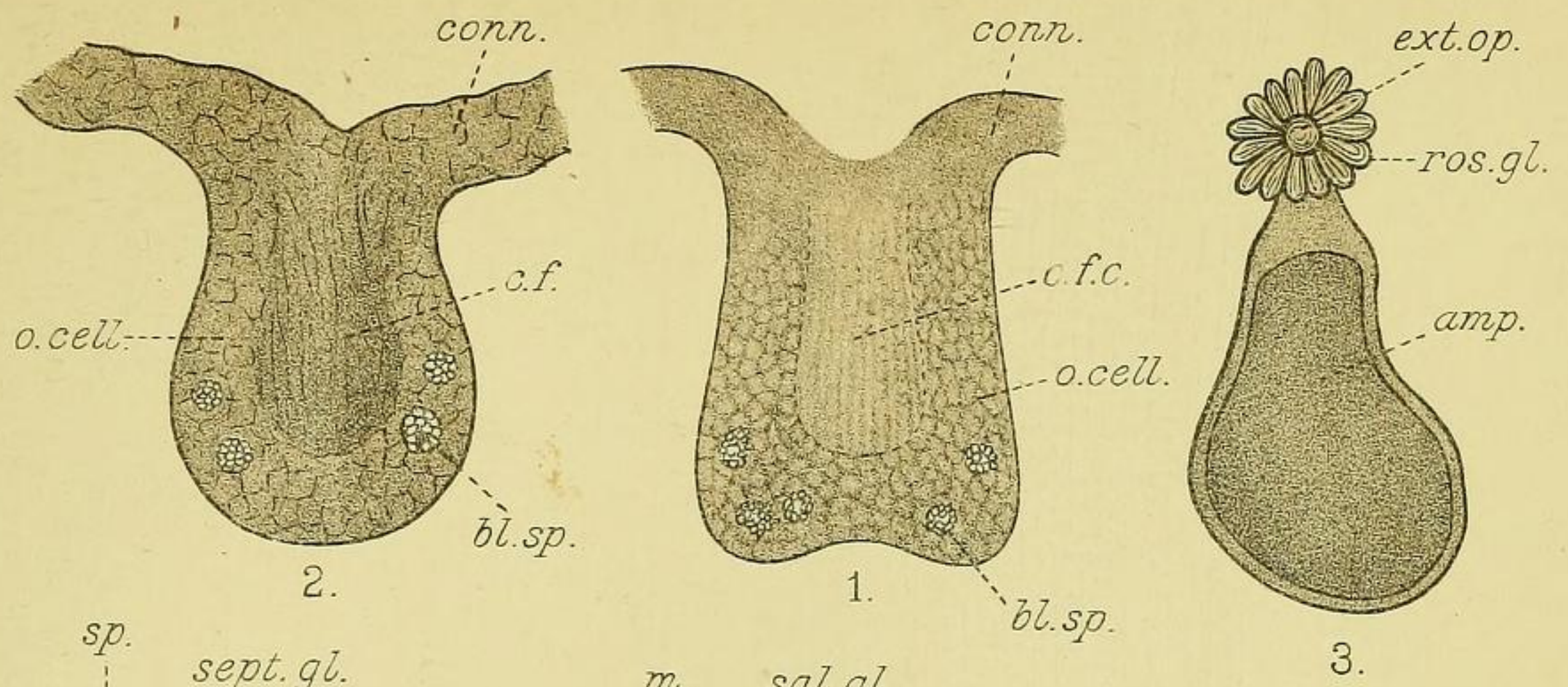
The object of the following paper is to give as full a description as possible of a typical Enchytræid or "white worm." In spite of the descriptions of Enchytræids given by Vejdovsky (16), Michaelsen (8, 9, 10), Friend (5, 6), Southern (11, 12, 13), etc., there seems to be need for such a straightforward description, especially of certain points about which much vagueness and difference of opinion exists. The knowledge of our British Enchytræids is increasing rapidly every year, chiefly owing to Southern in Ireland and Friend in England, but almost all recent work in connection with Enchytræids has been purely systematic, species new to the British Isles and also new to science being discovered quite frequently.

* Festschr. für C. Gegenbaur, Part I. 1896, p. 295.

† Trans. Zool. Soc. London, vol. xvi. pt. vii. p. 329.

‡ Communicated by Prof. F. W. GAMBLE, F.R.S., F.Z.S.

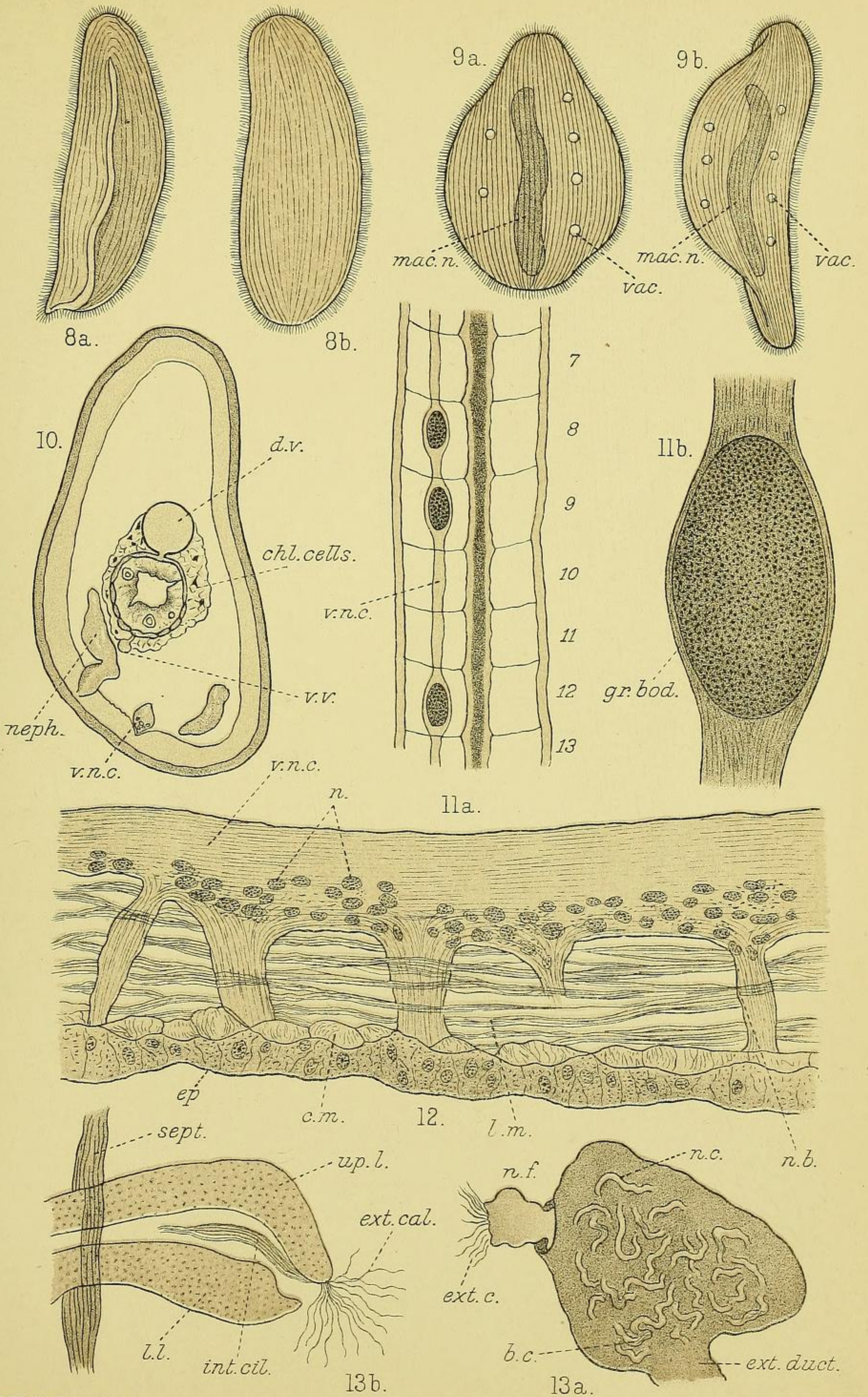
§ For explanation of the Plates see pp. 320-321.



