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, Anglian Institute of Agriculture, Chelmsford ‡.

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

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

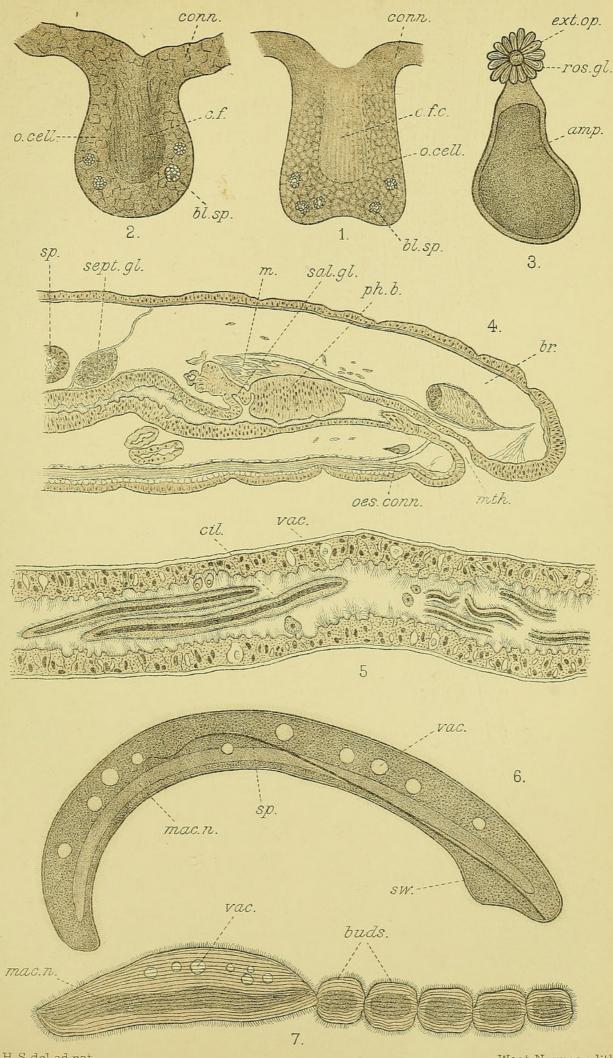
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## Introduction.

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.

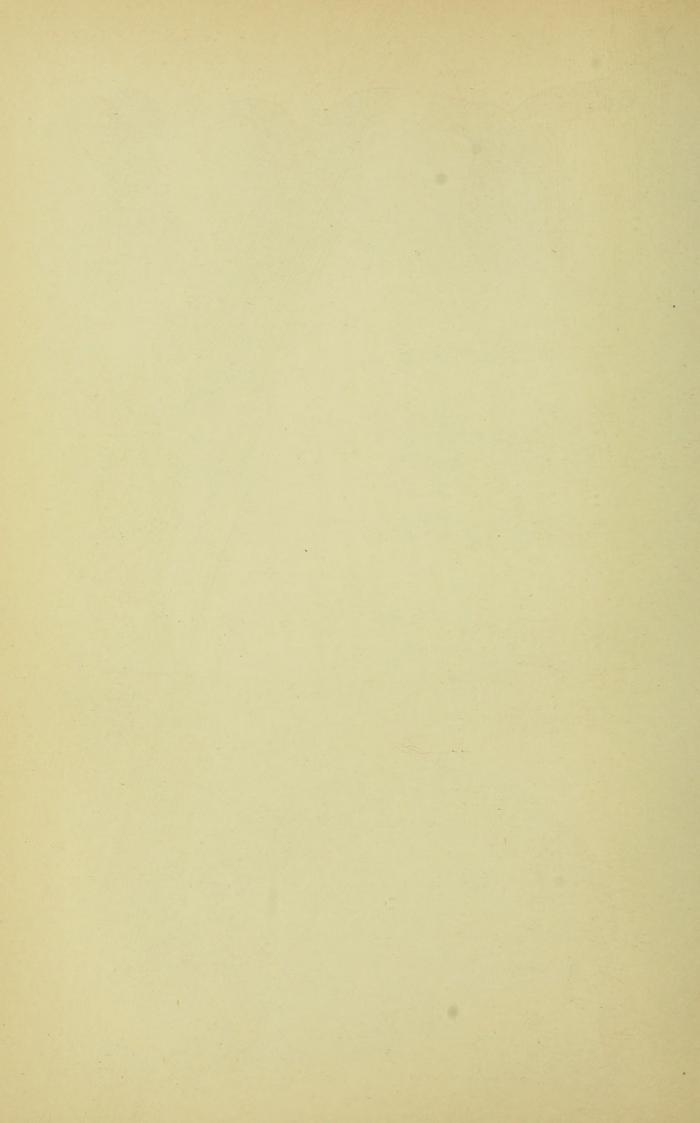
<sup>\*</sup> Festschr. für C. Gegenbaur, Part I. 1896, p. 295.

