Contributions to the Anatomy of Earthworms, with Descriptions of some New Species.

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THE present paper contains some of the results of the examination of a quantity of material which I have been gradually amassing during the last few years. For this material I am indebted to the kindness of numerous friends at home and abroad who have interested themselves in the matter. For the most part the specimens which are described here were in a fit state of preservation for microscopical study.

I. On the Structure of three New Species of Acanthodrilus, with Remarks on other Species of the Genus.

Some time since I received from the Falkland Islands eight or nine examples of a small species of Acanthodrilus. The specimens were collected and preserved by Dr. Dale at the request of Mr. Coleman, the Secretary of the Falkland Islands Company.

It happens that the only species of Earthworms known from that quarter of the world belong to the same genus. Mandane littoralis of Kinberg from Patagonia has been recently shown by Perrier (**34**) to be an Acanthodrilus. I have myself examined an individual of this same species which is contained in the National Collection at South Kensington, and can quite confirm Perrier's identification. It follows, therefore, that, strictly speaking, the name Mandane should be retained for the genus, and the name Acanthodrilus allowed to drop.[1] The remaining species is Acanthodrilus georgianus, from South Georgia (see Michaelsen, **31**).

The species which I describe here may be identical with Acanthodrilus (Mandane) littoralis, but I have no means of coming to a certain conclusion;[2] as it hardly differs from A. georgianus in any characters to which Michaelsen has directed attention I refer it to that species, of which I am able to give a rather fuller account than that contained in Michaelsen's paper. The largest individual measures about three inches in length.

The setæ are disposed like those of A. multiporus, i. e. in four series of pairs with a rather greater interval between the two setæ of the dorsal pair than between the two setæ of the ventral pair.[3]

The clitellum occupies segments XIV—XVI and a portion of segment XIII; the boundaries of the several segments were in every case quite distinguishable. The median ventral part of the clitellar segments lying between the innermost seta of each side showed no absence of glandular development.

The prostomium (fig. 22) has the shape illustrated in the figure; it does not divide completely the buccal segment.

[1] Since writing the above, I find that Kinberg used the name Mandane twice in the same paper! Vaillant has called attention ('Suites à Buffon,' "Annelés") to this flagrant case of disobedience to the rules of nomenclature.

[2] If the specimen in the British Museum be really Mandane littoralis it is different from this species.

[3] The actual proportion of the distances between the setæ are as follows:— 1l. – 1r. = 4; 1r. – 2r. = $2\frac{3}{4}$; 2r. – 3r. = 3; 3r. – 4r. = $3\frac{1}{2}$; 4r. – 4l. = 8.

The nephridiopores open in front of the lower seta of the dorsal pair; these orifices were particularly obvious upon the clitellar segments.

The apertures of the atria are upon segments XVII and XIX, and correspond to the ventral setæ, which are here modified and form special penial setæ, as in all other species of Acanthodrilus; these apertures are surrounded by a ridge, and a narrow groove connects the two apertures of each side of the body; this no doubt enables the secretion of the atria to mingle with the sperm, which is discharged from the orifice of the vasa deferentia upon the eighteenth segment within the said groove.

The oviducal pores were not visible.

Alimentary Tract.—Dr. Michaelsen mentions that in A. georgianus there is a dorsally-placed diverticulum of the gut in the fifth segment. If this refers to a diverticulum of the pharynx, then I can confirm him, and state also that other species of the genus agree with A. georgianus; this diverticulum can be plainly made out from a series of transverse sections. In the Oligochæta generally the dorsal wall of the pharynx is specially thickened, while in other Annelids, e. g. embryo Serpula, the ventral wall is thickened, and forms a diverticulum (see Weldon, **41**). It does not appear to be novel for the dorsal wall of the pharynx to form a diverticulum, as is often the case in Acanthodrilus; but in Acolosoma tenebrarum (Vejdovsky, **39**) the pharynx is furnished with two minute diverticula, which probably correspond to the unpaired diverticulum of Acanthodrilus georgianus. It is interesting to note that the dorsal position of the pharynx in the Oligochæta, and of the diverticulum where such is present, contrasts with its ventral position in Polychæta.

A. georgianus does not possess a well-developed gizzard. In the fifth segment the muscular walls of the œsophagus become thickened, but the chitinous lining of this part of the gut is thinner than the external chitin; but the proportion of the muscular coat and the lining epithelium (see fig. 33) are very much less than in other worms which have a well-developed gizzard. In comparing this gizzard with that of Pontodrilus I do not find a great difference between them. On a dissection of A. georgianus it is impossible to recognise the gizzard at all; it is clear, therefore, that in this species the gizzard is either disappearing or in course of development, as it is in Pontodrilus. Michaelsen makes no remark upon the presence or absence of a gizzard in A. georgianus. The seven anterior segments are large, occupied by the masses of cells which are usually termed salivary glands; these extend back beyond the pharynx and cover the beginning of the œsophagus. It is necessary to dissect them away before the œsophagus can be seen or the septa, which begin to be obvious between segments 5, 6. In the tenth segment the œsophagus alters its character; the lining epithelium no longer consists of tall narrow cells, as in the preceding section; the cells become smaller and cuboid in shape, and the whole epithelium becomes much more folded; at the same time a blood-sinus is developed between the epithelium and the muscular walls. I imagine that this part of the œsophagus represents an undifferentiated condition of the calciferous glands; in any case there was no other trace of the calciferous glands in the three specimens which were dissected or cut into sections. In the fifteenth segment the œsophagus again alters its character, the blood-space disappears, and the lining epithelium acquires a columnar character; in the sixteenth segment the œsophagus abruptly widens and becomes the intestine.