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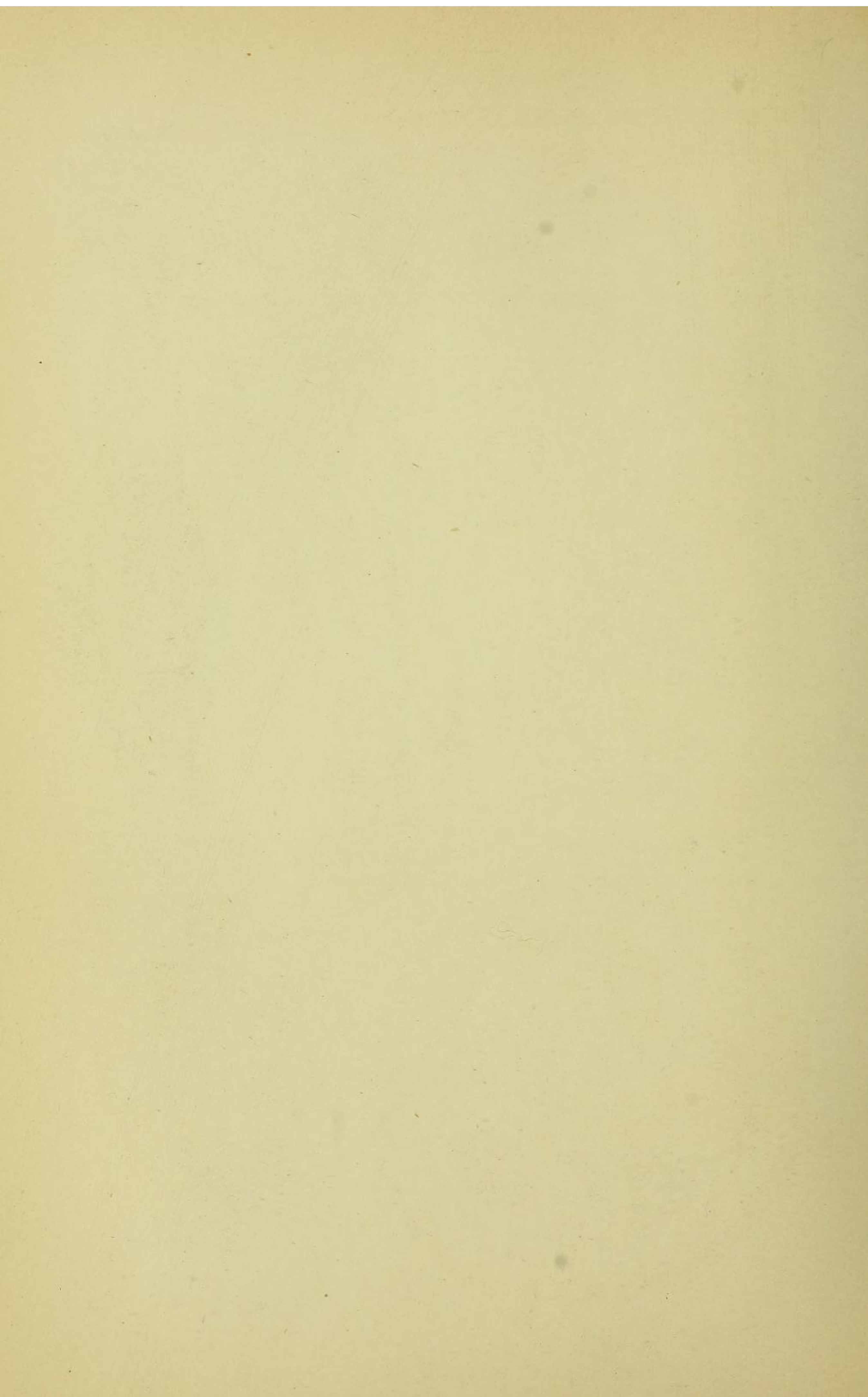
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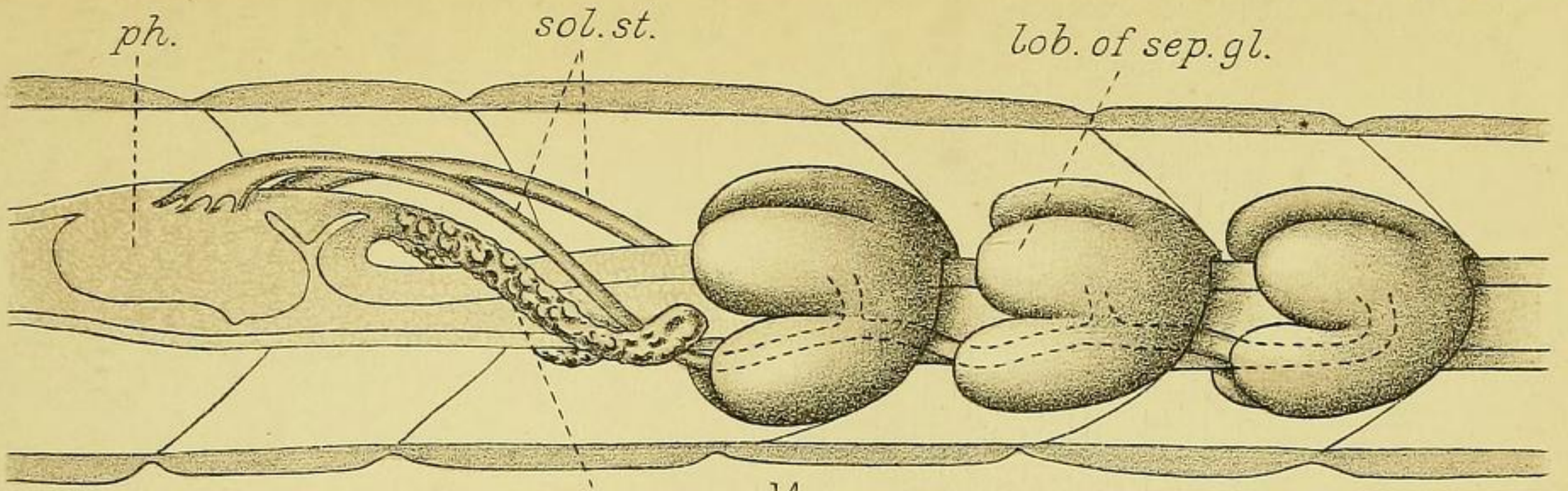
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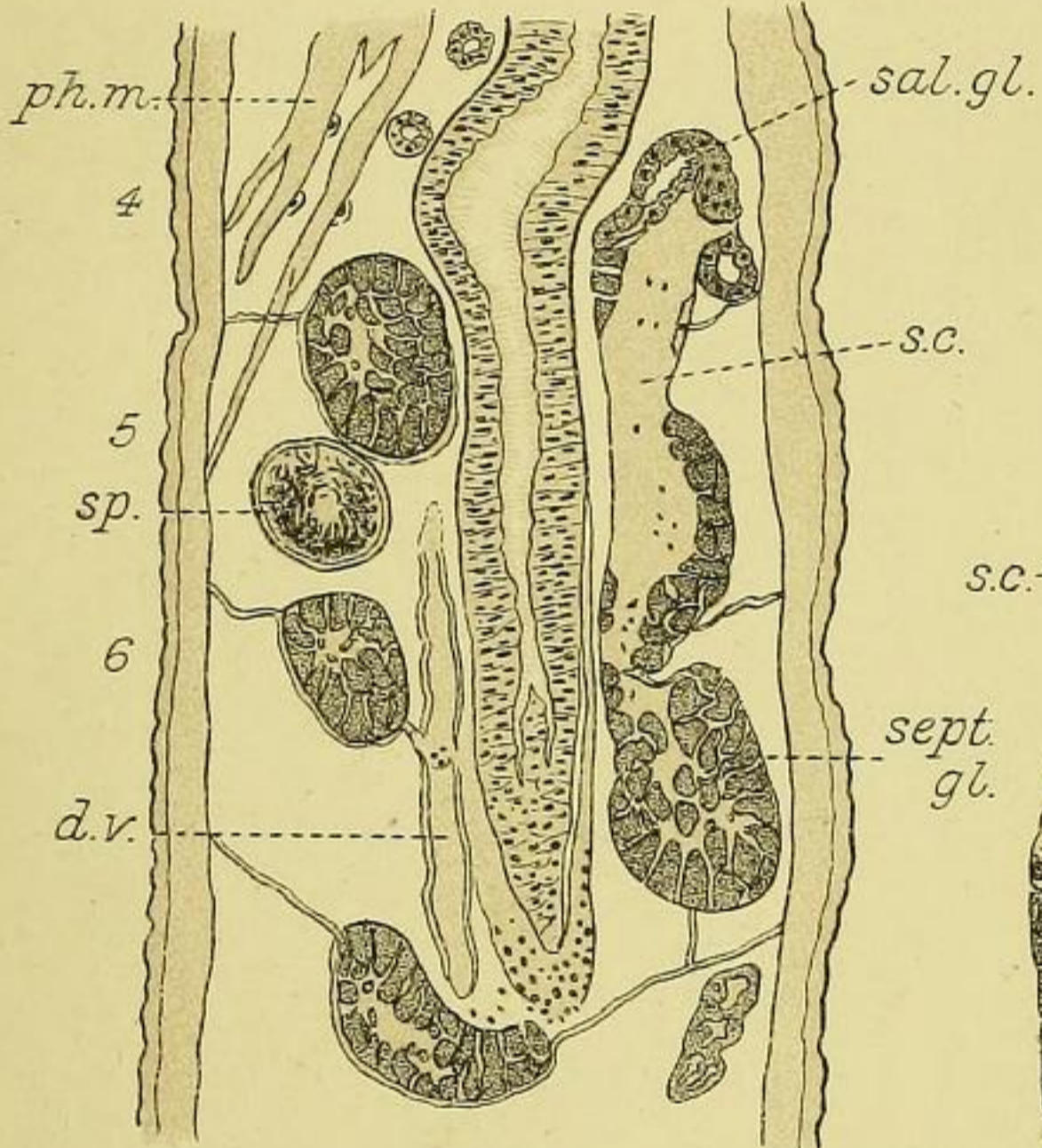
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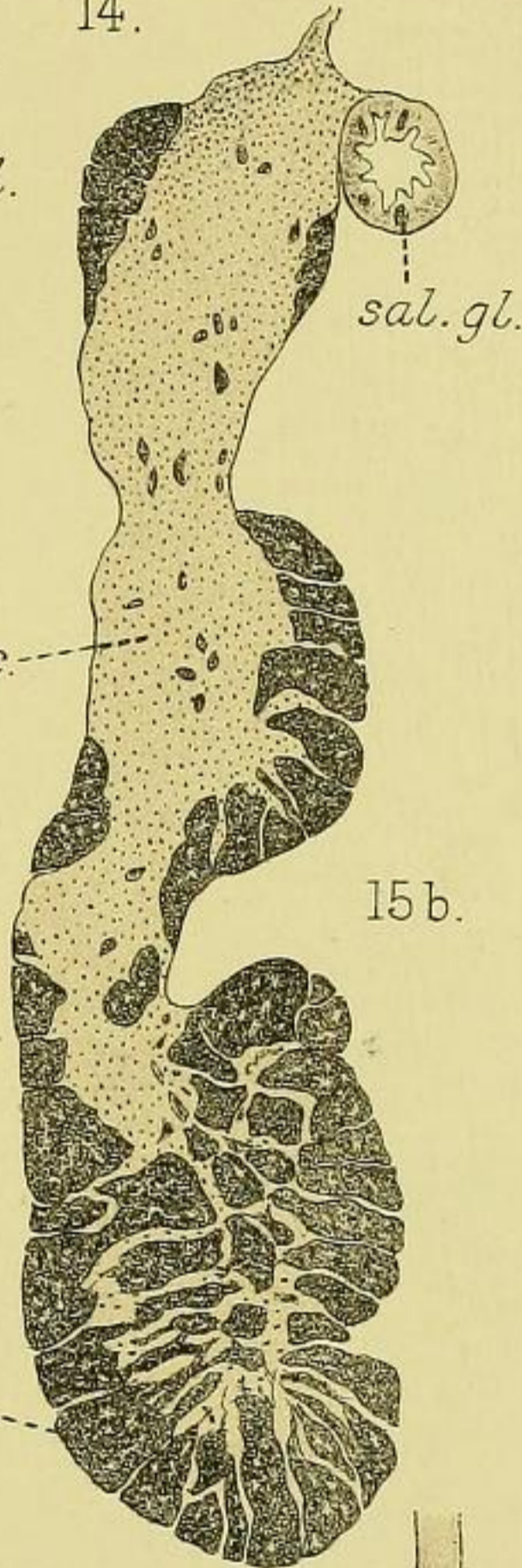