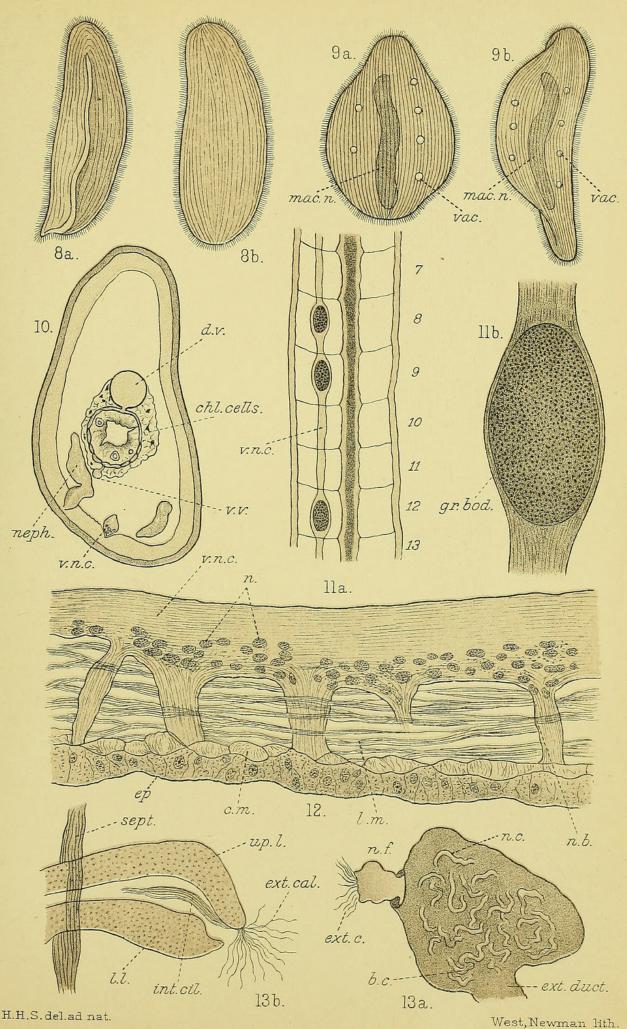
<sup>†</sup> Trans. Zool. Soc. London, vol. xvi. pt. vii. p. 329.
† Communicated by Prof. F. W. Gamble, F.R.S., F.Z.S.
§ For explanation of the Plates see pp. 320-321.



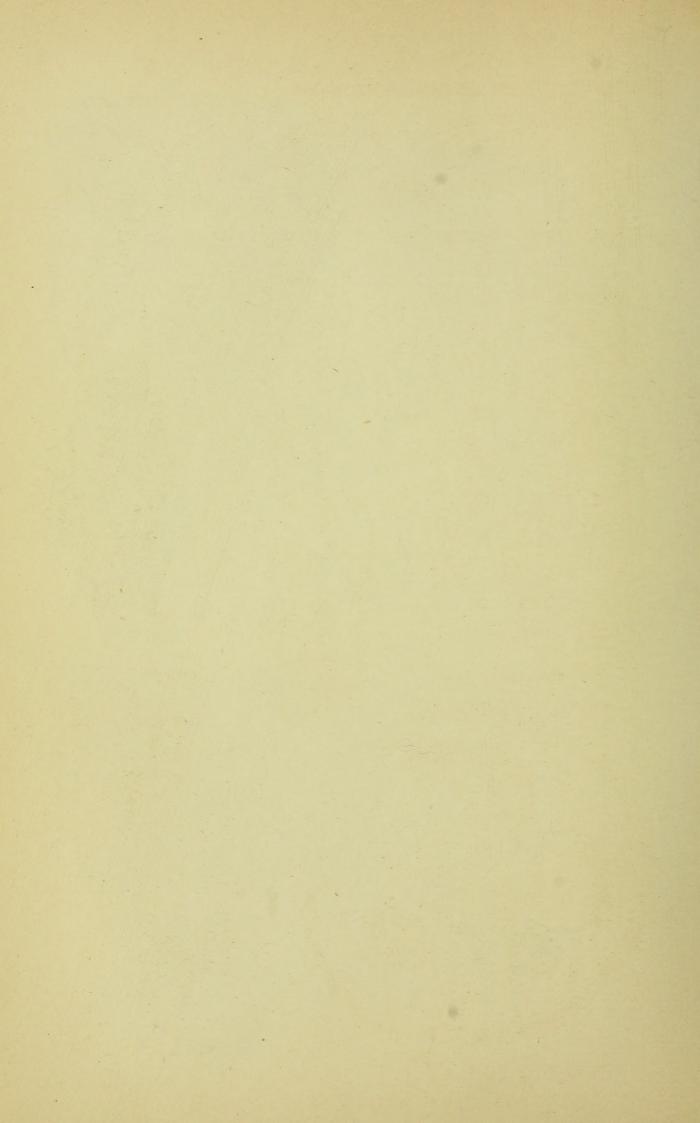
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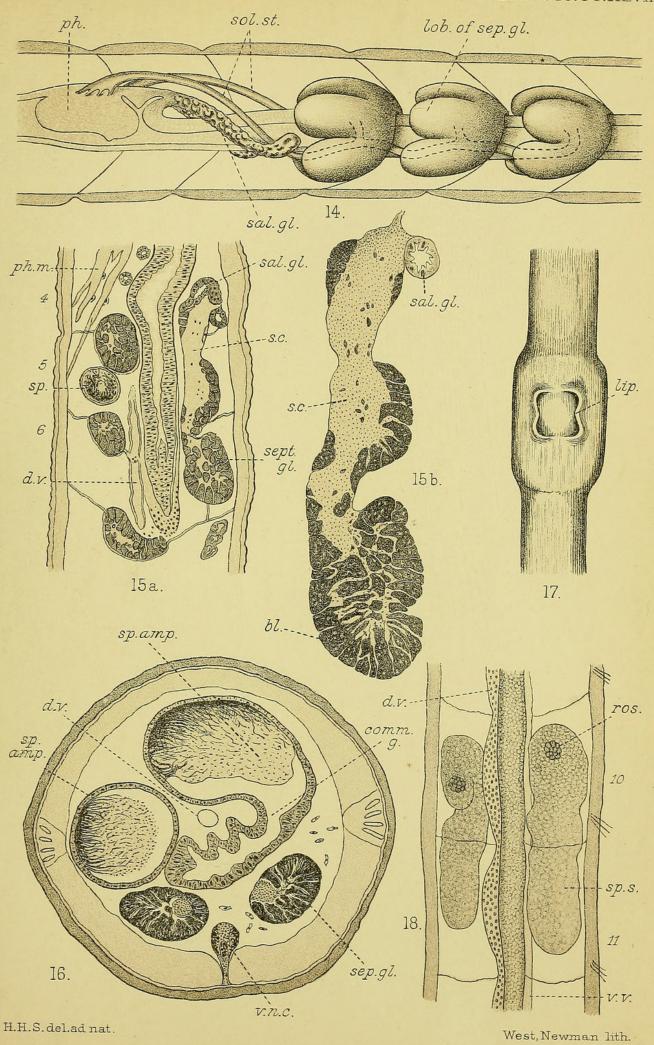
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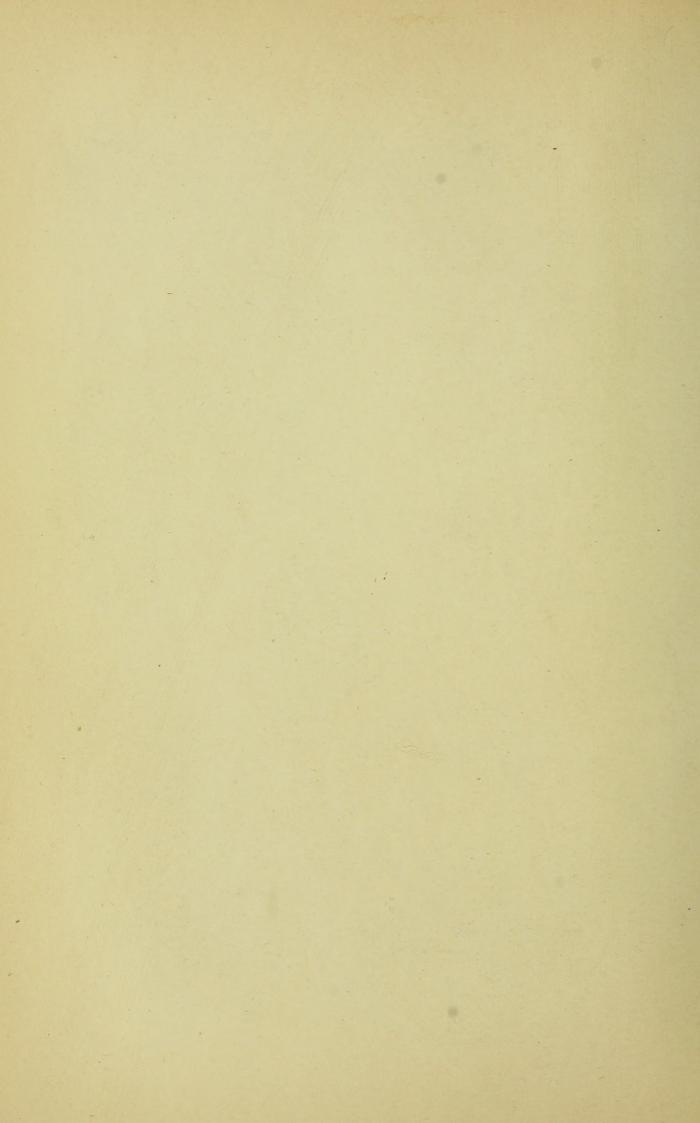