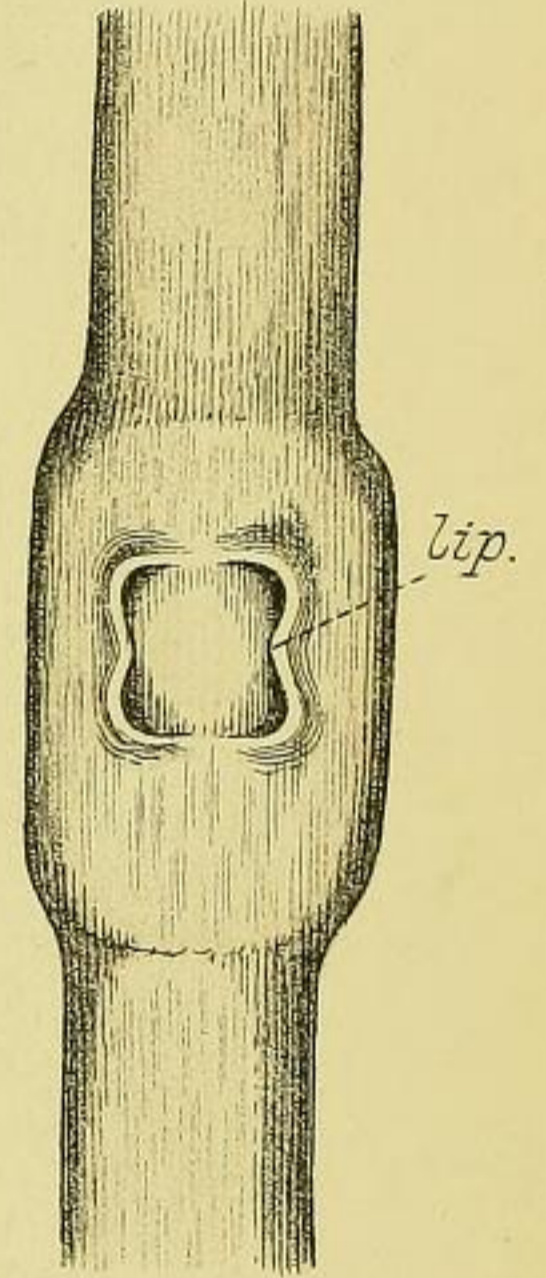
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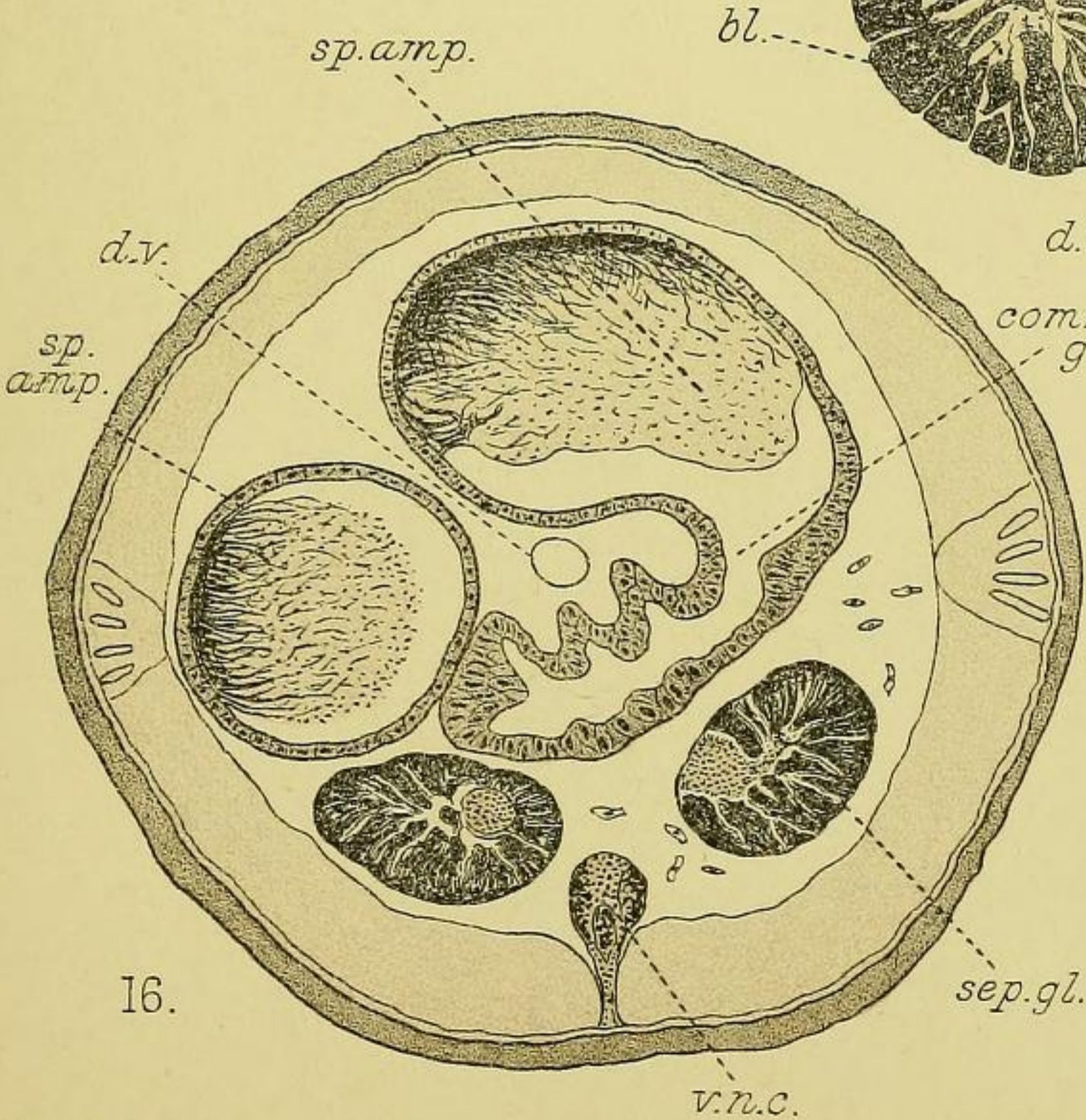
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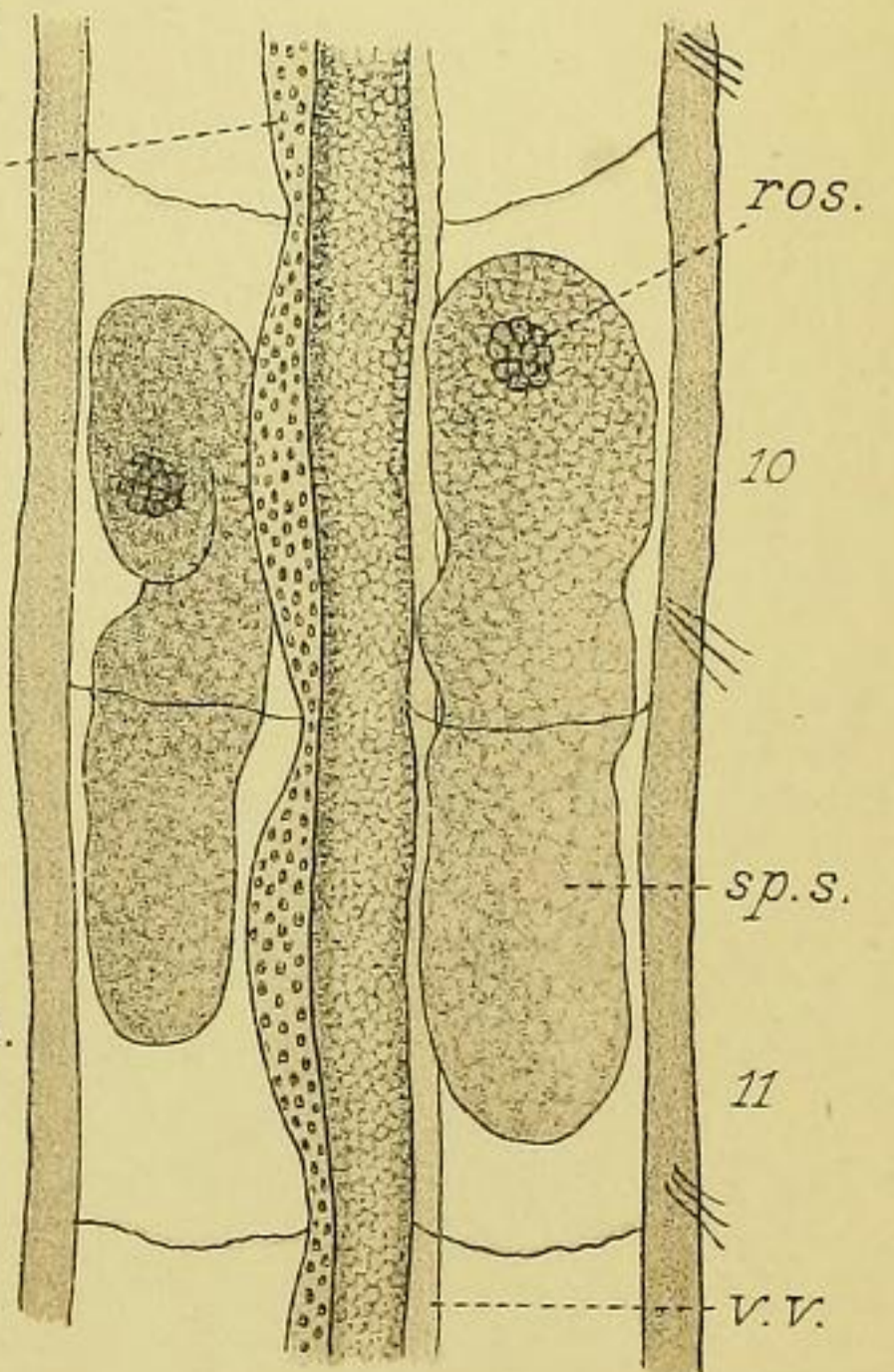
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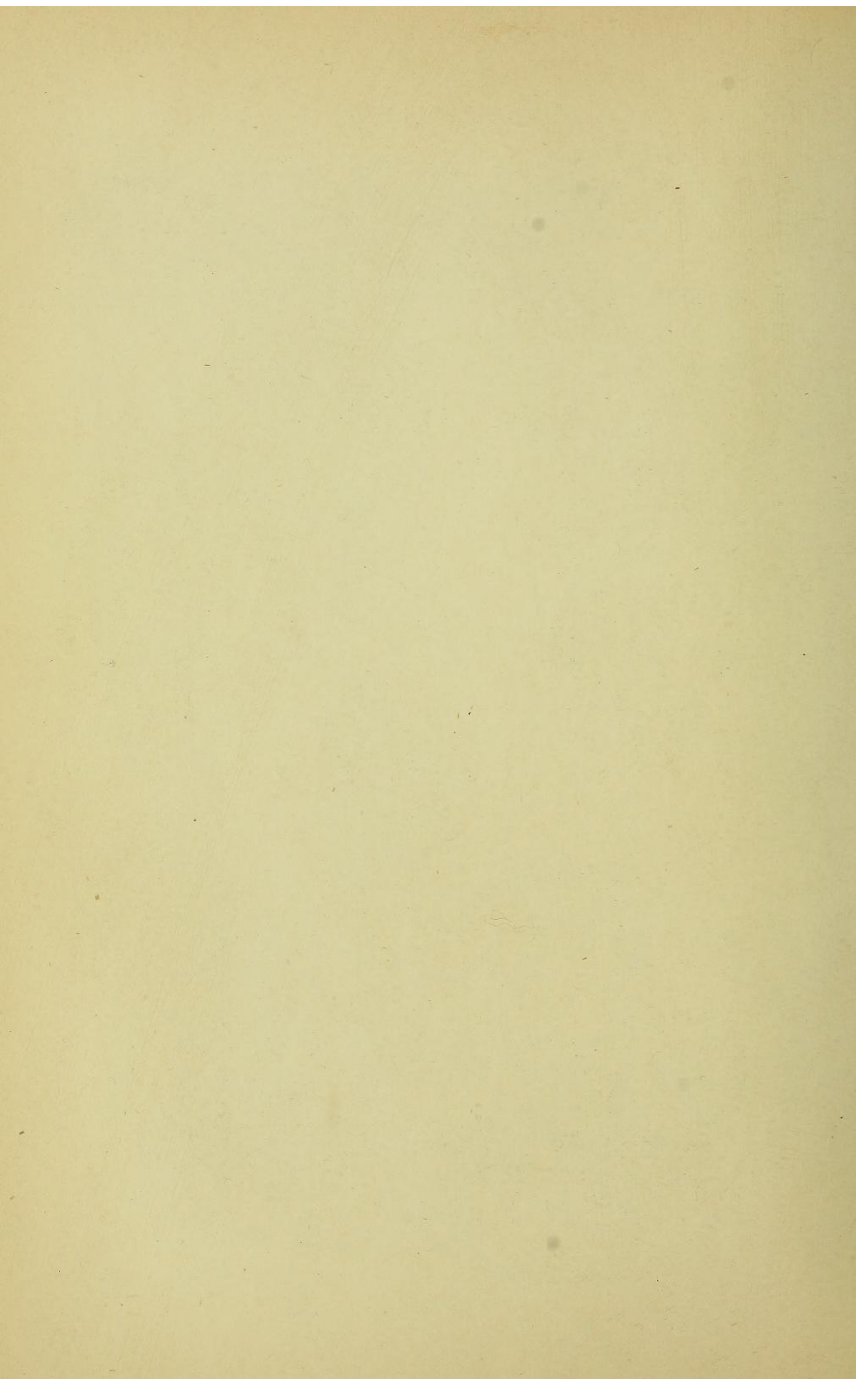


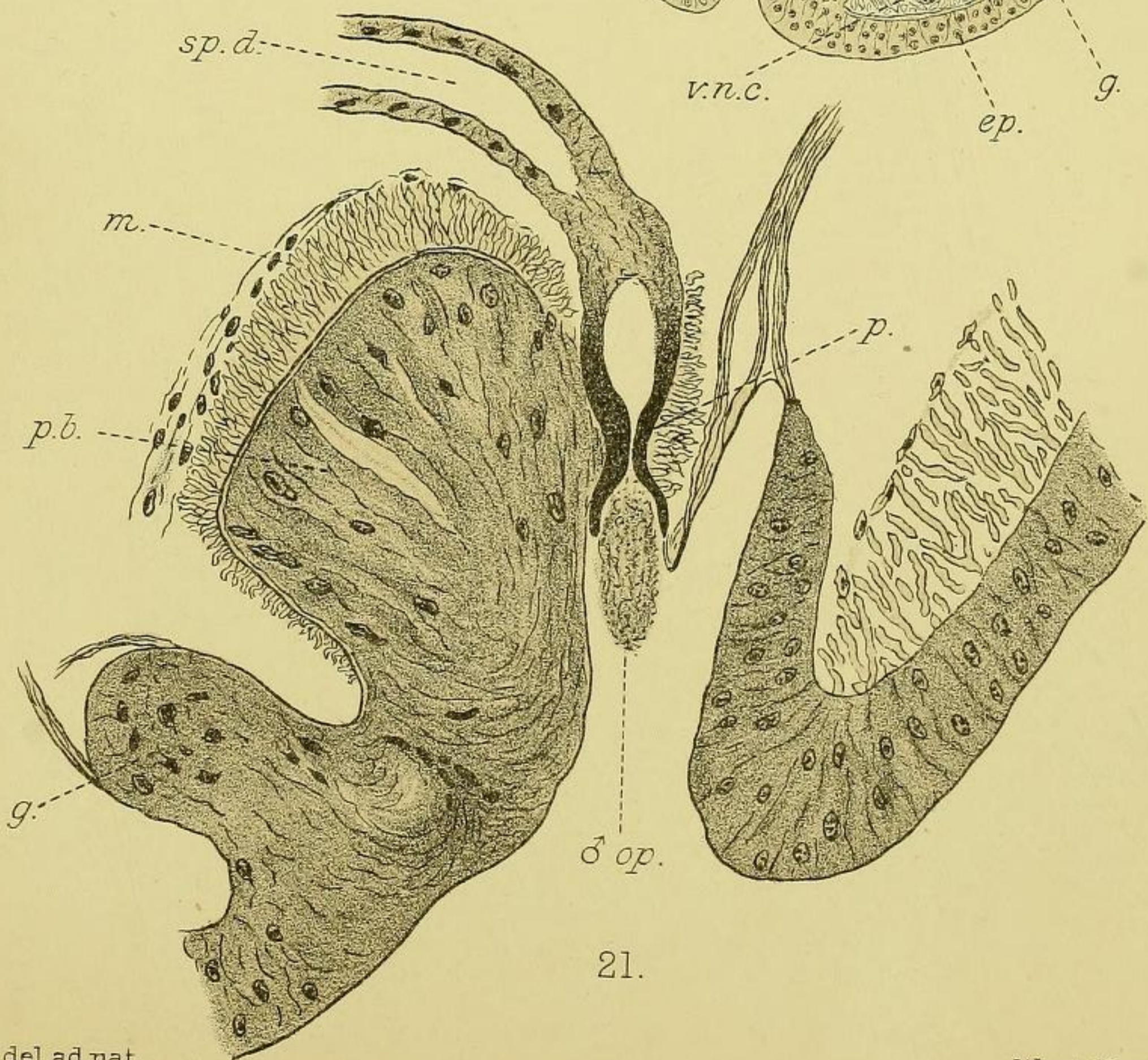
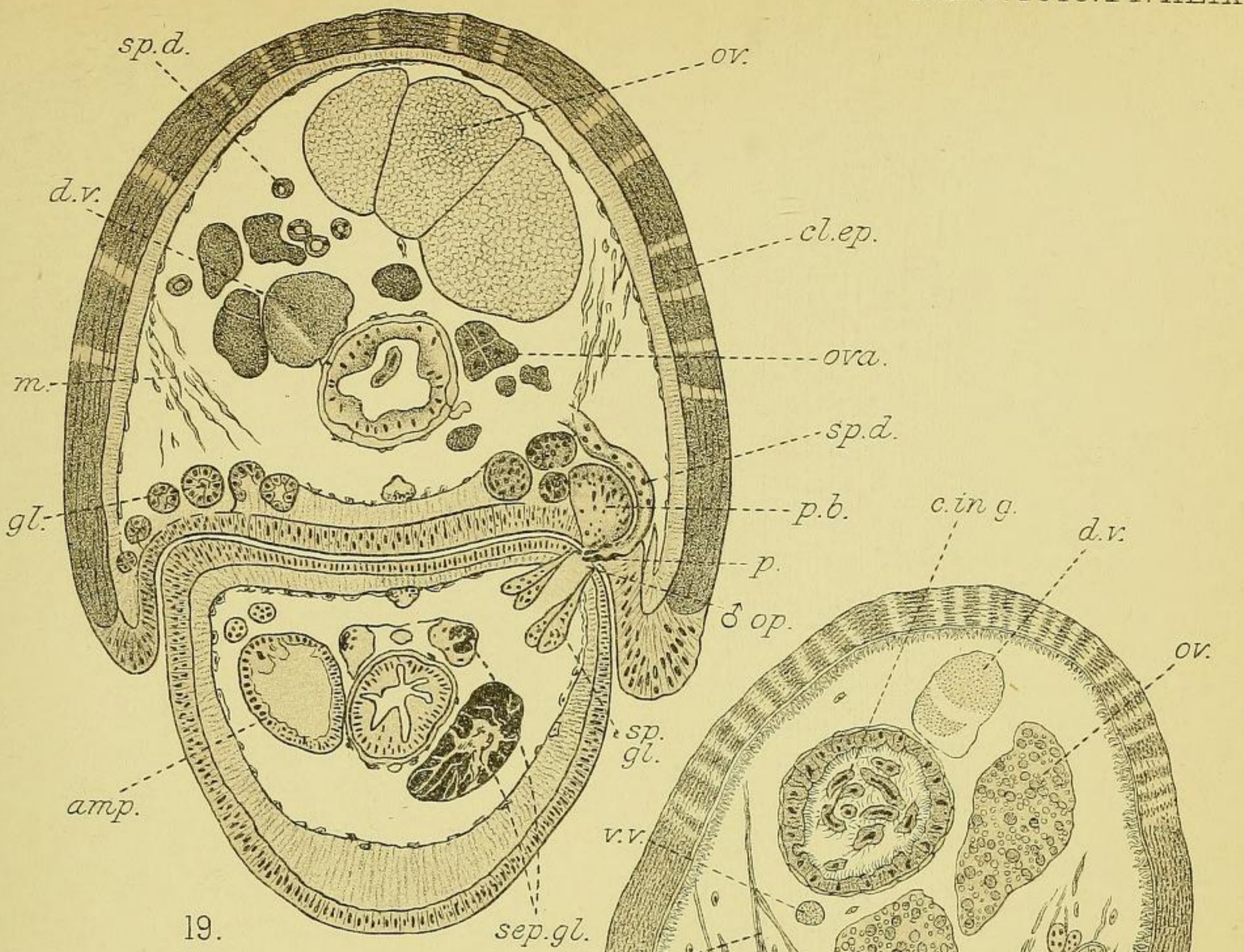
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ANATOMY OF ENCHYTRÆID WORMS.