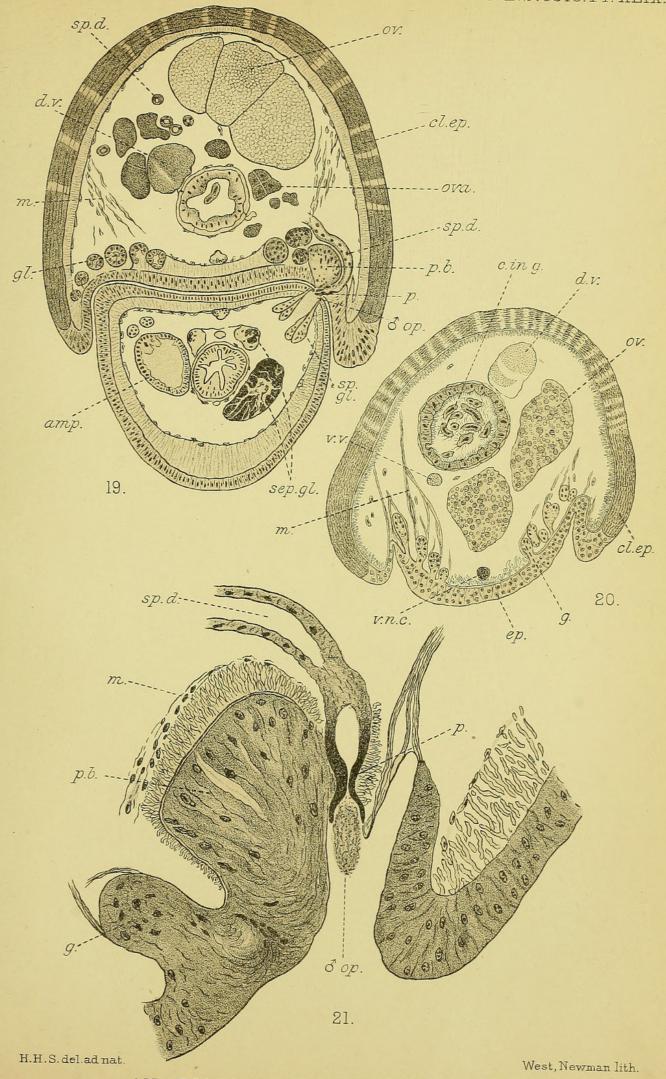
ANATOMY AND PROTOZOAL PARASITE OF ENCHYTRÆID WORMS.



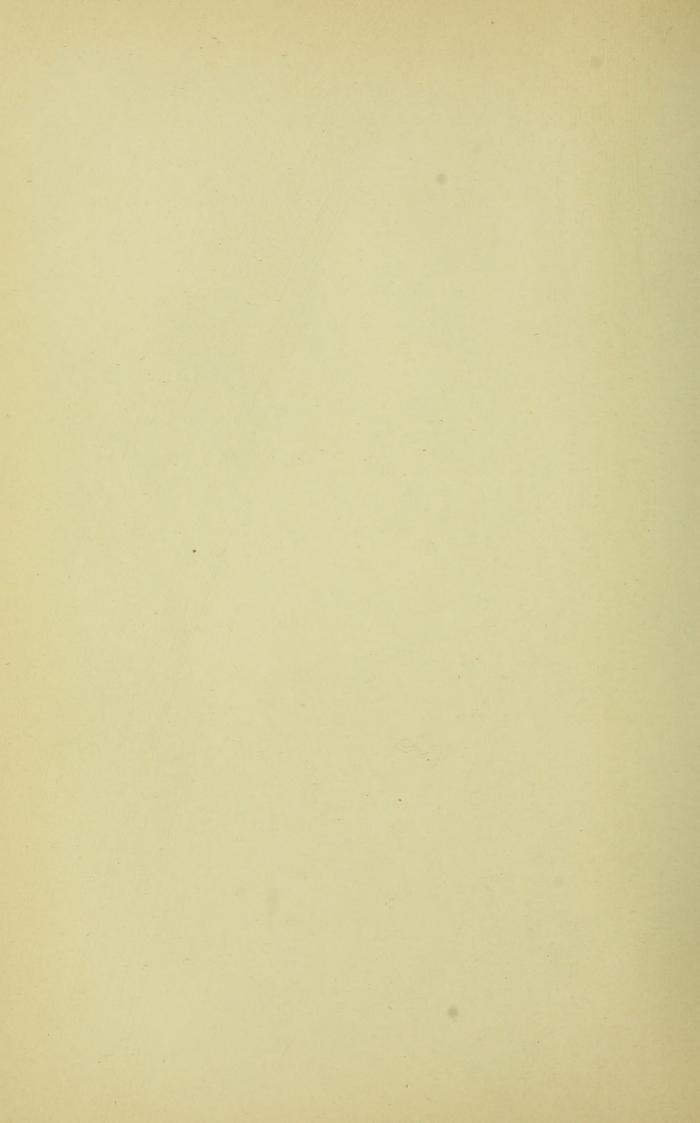


ANATOMY OF ENCHYTRÆID WORMS.





ANATOMY OF ENCHYTRÆID WORMS.



Goodrich (7) gives a good description of the nephridia and coelomic 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 spermathece. 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. 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 The number of segments varies, but is 20 mm. in length. 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 beechleaves 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 Enchytraids 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-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 bodywall. 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 Esophagus gradually merges into the intestine; the actual point where esophagus 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 gutwall, they are seen to be spherical, and contain numerous oilglobules 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 esophagus 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 ampulla. Although these two simple tubular glands converge towards the same point just behind the pharynx, they open into

the esophagus quite separately on the dorsal side.