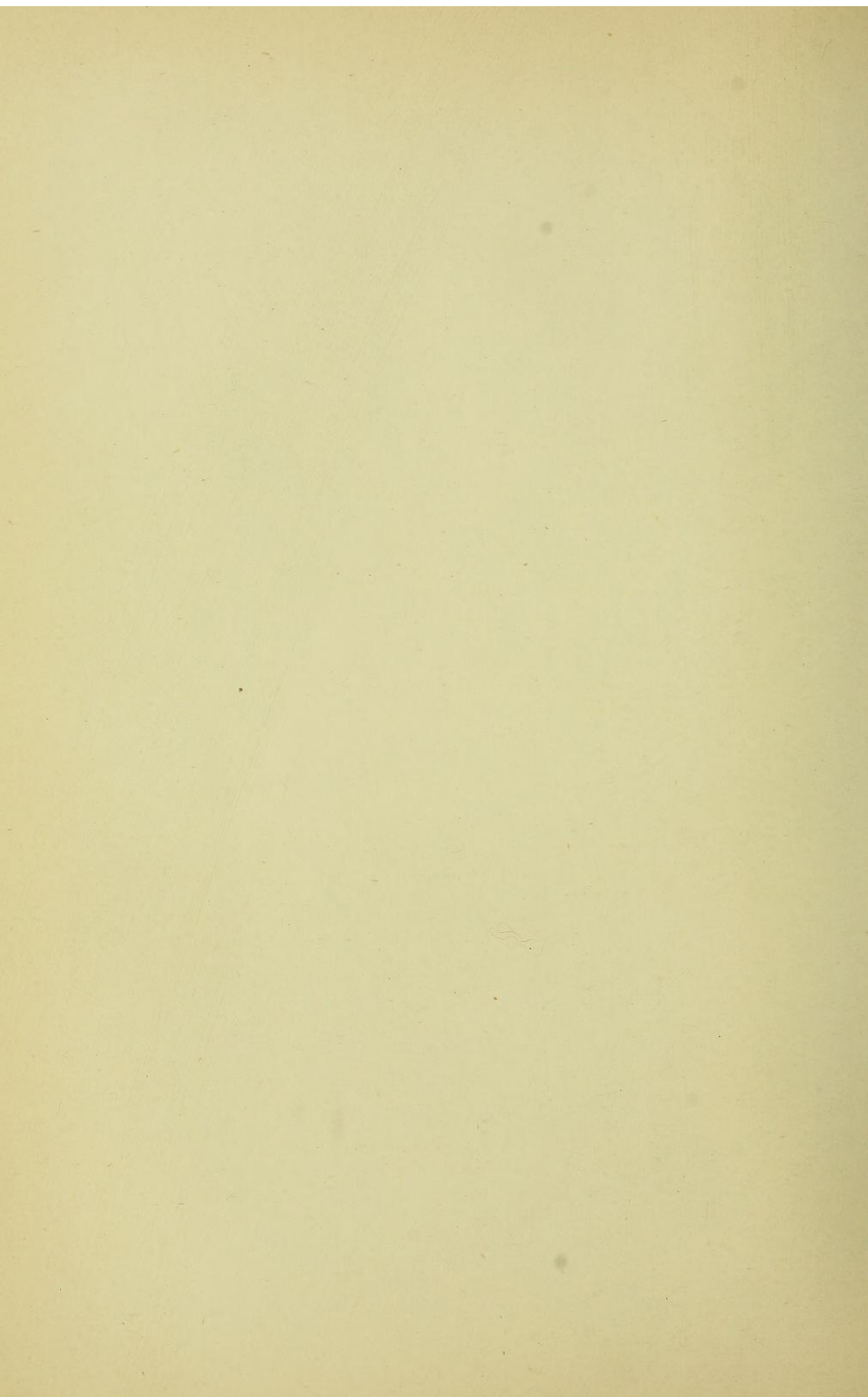




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West, Newman lith.

ANATOMY OF ENCHYTRÆID WORMS.



Goodrich (7) gives a good description of the nephridia and cœlomic corpuscles of a species of *Enchytræus*, but says very little about any other organs.

The Enchytræids are amphibious in their habits. They may be found in comparatively dry places, as in soil or leaf-mould; but they are also found in certain places where they are practically living an aquatic mode of life. A common resort of these Enchytræids is on the sea-shore, but when found here they are most abundant at the point where fresh water is running into the sea. Consequently, they are not purely land or aquatic animals, nor yet are they purely fresh-water or marine.

The Enchytræids or "white worms" have been found in recent years to be much more plentiful than was formerly supposed. They are found most abundantly wherever there is decaying vegetable matter, such as in leaf-mould, dead and decaying plants, etc. But they are also found, sometimes in large quantities, at the roots of living plants, and ultimately cause the death of these plants. Hewitt (18) found that an Enchytræid, viz. *Fridericia bisetosa* Levinsen, was the direct cause of the death of a number of larch seedlings. It became a great pest in the nursery, killing off the seedlings by eating away the living cortical tissue of the main root.

I, also, have found Enchytræids at the roots of living plants. In this case, the plant attacked was *Antirrhinum* from a garden in Edgbaston, Birmingham. The particular Enchytræid causing the damage was *Enchytræus argenteus* Mich. As in the case of the larch seedlings, the Enchytræids were found at the roots, destroying the living cortical tissue and leaving the central woody cylinder exposed.

On account of this the Enchytræids are probably of great interest from an agricultural point of view, and this paper is a preliminary attempt to discover the economic significance of these "white worms."

The Enchytræid I have chosen for this paper is *Enchytræus pellucidus* Friend (5), chiefly because I have an abundant supply of these worms, but also because I think this species is a good type of the whole genus *Enchytræus*.

There is a difficulty in determining some species of the Enchytræidæ, since the specific differences are sometimes very small. After having closely examined many specimens of *Enchytræus pellucidus* and also specimens of *Enchytræus albidus* Henle, which I was able to obtain in large quantities, I have come to the conclusion that *E. pellucidus* cannot be regarded as a distinct species, but only as a variety of *E. albidus*, and differing only slightly from it. According to Michaelsen (10), thirteen authors have, in eighteen papers, given to this worm, *Enchytræus albidus*, five generic and twelve specific names, so that it is evidently fairly common and probably varies in different localities.

Two of the chief distinctions between *E. albidus* and

E. pellucidus lie in the structure of the *brain* and *spermatheca*. The brain of *E. albidus* is definitely concave behind (Pl. XLVI. fig. 1), whilst that of *E. pellucidus* is rounded or convex behind (fig. 2); but this is a variable character, according to the state of tension of the worm, as I have seen the brain of *E. albidus* quite straight behind with no concavity at all, and also the brain of *E. pellucidus* with slight indications of a concavity behind. The spermatheca of *E. albidus* has a definite rosette of glands around the external opening of the duct (fig. 3), whilst *E. pellucidus* is described as having no such glands. But the duct of the spermatheca of *E. pellucidus* is irregular in outline, and in my sections it is seen that these irregularities are due to simple glands, which are not, however, in the form of a definite rosette as in *E. albidus*. Again, the habitat of these two species is the same, viz. old stable-manure and leaf-mould. In all other respects they are very similar.

Short Description of the most easily observed Characters of E. pellucidus.—It is a white transparent worm, from 15 to 20 mm. in length. The number of segments varies, but is usually about 60. The setæ are straight with the innermost ends slightly curved, giving them the appearance of hockey-sticks; the number of setæ is not absolutely constant, but is usually 4 in each bundle in front and 3 behind the clitellum. The brain is twice as long as broad when stretched to the fullest extent, and convex behind with pigment-spots at the posterior end. The nerve-cord is equally broad throughout. Salivary glands (peptonephridia) are present; they are not branched, but simply tubular and slightly coiled or undulating; the free ends are slightly swollen. Blood colourless; sperm-duct very long, often extends 10 or 12 segments behind the clitellum; it is internally ciliated very strongly along its whole length. Spermathecæ in segment 5 (external opening at intersegment 4/5), communicate with alimentary canal; ampulla large, filling up the whole of segment 5; no rosette of glands around the external opening of the duct.

Habitat.—My material of *E. pellucidus* was found abundantly in a heap of refuse which consisted for the most part of leaf-mould. In the heap were autumnal sweepings of leaves, grass cut from the lawn, soil, stones, and occasionally bundles of soaked brown paper. Although single worms were common throughout the whole heap, I often came across large quantities of these Enchytræids quite unexpectedly. When I did so, these worms always looked bigger and healthier, and a large percentage of them was always mature. I have always been able to get mature worms from this heap, whatever the month of the year; this points to the fact that they may be mature all the year round. In the laboratory I kept the Enchytræids in tin boxes with the leaf-mould in which they were found. They lived quite well here, but I always found that the number of mature worms

steadily decreased until, in about a month's time, I could not find a single mature worm. This heap of leaf-mould, which was situated in a garden in Edgbaston, Birmingham, has been my chief source of material. In the same heap were also numbers of the "Gilt-tail," *Dendrobæna subrubicunda*; this is interesting, as Friend has also noticed that certain Enchytræids are often associated with certain of the larger earthworms. A favourite retreat of the Enchytræids was between 2 or 3 decaying beech-leaves that had been tightly compressed, a handful of such decaying leaves often yielding 40 or 50 worms, many of which were quite mature. But I have also found groups of these worms between sheets of damp compressed paper in the heap, although one would be surprised if they obtained much nourishment from that. They were also fairly abundant on the under side of stones. They were very rarely present in any loose material, but seemed to prefer compressed material. Occasionally I have seen these Enchytræids boring their way inside blackened decaying leaves between the upper and lower epidermis. They were feeding on the soft tissue of the leaf, as an examination of the contents of the gut showed, and this suggests that Enchytræids may be quite an important factor in the formation of leaf-mould. These Enchytræids are also very gregarious in their habits; one often wonders if this is due to the worms collecting together at some point where there is a special advantage, *e. g.* nourishment, or whether it is due in some manner to rapid multiplication, owing perhaps to a similar advantage. I have isolated numbers of specimens with a view to seeing whether Enchytræids are capable of fission, but so far with a negative result.

ANATOMY.

The Pharynx, which is just behind the buccal cavity and occupies segment 2, is interesting because of a large pharyngeal ingrowth. This is an ingrowth of cells from the dorsal side of the wall of the pharynx. It occupies segments 2 and 3, and is composed of elongated spindle-shaped cells, which run dorso-ventrally. The nuclei of these cells are large, elongated, and distinct (Pl. XLVI. fig. 4). This pharyngeal ingrowth almost obliterates the cavity of the gut, reducing it to a small ventral channel. There is some connection between this ingrowth and the septal glands, but this will be referred to later. In this Enchytræid there is nothing in the nature of a stylet attached to the pharyngeal ingrowth, which has been described in *Enchytræus buchholzii* Vejd. (16). This stylet was said to be used for clinging to the roots of plants. The function of the pharyngeal ingrowth is not quite plain, but it may be some kind of sensitive organ, as these Enchytræids, when irritated, often evert the whole of the pharynx spasmodically, the pharyngeal ingrowth then hanging out like a tongue. The pharynx is extremely muscular, the muscles running obliquely backwards from it to the body-

wall. These are the muscles used when the pharynx is everted and then withdrawn. There is another ingrowth of cells from the ventral side, anterior to the pharyngeal ingrowth, but this is much smaller (fig. 4).

The Œsophagus gradually merges into the intestine; the actual point where œsophagus ends and intestine begins cannot be defined.

The Intestine can be seen quite plainly owing to its darker colour, due partly to the food in it and also to its external covering of cells which contain many oil-globules. It is constantly undergoing peristaltic contractions, the waves running from behind forwards. The intestine is covered over its whole length with chloragogen-cells. When these cells break away from the gut-wall, they are seen to be spherical, and contain numerous oil-globules of various sizes. The cells are about $16\ \mu$ in diameter. The intestine is internally strongly ciliated. Owing to the chloragogen-cells which cover the gut, I have never been able to see whether the ciliary current in the intestine begins at the anus and runs forward, or whether it runs backwards to the anus. Stephenson (17) has recently published some interesting considerations on the phenomena of antiperistalsis and ascending ciliary action in the intestine of aquatic Oligochætes. He has never observed ascending ciliary action from behind forwards in the Enchytræidæ, but thinks that it is very possible that such an action will be found to occur in this group. His reason for this is that "the inhalent function of the intestine is common in the aquatic Oligochæta, and is evidenced by a widely occurring ascending ciliary current in the intestine" (17, p. 74).

The problem of the nutrition of these Enchytræids is highly important. As already mentioned, I have seen Enchytræids situated *inside* decaying leaves and literally eating their way through the soft tissue of the leaf. When the contents of the gut is examined, it is found to consist chiefly of disorganized vegetable cells. These are usually brown and dead, but I recently examined the contents of the gut of an Enchytræid which had been feeding on the green living cells of a plant. In this case the contents of the gut was green in colour, and a greenish fluid was also slowly oozing out from the anus whilst the worm was under pressure. Green vegetable cells could be recognized, although they were being gradually disorganized. These were the soft parenchymatous cells of the leaf or stem. In contrast with these cells, the long vessels and tracheides of the vascular bundles were always extruded quite whole and apparently little changed. This would be due, no doubt, to their thick walls resisting the action of the digestive juices.

The epithelial cells of the gut are strongly ciliated (Pl. XLVI, figs. 4, 5). The nuclei of these cells stain deeply, and there are present numerous large vacuoles or spaces, which often contain masses of material; this material has no affinity for any stains, but is almost colourless. They suggest to me that nutrition may

take place, at least partly, by actual ingestion as well as by diffusion of liquid nutriment. To try to prove this I have made numerous experiments, but they were all unsuccessful. I kept worms alive for a time in a weak solution of methylene-blue, and then examined the cells of the gut to see if any of the solid indigestible particles had been ingested by the cells, but this was unsuccessful. I also tried feeding them on the scum from a hay infusion, which contained numerous cysts, but this was again unsuccessful. If the almost colourless material inside the vacuoles is not actually ingested from the gut, I can only think that it is some digestive liquid, formed by the epithelial lining of the gut in these vacuoles, and then gradually forced into the gut-cavity. This would mean that the vacuoles would be in the nature of small digestive glands. Still, the fact that the cells of the gut are so strongly ciliated, and the presence of these large spaces in the wall of the gut filled with masses of almost colourless material, point at least to the possibility of nutrition being partly by ingestion.

Salivary Glands.—The salivary glands extend as far back as the first pair of septal glands, which are situated in segment 4. They enter the œsophagus just behind the pharyngeal ingrowth (fig. 4). They are paired structures, each being a simple, undulating, tubular gland. Transverse sections show that each gland is of almost uniform thickness, ending in a slight swelling or ampullâ. Although these two simple tubular glands converge towards the same point just behind the pharynx, they open into the œsophagus quite separately on the dorsal side.

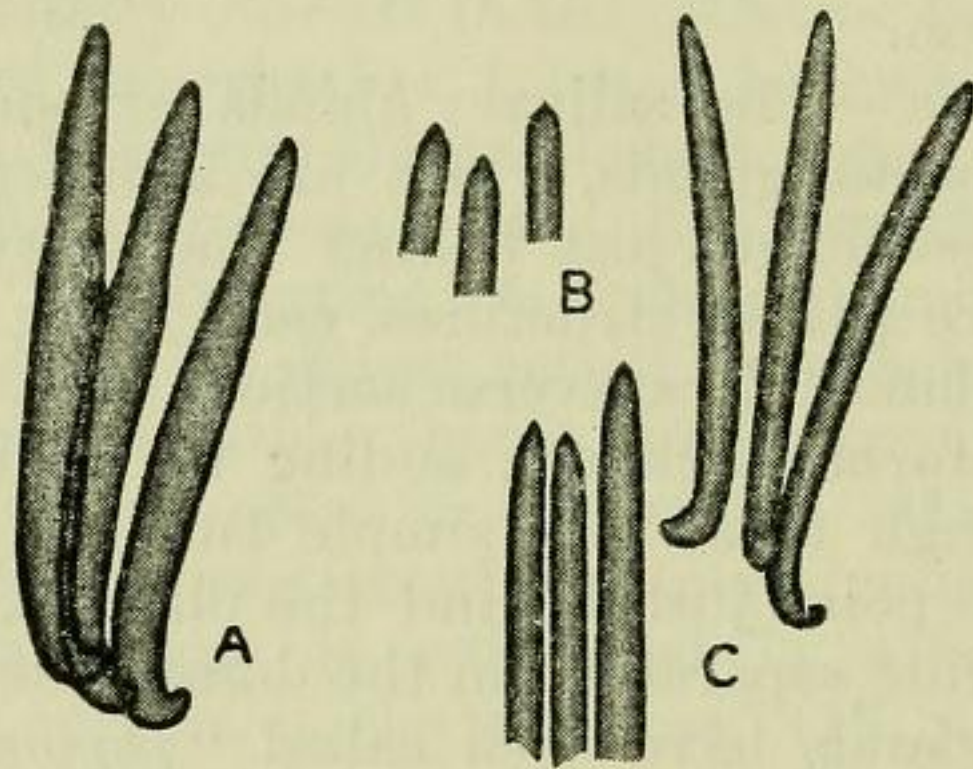
The salivary glands have been called "*peptonephridia*." The main characters which distinguish these glands from nephridia are (1) there is no opening to the cœlom, (2) there is no trace of a funnel, (3) the tubes are not ciliated, and in no Oligochætes are there nephridia which are entirely without cilia. On the other hand, the segments occupied by the salivary glands are devoid of other nephridia; and Beddard (1, p. 47) found that in *Octochætus multiporus*, the study of the development revealed the fact that the "salivary glands" were undoubtedly formed by the fusion of at least two pairs of nephridia, which were at first distinct and each provided with its own cœlomic funnel which is subsequently lost. This suggests that it is quite possible that in the earlier stages of the development of Enchytræids, the "salivary glands" might have had an opening into the cœlom, and if so, this would do away with one of the chief arguments against the nephridial nature of these "salivary glands." On the whole, however, it seems best to leave the nephridial or non-nephridial nature of the "salivary glands" an open question.

Setæ.—As before mentioned, the setæ are straight with the innermost ends curved like a hockey-stick. The setæ are slightly swollen in the middle (text-fig. 61 A). New bundles of setæ are constantly being formed by the side of the old ones. Text-fig. 61 B shows three setæ just beginning to be formed, and

text-fig. 61 C shows three setæ almost formed with the three old setæ close beside them.

Blood-system.—The intestine is surrounded by a blood-sinus which is in very close contact with the epithelial lining of the gut. In segment 15 the dorsal portion of this blood-sinus becomes swollen and is gradually pinched off to form a large dorsal vessel. The fact that this dorsal vessel is postclitellar in origin is an important generic character distinguishing the genus *Enchytræus* from most of the other genera in the family Enchytræidæ. This dorsal vessel is continued forward until it reaches segment 1. It then divides into two, each branch going backwards to the ventral side and uniting to form the ventral vessel. This ventral vessel continues, just ventral to the gut, to the posterior end of the worm. Both dorsal and ventral vessels are

Text-fig. 61.



Enchytræus pellucidus.

- A. Three setæ. B. Three new setæ just being formed.
C. Three setæ almost formed with the three old setæ close to them.

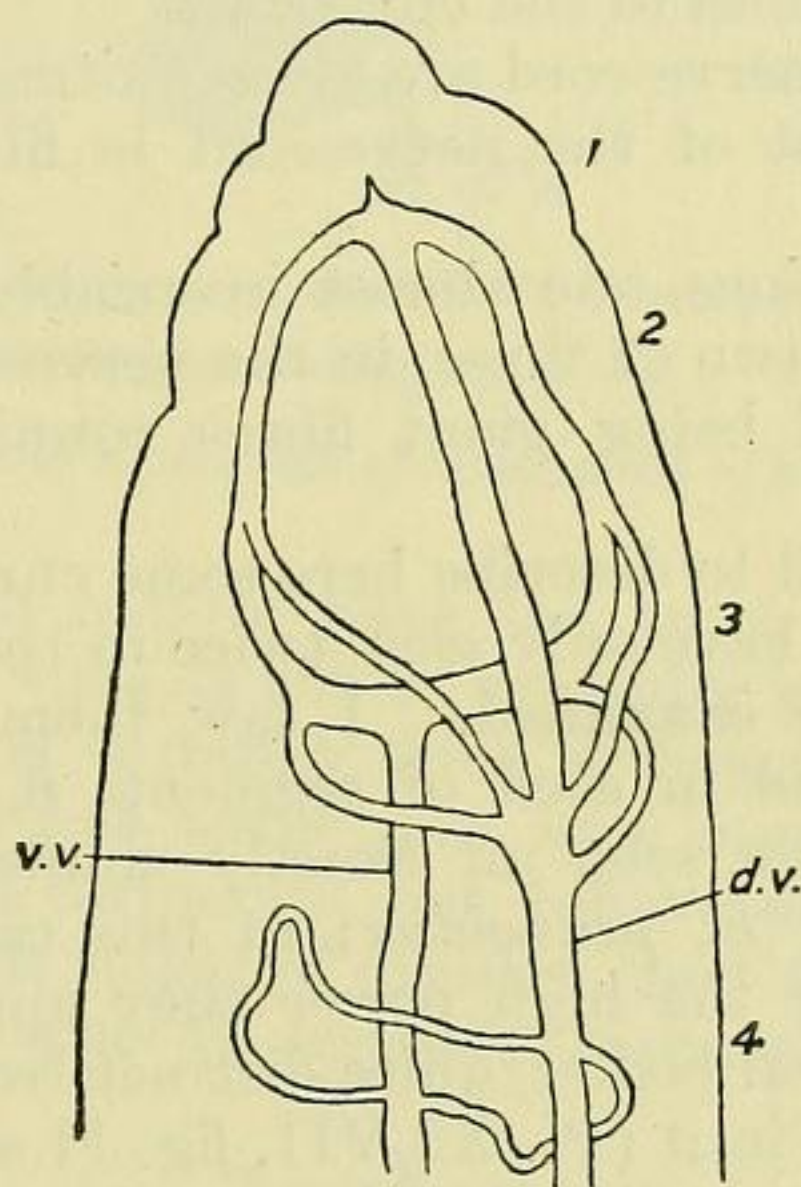
joined at intervals to the gut-sinus by small vessels (Pl. XLVII. fig. 10). There are three pairs of lateral vessels also in the anterior blood-system; two pairs are given off close together and join the two branches which form the ventral vessel, and one pair is given off just behind this and joins the ventral vessel proper. Text-fig. 62 represents this anterior blood-system.

The dorsal vessel, which is very large at its point of origin, is partly covered with chloragogen-cells, which also extend round the gut. At the point where the dorsal vessel arises, it swells and contracts rhythmically, sending the blood forward. I have seen no trace of the cardiac body, "a solid rod of cells attached to the ventral side of the dorsal blood-vessel, and extending along its whole length" (1, pp. 77-78), in *Enchytræus pellucidus*. This cardiac body was first described by Michaelsen in the genus *Mesenchytræus*. He suggested that this solid rod of cells served to ease the contractions of the dorsal vessel. The blood is a colourless fluid with no blood-corpuscles.

Nervous System.—The brain is dorsal in segment 1. Anteriorly it gives off two connectives which unite ventrally to form the ventral nerve-cord. The connectives can be traced in sections; they are in close approximation with the body-wall of the 1st segment and seem to be connected at this point with a ring of tissue which appears to be nervous. It may be this nervous ring of tissue which makes the 1st segment, including the prostomium, so extremely sensitive.

The brain is twice as long as broad when stretched to its fullest extent, and oval in shape. Posteriorly it is rounded, but occasionally shows signs of a concavity. The brain itself seems to be composed of two parts, a central core and an outer portion (Pl. XLVI. figs. 1 & 2). The outer portion is cellular in structure;

Text-fig. 62.

Anterior blood-system of *Enchytræus pellucidus*.

d.v., dorsal vessel; *v.v.*, ventral vessel.

the cells are small and numerous, and each one has a prominent nucleus. In preparations, the outer portion stains very deeply owing to the large number of nuclei. The central core is fibrous in structure with no nuclei showing.

Pigment-spots in the Brain.—At the posterior end of the brain there are numerous black spots in the outer cellular portion (fig. 2). These vary in number, usually 4 to 8, and are not regularly or symmetrically placed. Although these bodies have been mentioned by some authors, I have never seen them fully described, nor have I seen any suggestions as to their possible function. If the brain be carefully dissected out and examined under the high power of a microscope, the pigment-spots seem to be dark, granular or oily, with a clear spot in the centre. They are always present in this worm. Each black spot is composed

of a number of small, rounded, highly refractive bodies. From their appearance one would almost think they were ocelli of some kind. However, their function is, I believe, unknown, and more work is required upon them before they could definitely be called ocelli.

In *E. pellucidus* there is nothing in the nature of winged expansions to the nerve-cord, which have been described in some Enchytræids (6). The so-called "copulation-glands," which is the name given to masses of large cells which almost surround the nerve-cord in segments 13 and 14 (14), are not present in *Enchytræus pellucidus*.

The ventral nerve-cord sends out numerous branches to the body-wall. Fig. 12 (Pl. XLVII.) shows a longitudinal section of the body-wall passing through the nerve-cord. Here the nerve-branches are very thick strands and can be seen passing through the longitudinal muscles to the epidermis.

The nuclei of the nerve-cord are always situated in the ventral region only; the rest of the nerve-cord is fibrous in structure and has no nuclei.

In transverse sections, one almost invariably sees a number of clear spaces, usually two or three, in the nerve-cord. These have every appearance of being giant fibres running longitudinally along the cord.

It would be as well to describe here some curious bodies in the nerve-cord, which I have only seen twice in the large number of Enchytræids I have examined. I saw them first in a small immature Enchytræid in each of segments 8, 9, and 12. Just recently I have again seen an exactly similar body in a fully mature specimen of *E. pellucidus*; in this case it appeared in segment 14. Under the high power they appeared to be very granular, definite, oval bodies, quite distinct from the nerve-cord itself, but embedded in it (Pl. XLVII. fig. 11 *a, b*). I have seen no description of these bodies elsewhere, and am inclined to think that they were of a parasitic nature, but since I have only seen them twice, I have been unable to do more than describe them.