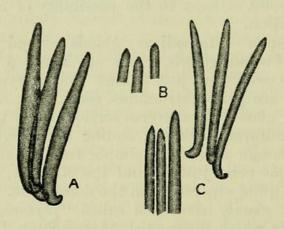
The salivary glands have been called "peptonephridia." The main characters which distinguish these glands from nephridia are (1) there is no opening to the colom, (2) there is no trace of a funnel, (3) the tubes are not ciliated, and in no Oligochætes are there nephridia which are entirely without cilia. 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 colomic 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 colom, 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.

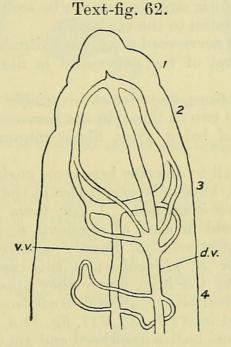
joined at intervals to the gut-sinus by small vessels (Pl. XLVII. fig. 10). There are three pairs of lateral vessels also in the anterior blood-system; two pairs are given off close together and join the two branches which form the ventral vessel, and one pair is given off just behind this and joins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



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 occili of some kind. However, their function is, I believe, unknown, and more work is required upon them before they could definitely be called occili.

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 nervebranches 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.

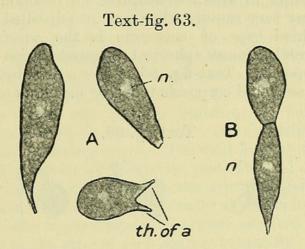
Cælomic Corpuscles.—The cælomic corpuscles in E. pellucidus are comparatively few in number. In some Enchytræids they are so numerous that it is very difficult to examine the various organs in the living worm; but E. pellucidus is so transparent

that the nephridia, brain, etc., can be seen quite easily.

My observations on the colomic 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  $\mu$  to 23  $\mu$  in length and from 12  $\mu$  to 8  $\mu$  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 celomic 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



A. Cœlomic corpuscles of Enchytræus pellucidus.

B. Corpuscle just dividing into two.

n., nucleus; th. of a., threads of attachment to the colomic 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 colomic corpuscle (text-fig. 64) is

# ref. bod. coil. th.

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

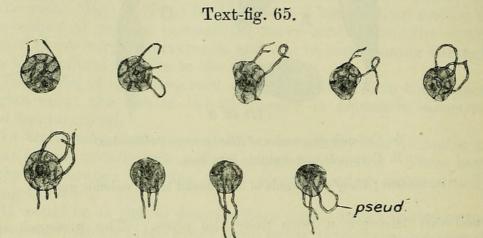
Ref.bod., refringent body; coil.th., coiled thread; n., nucleus.

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 celomic corpuscles, as they disappear very rapidly when put into distilled water.

(c) The third type of corpuscle is the amæboid 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 amæboid corpuscle taken at intervals of about half a

minute.



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.

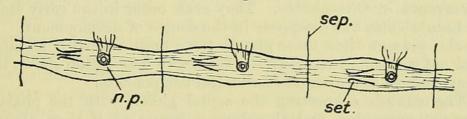
Nephridia.—Goodrich (7) has given a full account of these organs in E. hortensis, a species closely allied to, if not identical with, E. albidus, and I have been able to confirm his excellent

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. 13b). 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 flattened body of the nephridium consists of the funnel. 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 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 semidiagrammatic 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 Oligochetes. They even occur in the early stages of Lumbricide, 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

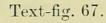
pores, are still unsolved.

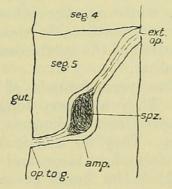
According to Michaelsen (9), "The reproductive apparatus of Enchytræids varies very little. The testes are formed on the posterior side of the septum between segments 10 and 11, and the ovaries on dissepiment 11/12. Two sperm-funnels are present in segment 11. The sperm-ducts lead from the sperm-funnels, 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.





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



1913. "A descriptive study of an Oligochaete worm of the family Enchytraeidae; with an appendix on certain commensal Protozoa." *Proceedings of the Zoological Society of London* 1913, 300–321. https://doi.org/10.1111/j.1469-7998.1913.tb07581.x.

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