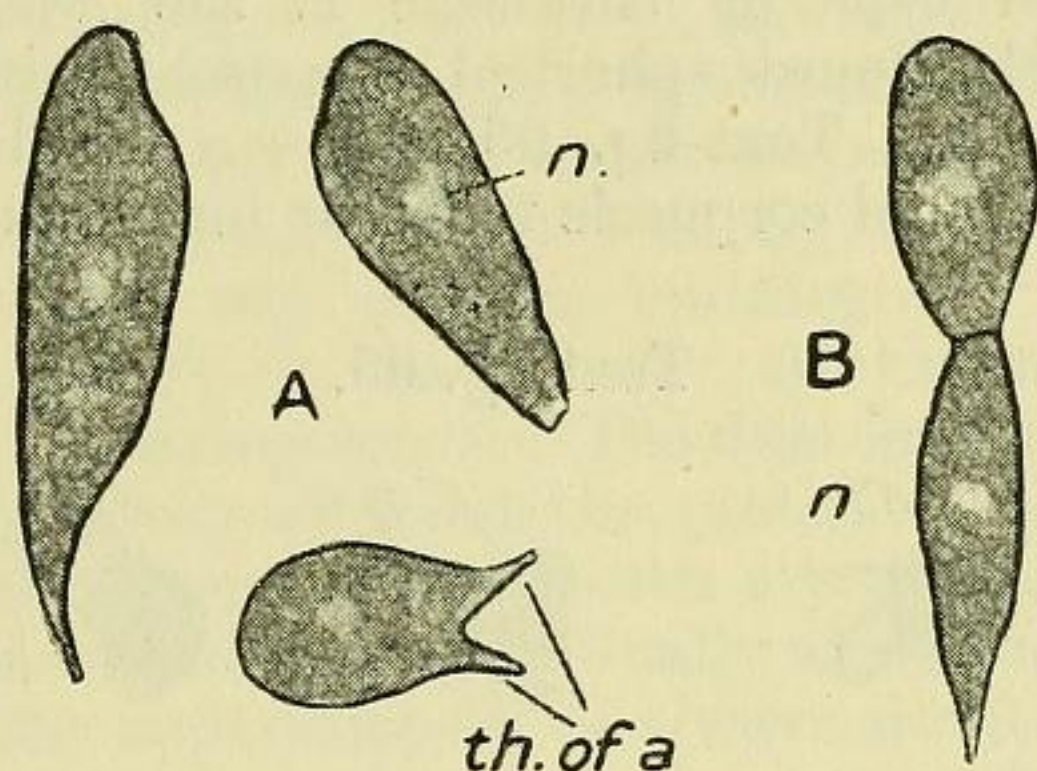
Cœlomic Corpuscles.—The cœlomic corpuscles in *E. pellucidus* are comparatively few in number. In some Enchytræids they are so numerous that it is very difficult to examine the various organs in the living worm; but *E. pellucidus* is so transparent that the nephridia, brain, etc., can be seen quite easily.

My observations on the cœlomic corpuscles agree very closely with those of Goodrich in his description of *E. hortensis* (7).

(*a*) By far the commonest and largest type of corpuscle is oval in shape and flattened (text-fig. 63 A). It varies from 47 μ to 23 μ in length and from 12 μ to 8 μ in breadth. It is very granular, with a clearer spot in the centre, the nucleus. It is usually rounded at one end and at the other end drawn out into one or two threads, the points of attachment to the cœlomic epithelium. Whilst examining the living worm, one can always see a number of these corpuscles attached to the walls of the

cœlomic cavity and the free ends moving about with the flow of the cœlomic fluid. The pressure of the cover-slip on the worm is all that is necessary to obtain these corpuscles, which are forced out through the *head-pore* to relieve the pressure. The head-pore is situated between the prostomium and the 1st segment in the dorsal median line. Very often, also, the cœlomic contents are

Text-fig. 63.



A. Cœlomic corpuscles of *Enchytræus pellucidus*.

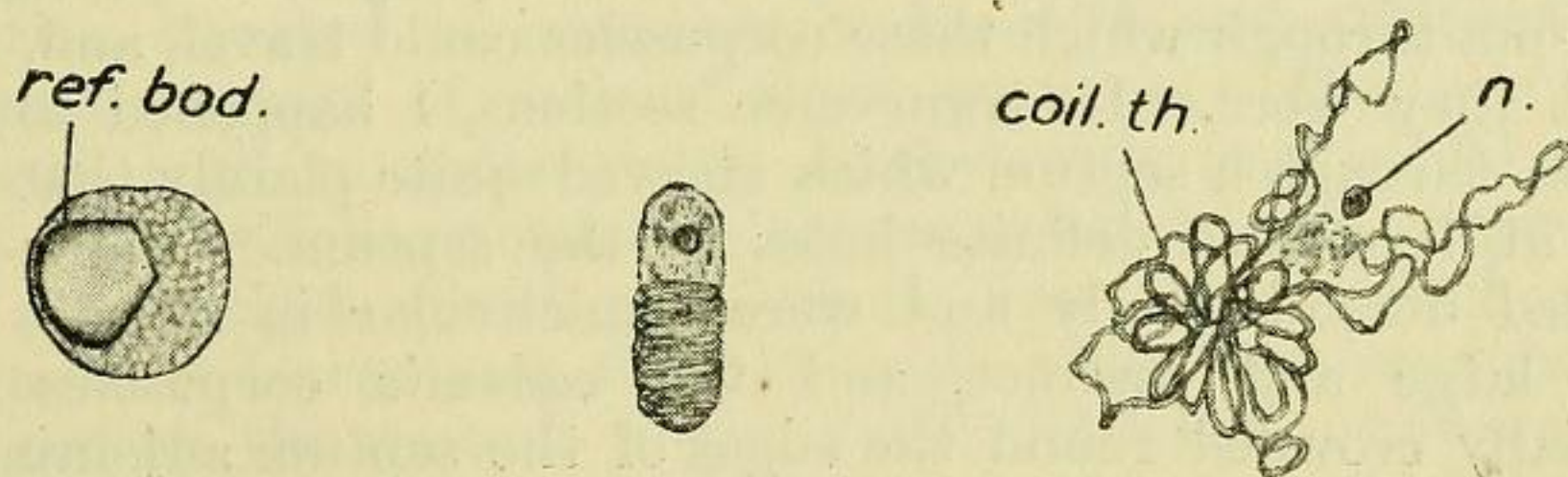
B. Corpuscle just dividing into two.

n., nucleus; *th. of a.*, threads of attachment to the cœlomic wall.

forced out through a pore near the anus. The presence of this pore near the anus is not so generally known as that of the head-pore, but it is certainly there, although rather difficult to see. Goodrich (7) has never seen any cases of multiplication by division of these corpuscles, but I have often observed these corpuscles in various stages of division (text-fig. 63 B).

(b) The second type of cœlomic corpuscle (text-fig. 64) is

Text-fig. 64.



Three stages in the disintegration of a cœlomic corpuscle of *Enchytræus pellucidus*.

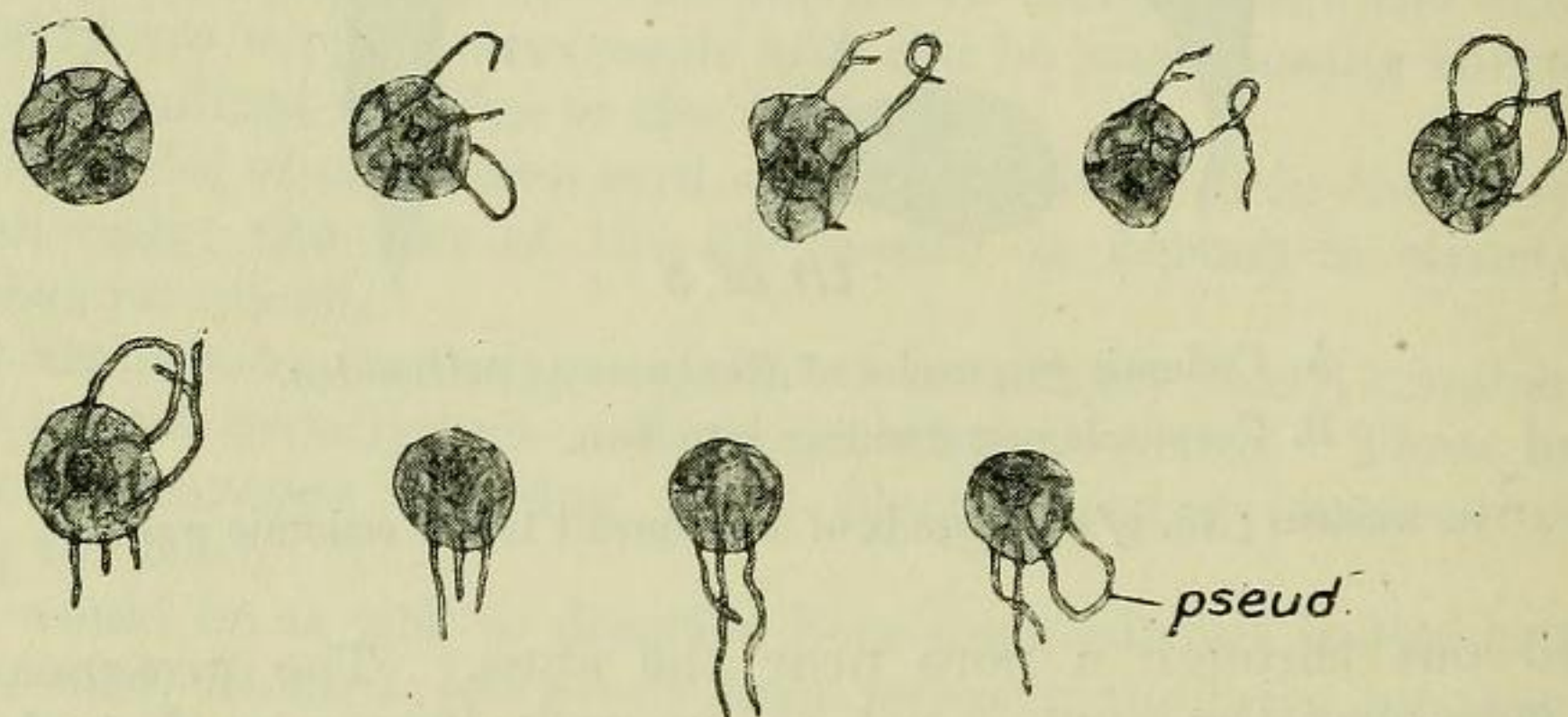
Ref.bod., refringent body; *coil.th.*, coiled thread; *n.*, nucleus.

smaller and not uniformly granular, but certainly seems, as Goodrich suggests, to be a variety of the first kind of corpuscle. In it there is a colourless and very refringent body, whilst the rest of the corpuscle is granular. The curious fact is that when

this corpuscle comes into contact with a strange fluid, such as distilled water, the colourless body swells and begins to show that it is really formed of a long thread of transparent substance. This long thread is very much coiled, and as it swells out the rest of the cell disintegrates. Text-fig. 64 shows three stages in the disintegration of one of these corpuscles. Salt solution is much the best medium in which to examine the cœlomic corpuscles, as they disappear very rapidly when put into distilled water.

(c) The third type of corpuscle is the *amœboid corpuscle*. This is a small, almost spherical corpuscle, with a number of clear pseudopodia. Text-fig. 65 shows a number of drawings of the same amœboid corpuscle taken at intervals of about half a minute.

Text-fig. 65.



Drawings of the same amœboid corpuscle of *Enchytræus pellucidus* taken at intervals of half a minute.

Pseud., pseudopodia.

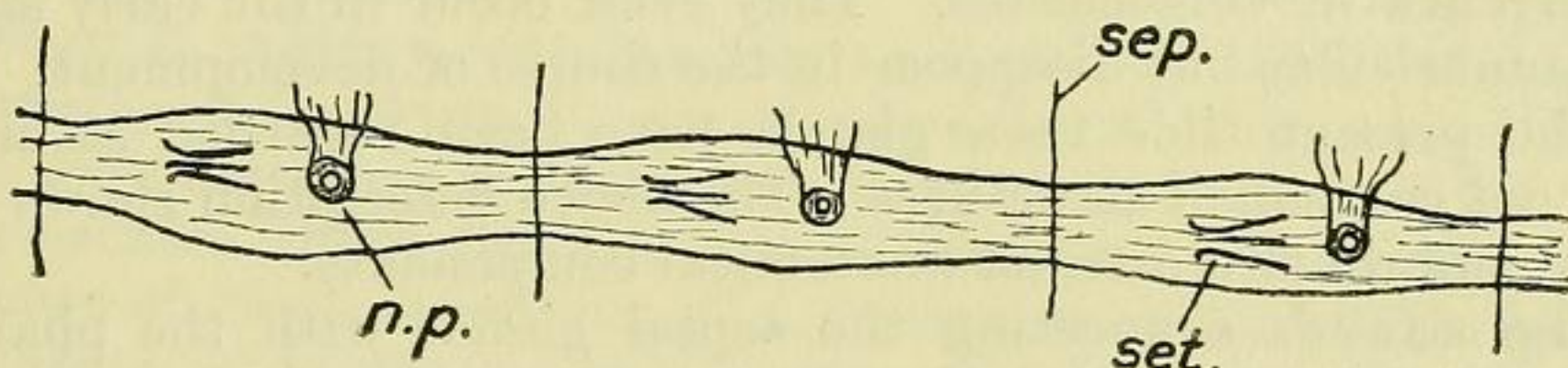
In the living worm one often sees the free cœlomic contents moving apparently through the septa from segment to segment. I often wondered whether there were any *definite* apertures in the septa through which these corpuscles could travel, and, if so, where they were. In transverse sections, I happened to get a section through a septum which showed quite plainly that there were at least two definite holes in the septum. These were situated dorso-laterally and were semicircular in shape. They were large and distinct, and the cœlomic corpuscles were especially crowded round the edges of the septum adjoining the hole.

Nephridia.—Goodrich (7) has given a full account of these organs in *E. hortensis*, a species closely allied to, if not identical with, *E. albidus*, and I have been able to confirm his excellent description in most particulars.

There are no nephridia in the first six segments, the first nephridium occurring in segment 7. The nephridium is a lobed flattened body (Pl. XLVII. fig. 13 a). It is composed of three parts, an anteseptal portion, the flattened body of the nephridium,

and the duct leading to the exterior. The anteseptal portion is small and consists of the funnel (fig. 13*b*). This funnel is composed of two lips. From the extremity of the upper lip are given off numerous very fine cilia, which wave about independently in the body-cavity. From the inner surface of the upper lip there also arises a number of long cilia, but unlike the external cilia these move simultaneously and rhythmically, forming an undulating bunch. The function of this bunch of undulating cilia is undoubtedly to propel liquid down the canal which leads from the funnel. The flattened body of the nephridium consists of granular cells, through which runs the nephridial canal. At numerous points (usually about 4 or 5), but not continuously through this canal, one can see bunches or "flames" of cilia similar to the bunch in the funnel. All this ciliary action can be observed in the living worm. The duct leading to the exterior is broad, and is given off from the posterior end of the body of the nephridium. The nephridiopores are arranged definitely on a band of tissue running longitudinally along each ventro-lateral surface, and the nephridiopore is always situated on this band just anterior to the setæ of each segment (text-fig. 66).

Text-fig. 66.



Drawing to show the position of the nephridiopores in *Enchytræus pellucidus*.

sep., septum; *set.*, setæ (ventral); *n.p.*, nephridiopore.

Septal Glands.—The septal glands are organs of unknown function situated in segments 4, 5, and 6, and attached to the posterior septum of each of these segments. They are always present, both in quite young *Enchytræids* and in old mature ones. In the living worm they appear as lobed organs surrounding the gut. Each gland consists of four lobes, which project forwards and surround the gut, being united on the dorsal side but not on the ventral. Fig. 14 (Pl. XLVIII.) shows a semi-diagrammatic drawing of these organs *in situ*, which has been obtained by reconstruction from a series of transverse and longitudinal sections. The septal glands are solid organs with no central cavity. I have examined numerous series of transverse sections, but have never been able to discover any opening into the gut. The gland itself (Pl. XLVIII. fig. 15*a* & *b*) consists of two parts; one part, which comprises the bulk of the gland, is composed of solid blocks of tissue. These are remarkable for the readiness with which they take up stains such as Hæmalum,

Hæmatoxylin, etc. The other part is in the nature of a connecting-link, and might be called the "core" of the septal glands. It consists of two solid nucleated strands, one on each side of the gut, which only stain slightly and connect together all the septal glands. Now, if these connecting-strands were hollow or tubular, one could easily understand that the septal glands were, in reality, glands, and that the connecting-strand was a duct to carry off their secretions. But the connecting-strands are solid, and appear quite incapable of carrying any liquid secretion. I have also been struck by the resemblance which these connecting-strands bear to nervous cords or strands, but in tracing them through series of sections I have been unable to find any connection with the main nervous system.

In segment 4, these solid strands leave the substance of the first septal gland and travel forwards parallel and close to the salivary glands. They then move towards the dorsal side and finally enter the substance of the large pharyngeal ingrowth on the dorsal side, first dividing into four or five branches (fig. 14).

Significance of Septal Glands.—Owing to the lack of observation upon the development of these organs there is considerable doubt as to their morphology, and still more as to their function. Beddard (1), quoting Vejdovsky, shows that they are of widespread occurrence in Oligochætes. They even occur in the early stages of Lumbricidæ, but disappear in the course of development. Up to the present time these glands have been regarded as single and not compound structures. The above description shows that they contain two distinct anatomical components.

The strands connecting the septal glands with the pharynx are not muscular, and therefore it seems as if they are not merely supporting strands. Neither are they ducts, and therefore, if the septal glands have a glandular function, one wonders how this internal secretion is transmitted to its destination. I am inclined to the view that the connecting solid strands are nervous, and if some connection with the central nervous system could be found, it would make the problem of solving what these organs are, considerably easier. If the connecting-strand is an epithelial structure, it is quite possible that it may originate as an outgrowth from the pharynx (*cf.* Outgrowths in Capitellids of Eisig), but even this will not explain the "core," which has such a delicate fibrillar structure. Nor can a simple septal origin be accepted, since in that case it would be difficult to understand the "gland" opening into the pharynx.

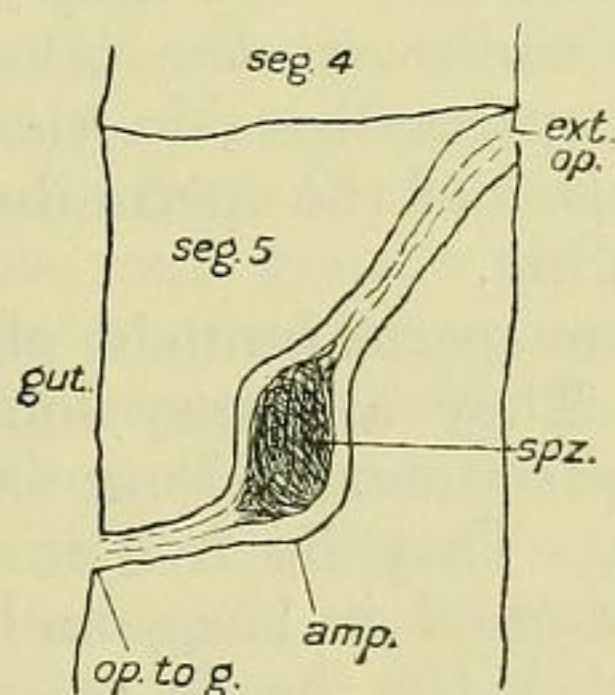
Reproductive Organs.—All existing accounts of the reproductive organs of Enchytræids are vague and incomplete. Certain of the reproductive organs are well understood, *e. g.* the male efferent apparatus consisting of the sperm-funnel and sperm-duct; but, on the other hand, the question of the female opening, the oviducts (if present), and the problem as to how such large ova as are found in Enchytræids escape by such insignificant female pores, are still unsolved.

According to Michaelsen (9), "The reproductive apparatus of *Enchytræids* varies very little. The testes are formed on the posterior side of the septum between segments 10 and 11, and the ovaries on dissepiment 11/12. Two sperm-funnels are present in segment 11. The sperm-ducts lead from the sperm-funnels, and each opens in a penis-like swelling on the ventral side of segment 12. A pair of oviducts open on the ventral side of segment 13. The spermathecæ lie in segment 5 and open externally on the intersegmental furrow, segments 4/5. The clitellum covers segment 12 and often parts of segments 11 and 13."

Spermathecæ.—In *Enchytræus pellucidus* the spermathecæ are present in segment 5. In the fully mature worm they are large organs, filling up practically the whole of the body-cavity in that segment. They open at intersegment 4/5.

The ampulla of the spermatheca is large and pear-shaped, with the narrow end anterior. In a mature worm, after copulation has taken place, the spermatozoa can be seen through the walls of the ampulla, giving it a definite golden-brown colour. The duct leading to the exterior is not so long as the ampulla, and in *E. pellucidus* has not got a definite rosette of glands around the external opening. Fig. 3 (Pl. XLVI.) shows the spermatheca of *E. albidus*, with the rosette of glands round the external aperture—it had been dissected away from the worm, and therefore the connection with the gut is not seen. To show how this spermatheca differs from the spermatheca in other species, I give a figure of the spermatheca of a mature specimen of *Enchytræus argenteus*. In this worm the ampulla of the spermatheca is merely a slight swelling of the spermathecal tube.

Text-fig. 67.



Spermatheca of *Enchytræus argenteus*, for comparison with fig. 3 (Pl. XLVI.)

spz., sperms in the ampulla; *amp.*, ampulla; *op. to g.*, opening of spermatheca into the gut.

The spermatheca always communicates with the gut (Pl. XLVIII. fig. 16), sometimes by a long connection and sometimes by a short one. In *E. pellucidus* the connection with the gut is short and wide. The fact that the spermatheca communicates

with the gut has been known for some time, but it has never been satisfactorily explained why this is so. My own observations show that spermatozoa are occasionally seen in the tube connecting the ampulla with the gut, but by far the majority are stored in the ampulla with their heads buried in the wall and their tails free in the cavity of the ampulla. In transverse sections, at the point where the spermatheca opens into the gut, I have occasionally seen a number of spermatozoa actually in the gut. Although they were quite near to the spermathecal opening, I think this observation supports the view that this connection between spermatheca and gut has some definite function, probably to allow the excess spermatozoa to escape from the spermatheca.

One can always see where the gut ends and the spermatheca begins, because the epithelial cells of the gut are ciliated, whilst those of the spermatheca are not.

Some time ago I had the good fortune to observe two Enchytræids in copulation. They were lying quite still, with the ventral surfaces very close together, so that the spermathecal opening in each worm was directly in touch with the male opening of the other worm. They were so tightly fixed together that even whilst killing and fixing them they did not separate, and so I was able to obtain sections through this region. Fig. 17 (Pl. XLVIII.) shows a drawing of the ventral clitellar region. From this it is seen that there is a shallow depression, overhung on each side by a lip. Underneath each lip and in the groove is the male opening. During copulation the fifth segment of one worm fits closely into this shallow depression and is held in position partly by the overhanging lip, but also probably by the secretion of certain glands in this region, to be described later. Fig. 19 (Pl. XLIX.) shows a drawing of a section through these two copulating Enchytræids. The ampulla of the spermatheca is seen on one side, whilst on the other side is the external opening of the other spermatheca in close approximation with the penis-like termination of the sperm-duct, which is protruding through the male opening.

Sperm-funnels.—The sperm-funnels of *E. pellucidus* occupy the clitellar region. They are very long, sometimes being as much as seven or eight times as long as broad, and are often bent upon themselves. They lie free in the body-cavity. The mouth of the sperm-funnel is large and has a swollen ridge, in which are embedded the heads of numerous spermatozoa. The tails of the spermatozoa hang out stiff and straight like the bristles of a brush, and when viewed in the living worm are of a beautiful golden-brown colour. The sperm-duct leads from the sperm-funnel and is very long and coiled. It is very strongly ciliated internally along the whole of its length. The coils of this sperm-duct are free in the body-cavity and often extend a dozen segments behind the clitellum before finally ending in the male opening on segment 12.

We now come to some gland-like bodies which are present in the clitellar region, and which I have not seen described before (Pl. XLIX. fig. 20). These bodies protrude into the body-cavity in the ventral region of segment 12 on both sides of the male openings. They are continuous with the epidermis, which in the ventral region is composed of true epidermal cells, as the clitellar epithelium does not extend over the ventral region. These bodies are usually solid and composed of a few cells; they are oval in shape and the cells have prominent nuclei. I have occasionally seen signs of slit-like cavities in them, but even then there has been nothing approaching a duct to the exterior. One can see quite clearly that the cells forming these glands are continuous with the epidermal cells, and they have evidently been formed as impittings from the epidermis. The muscular system in this region is also slightly modified. Surrounding these glands are strong muscles, which are continued obliquely across the body-cavity to the lateral wall. These oblique muscles are not found anywhere else, except in the region of these glands. I think the most probable solution of the function of these glands is that they form some kind of secretion which helps to make the worms adhere together closely during copulation.

Male Opening.—The actual male opening is worthy of note. The sperm-duct ends in a peculiar chitinous-like thickening (Pl. XLIX. fig. 21). This penis-like thickening of the sperm-duct opens to the exterior in a groove. It does not pass through the so-called penial bulb, but only skirts the edge of it. The penial bulb (fig. 21) has every appearance of being simply one of these ventral clitellar glands just described, but it is always rather bigger. The cells composing it are continuous with the epidermis, and it has a very strong muscular coat.

Sperm-sacs (Vesiculæ Seminales).—Beddard, in his 'Monograph of the Oligochæta,' says: "In only one family of Oligochætes are the sperm-sacs nearly always absent; this family is the Enchytræidæ. The genus *Mesenchytræus*, however, has paired sperm-sacs which originate from the septum bounding posteriorly the segment in which the male gonads lie."

In *E. pellucidus* there are two large sacs filling up almost the whole of the body-cavity in segments 10 and 11. These sacs are filled with sperm mother-cells and masses of spermatozoa in various stages of development. Since 'sperm-sacs' is the name given to sacs in which the sperm undergoes most of the stages of its development, then these sacs in *E. pellucidus* are undoubtedly sperm-sacs, and not testes. As to the true testes, I cannot say that I have ever seen them, but the following may have some reference to them.

In certain Enchytræids which are not quite sexually mature, *i. e.* when the ovaries and sperm-funnels are small, I have noticed a peculiar rosette of small cells in the anterior end of each sperm-sac. This mass of cells, when seen in the living animal, is of a definite golden-brown colour (Pl. XLVIII. fig. 18).

Ovaries and Oviducts.—The ovaries are situated in segment 12. In the mature worm the ova are so large that they almost fill up the whole of the body-cavity in that region, and are of a pure white colour. When ripe, they break away from the ovary and lie apparently quite freely in the body-cavity.

In the lower Oligochætes there are no special ducts for the ova, e. g. *Æolosoma* simply has a median pore. Beddard (1) says that "the structure of the oviducts in Enchytræids is such as to suggest a degenerate condition." D'Udekem's opinion was that the sperm-ducts served as ducts for the ova also. Later it was suggested that there might simply be pores in the body-wall through which the ova might escape to the exterior. For some time these pores could not be found, but Claparède (4) at last described a pair of pores behind the male pores in *Enchytræus vermicularis*, and these were afterwards verified by Vejdovsky and Michaelsen. However, both Vejdovsky and Michaelsen regarded them as mere pores for the escape of the ova without any trace of oviducts. Beddard (2) has described the oviducts in *Pachydrilus* (Enchytræidæ). They consist of a few pear-shaped cells, not ciliated, which fringe the orifices. He regards them as degenerate oviducts.

My own observations on *E. pellucidus* show that there is certainly a pair of these pores in the body-wall in segment 13. But, instead of a few non-ciliated cells fringing these openings, it is quite plain that these two pores communicate with a single, large, thin-walled sac, which fills up almost the whole of the body-cavity in this region. Since the mature ova in this Enchytræid are large, then either the ova are capable of altering their shape with ease or else these pores are capable of great distension. The former seems to be most likely, as there are no extra muscles connected with these female pores.

APPENDIX.

Astomatous Ciliate Protozoa in the Gut.

Whilst working at the alimentary canal of this worm, I was surprised to come across numbers of large ciliates living commensally in the gut. They were usually found in the middle region, and not at the posterior or anterior ends of the gut. There were often so many of them present that they almost filled the cavity of the intestine. Many of these ciliates showed signs of budding; it was quite a common occurrence to come across a ciliate with anything from one to six buds at the hinder end, and the pressure of the cover-slip was only required to make one or two of the buds break off and swim about independently.

The largest and commonest of these ciliates living in the gut was *Mesnilella fastigiata* (3). The length of this ciliate varies considerably, but an average length is .3 to .4 mm. It is elongated and cylindrical in shape, with a

curious swelling at the anterior end on one side. The most characteristic feature is a strong chitinous-like spicule running from one end through the body of the ciliate, and ending at about two-thirds the length of the body in a fine curled thread, almost like the lash of a whip (Pl. XLVI. fig. 6). The protoplasm is granular, and there are parallel ridges running along the whole length of the body, on which rows of cilia are constantly in motion. The macronucleus is very long, extending the whole length of the body, and there are numerous vacuoles present. The micronucleus could not be seen in my own preparations, and is, I believe, unknown. Fig. 5 shows a longitudinal section through the gut, in which a number of these ciliates is present.

Less frequently I have found three other ciliates in the gut. The first is shown in fig. 7. It is somewhat similar to *Mesnillella*, although not usually so large. It is chiefly distinguished from *Mesnillella* by the absence of the spicule. The ciliate shown in fig. 7 had five buds attached.

The next ciliate was much smaller, and I have never seen any signs of it budding. Its shape is difficult to describe, and can be best realized from two drawings illustrating the ciliate turning round on its short axis (Pl. XLVII. figs. 8 *a* & 8 *b*). It measured 90 μ by 30 μ . This ciliate was also without a spicule.

The last ciliate I observed was again much smaller than *Mesnillella* and of a peculiar shape. It is best described as hat-shaped (figs. 9 *a* & 9 *b*). The macronucleus was long and slightly curved. Vacuoles were present, and were situated in two longitudinal rows. I have not been able to discover any description of the three last-mentioned ciliates.

Summary of New and Confirmatory Observations.

(1) *New Observations.*

(a) *The Presence and Structure of the peculiar Black Spots at the Posterior End of the Brain.*—These spots were not arranged definitely, but were scattered about in the outer *cellular* portion of the brain. When the brain was dissected out and examined under a high power ($\times 1000$), each of the spots was seen to be composed of a number of small, spherical, oil-like globules. Although at first I thought these bodies were very similar to ocelli, I have come to the conclusion that they are probably of the nature of very minute oil-globules. The reason for this is that they cannot be seen in any of my preparations or sections which have been treated with xylol or cedar-wood oil. However, the true meaning of these black spots in the brain is by no means clear as yet.

(b) *The Structure and Significance of the so-called "Septal Glands."*—Hitherto these glands have been regarded as single and not compound structures. The description given shows that they contain two definite anatomical components. The meaning of the connection of the septal glands with the pharynx is not

understood, and makes the question of the origin of the septal glands much more complicated. The structure of the strands connecting the septal glands with the pharynx leads one to try and discover whether these strands are connected in some manner with the nervous system, but my own observations prove most conclusively that they end blindly in the substance of the pharyngeal bulb.

The diagram of the septal glands (Pl. XLVIII. fig. 14), reconstructed from series of transverse and longitudinal sections, is useful in enabling one to understand the exact shape of these glands and also their relation with the gut and the solid strands connecting the glands. Most existing drawings of the septal glands are sketches taken from the living animal, and, although these give one a rough idea of their shape, they are never very satisfactory.

(c) *Presence of a thin-walled Ovisac which communicates with the Exterior by two Pores in Segment 13.*—Although in my preparations ova have not been actually seen in this thin-walled sac, there can be little doubt but that it is an ovisac. The fact that it communicates with the female pores on segment 13 proves that ova must, at some time, be present in the sac in order to escape to the exterior by the female pores.

(d) *The ventral clitellar Glands.*—It seems likely that the function of these glands is to secrete a substance which will enable two copulating Enchytræids to be held firmly together. My own observations on two copulating Enchytræids show that there is certainly something which enables the two worms to adhere very closely together.

It is difficult to account for the extraordinary muscles which cover these glands and extend obliquely across to the body-wall.

According to anatomical evidence, the "penial bulb" is simply an enlarged ventral clitellar gland. It is epidermal in origin like the ventral glands near it, and has a similar but slightly thicker muscular coat.

These ventral clitellar glands (although it is quite likely that they are "copulation-glands") must not be confused with the masses of large cells which almost surround the nerve-cord in some Enchytræids (segments 13 and 14), and which have also been called "copulation-glands."

(e) *Astomatous Ciliate Protozoa in the Gut of Enchytræids.*—Altogether four different kinds of these ciliates have been found in the gut of *E. pellucidus*. The commonest and largest of them was *Mesnillella*; this was also the only one which had the chitinous-like rod or spicule. This ciliate has already been recorded and described by Cépède in his extremely useful work on the Astomatous Infusorians (3), but I have not been able to find any records or descriptions of the other three ciliates, so that they may be quite new.

(f) *Observations on two Copulating Enchytræids.*—These observations on two Enchytræids in copulation are interesting, as one

rarely sees such convincing evidence as a transverse section passing through the male opening of one Enchytræid and the spermathecal opening of the other. The Enchytræids were evidently killed and fixed just after the sperms had been actually transferred to the spermathecæ by means of the sperm-ducts.

(2) *Confirmatory Observations.*

After a fairly exhaustive examination of the nephridia and cœlomic corpuscles, I have been able to confirm the excellent observations of Goodrich (7) in most particulars.

In conclusion, I must thank the Birmingham Natural History Society for helping me in this work by means of a grant from the Endowment of Research Fund, and I should also like to express my deep indebtedness to Professor Gamble for his kindly help and most valuable criticism.

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EXPLANATION OF THE PLATES.

PLATE XLVI.

- Fig. 1. Brain of *Enchytræus albidus* Henle.
2. Brain of *Enchytræus pellucidus* Friend. *cf.*, central fibrous portion; *o.cell.*, outer cellular portion; *conn.*, œsophageal nerve-connectives; *bl.sp.*, black spots on brain.
3. Spermatheca of *Enchytræus albidus*, dissected from the worm. *ext.op.*, external opening; *ros.gl.*, rosette of glands; *amp.*, ampulla.
4. Longitudinal sagittal section of *E. pellucidus* through the first four segments. *ph.b.*, pharyngeal bulb or ingrowth; *br.*, brain; *sal.gl.*, salivary gland opening into pharynx; *m.*, muscles attached to pharynx; *sept.gl.*, septal glands; *sp.*, spermatheca; *œs.conn.*, œsophageal nerve-connective; *mt.*, mouth.
5. Longitudinal section of the gut, to show ciliates in the gut and structure of gut-wall. *cil.*, ciliates in gut; *vac.*, vacuoles between the cells, sometimes containing a colourless mass.
6. *Mesnilella fastigiata*, found in the gut of *E. pellucidus*. *mac.n.*, macronucleus; *sp.*, spicule; *vac.*, vacuole; *sw.*, characteristic swelling at one end.
7. Ciliate with five buds, found in the gut. *mac.n.*, macronucleus; *vac.*, vacuoles.

PLATE XLVII.

- Fig. 8. Two views (*a*) and (*b*) of another ciliate from the gut.
9. Two views (*a*) and (*b*) of a fourth ciliate from the gut. *mac.n.*, macronucleus; *vac.*, vacuoles arranged in two longitudinal rows.
10. Transverse section to show the small blood-vessels connecting dorsal and ventral vessels with the blood-sinus surrounding the gut. *d.v.*, dorsal vessel; *v.v.*, ventral vessel; *chl.cells*, chloragogen-cells surrounding the gut; *neph.*, nephridium; *v.n.c.*, ventral nerve-cord.
11. (*a*) Diagram of segments 8-12, to show peculiar bodies in the nerve-cord. (*b*) Nerve-cord, with one of these bodies embedded in it (much higher power). *v.n.c.*, ventral nerve-cord; *gr.bod.*, granular bodies in the nerve-cord.
12. Longitudinal section through nerve-cord and ventral body-wall. *ep.*, epidermis; *c.m.*, circular muscles; *l.m.*, longitudinal muscles; *n.b.*, nerve-branch; *v.n.c.*, ventral nerve-cord; *n.*, nuclei.
13. (*a*) Nephridium. (*b*) Nephridial funnel. *n.f.*, nephridial funnel; *ext.c.*, external cilia; *n.c.*, nephridial canal; *b.c.*, bunch of cilia; *ext.duct.*, duct to the exterior; *sept.*, septum; *up.l.*, upper lip; *l.l.*, lower lip; *int.cil.*, internal bunch of cilia; *ext.cil.*, external independent cilia.

PLATE XLVIII.

- Fig. 14. Semi-diagrammatic drawing of the septal glands, obtained by reconstruction from sections. *ph.*, pharynx; *sal.gl.*, salivary glands; *lob. of sep.gl.*, lobe of the septal gland in segment 5; *sol.st.*, solid strands connecting septal glands with pharynx.
15. (*a*) Longitudinal sagittal section through segments 4-6, showing septal glands: *sp.*, spermatheca; *ph.m.*, pharyngeal muscles; *d.v.*, dorsal vessel; *sept.gl.*, septal gland in segment 6; *s.c.*, solid cord connecting the three septal glands; *sal.gl.*, salivary glands. (*b*) More magnified view of part of the previous section: *bl.*, solid blocks of tissue; *s.c.*, solid cord connecting the three septal glands.

- Fig. 16. Transverse section through the spermatheca, showing communication with the gut. *sp.amp.*, spermathecal ampulla; *comm.g.*, communication with gut; *d.v.*, dorsal vessel; *sep.gl.*, septal glands; *v.n.c.*, ventral nerve-cord.
17. Drawing of the ventral clitellar region. *lip*, lip overhanging the groove in which the male pore is situated.
18. Diagrammatic drawing of segments 10 and 11 of a young mature Enchytræid, showing the sperm-sacs. *d.v.*, dorsal vessel; *sp.s.*, sperm-sac; *v.v.*, ventral vessel; *ros.*, rosette of cells in the sperm-sac.

PLATE XLIX.

- Fig. 19. Transverse section through two copulating Enchytræids. *ov.*, ovary; *cl.ep.*, clitellar epithelium; *sp.d.*, sperm-duct; *p.b.*, penial bulb; *p.*, penis; *op.*, male opening; *sp.gl.*, spermathecal glands; *sep.gl.*, septal glands; *amp.*, ampulla of spermatheca; *gl.*, glands in the ventral clitellar region; *m.*, muscles attached to these clitellar glands and the body-wall; *d.v.*, dorsal vessel.
20. Transverse section through segment 12 to show gland-like bodies in the ventral clitellar region. *d.v.*, dorsal vessel; *ov.*, ovary; *cl.ep.*, clitellar epithelium; *g.*, gland-like bodies continuous with the epidermis; *ep.*, epidermis; *v.n.c.*, ventral nerve-cord; *m.*, muscles connecting gland-like bodies obliquely with the body-wall; *v.v.*, ventral vessel; *c. in g.*, ciliates in gut.
21. Highly magnified section through the male opening. *sp.d.*, sperm-duct; *p.*, penis-like thickening; *op.*, male opening; *p.b.*, penial bulb; *m.*, muscles around the penial bulb; *g.*, ventral clitellar gland.

25. The Relationship of the Big Game of Africa to the spread of Sleeping Sickness. By Dr. W. YORKE, Liverpool School of Tropical Medicine*. With an Appendix containing Remarks by Sir JOHN BLAND-SUTTON, F.R.C.S., F.Z.S.; GUY A. K. MARSHALL, F.Z.S.; Prof. E. A. MINCHIN, M.A., F.R.S., V.P.Z.S.; The Hon. L. WALTER ROTHSCHILD, D.Sc., F.R.S., F.Z.S.; Sir HENRY SETON-KARR, K.C.M.G., F.Z.S.; and Sir ALFRED SHARPE, K.C.M.G., LL.D.; and Reply by Dr. YORKE.

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Although Sleeping Sickness has been recognised as a disease on the West Coast for nearly two hundred years, human trypanosomiasis was unknown in Nyasaland and in the greater portion of Rhodesia until 1908. At the end of that year the first case of the disease was found in Nyasaland, and during 1909 and 1910 a considerable number of cases were discovered amongst the Europeans and Natives living in Nyasaland and Rhodesia. This state of affairs was not easy to understand, as the particular tsetse fly, *Glossina palpalis*, which is known to transmit Sleeping Sickness in other parts of Tropical Africa, has not been found in these countries.

In 1910, it was shown that the parasite causing the disease in Nyasaland and Rhodesia differed in certain respects from that

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