The intestine has just the merest trace of a typhlosole; this is represented by a very inconspicuous fold.

Vascular System.—The dorsal vessel is single, and is connected with the supraneural by five transverse vessels occupying segments IX—XIII. Of these the last four are the largest.

There is no subneural vessel. I have never met with this blood-vessel in any species of Acanthodrilus. Some remarks upon its presence or absence in other Earthworms will be found on p. 473.

In the œsophageal region immediately underlying the vascular tract of the œsophagus, and extending through two or three segments, is a longitudinal trunk, about the presence of which in other Earthworms there is some dispute. I have recognised it in A. georgianus, both in transverse and longitudinal sections. There can be no doubt as to its presence, the calibre of the vessel being quite as large as that of the supraneural trunk.

I have described this vessel in A. dissimilis and other New Zealand species (1).

It also occurs in Eudrilus sylvicola (see Beddard, 2) and among aquatic Oligochæta, in Bothrioneuron and Lophochæta (see Stolč, Tab. ii, figs. 5, 6, *sb*).

Professor Howes has figured a corresponding vessel in Lumbricus in his 'Atlas of Biology.' It is described in the 'Practical Biology' (p. 260) as the "subintestinal vessel;" but some doubt is thrown upon the existence of this vessel by Benham (10, p. 253) and by Jackson (27, p. 203, footnote).

I have failed to find any penetration of the capillaries within the epidermis either in this or in any other species of Acanthodrilus, except of course in the clitellum.

Generative Organs.—The testes and ovaries have been described by Michaelsen; they occupy the usual position—the testes in X and XI, the ovaries in XIII; these organs are attached, as is usually the case, to the anterior septum of their segment. The most striking variation from this normal position occurs in this genus; in A. annectens I have already (3) recorded the fact that the gonads are attached in the immediate neighbourhood of the funnels of the generative ducts to the posterior wall of the segment. I have taken the opportunity of re-examining the position of the gonads in A. multiporus, a species which comes near to A. annectens; I find that while the testes have the normal position, i.e. are attached to the front wall of their segment, the ovaries are, as in A. annectens, attached to the hinder wall of the thirteenth segment.

The vasa deferentia are described by Michaelsen as opening on to the exterior on the seventeenth and nineteenth segments, in common with "the large, lobulated prostates."

I find that in this, as in other species of the genus, the vasa deferentia open at the eighteenth segment quite independently of the atria, with which they have no connection. A species of Acanthodrilus has recently been described (**20**) from Illinois, U.S.A., under the name of Diplocardia communis; one of the principal structural characteristics of the species, which led the author to infer it to be a distinct genus, is the independent opening of the vasa deferentia on to the segment lying between those upon which the atria open; but this is no generic distinction, neither is the completely double condition of the dorsal vessel, which Mr. Garman also uses as a differential character, distinguishing Diplocardia from Acanthodrilus. The atria of A. georgianus, like those of other species, are tubular, not lobate; their minute structure, as well as their general anatomy, is precisely that of A. dissimilis and other species.

The sperm-sacs of A. georgianus are very remarkable; there are in the first place a pair of racemose organs attached to the front walls of segments XI and XII; these resemble the sperm-sacs of A. dissimilis, &c. (see Beddard, **1**, where they are, however, spoken of as testes), and were full of developing spermatozoa. In the ninth to the fifteenth segments inclusive is a median unpaired sac lying under the œsophagus and above the supraneural blood-vessel. This sac appears to be interrupted at the septa; its walls are very thin and appear to be muscular, with a coating of peritoneum (fig. 35). This structure recalls the unpaired sperm-sac of the Tubificidæ and other "Limicolæ" by its position and great extent, but I am unable to be certain whether it represents such a structure, at any rate physiologically, as there were hardly any developing spermatozoa within it; the few "sperm-polyplasts" that could be observed may have got there accidentally. The development of the sperm-sacs in the Oligochæta is but little known and in but few types. It seems possible, however, that the median unpaired sperm-sacs in this and in other Earthworms may represent the sperm-sacs, which are also median and unpaired, of many aquatic forms, while the paired sperm-sacs which are in A. georgianus quite independent of the median sac may be structures unrepresented in those forms. The extent of the median sac in A. georgianus through a number of segments is quite comparable to what is found, for example, in Clitellio.

The penial setæ are illustrated in figs. 15, 16. A remarkable fact about them is that there are two kinds; in one kind the extremity is ornamented with scallop-shell-like processes; in the other kind the extremity is plain; this is not a difference due to age. So far as I was able to ascertain, the ornamented setæ form one bundle, the plain setæ another.

Septal Sacs (figs. 31, 32).—A very characteristic feature, which I have not observed in any other species, and which Michaelsen has not mentioned, is the presence of a series of sacs attached to the septa. These are disposed in pairs and have the appearance of solid white bodies attached to the anterior septum of each segment, and hanging freely in the interior of the segment. They commence about the twentieth segment, and the first few pairs are commonly larger than the rest; they occupy all the segments lying behind the twentieth. These peculiar bodies suggest egg-sacs and sperm-sacs; they are rather larger than the former and smaller than the latter. Structurally they are merely outgrowths of the septa containing a spacious cavity which communicates by an aperture with the cavity of the segment in front; in their structure, therefore, they agree with the egg-sacs. The peritoneal epithelium covering these sacs was rather better developed than elsewhere upon the septum; these cells when stained with iodine assume a mahogany-brown which fades when the tissue is warmed, but reappears on cooling, indicating therefore (?) the presence of glycogen. The glycogen appears to be formed in the peritoneal cells of the septum generally as well as in those which cover the septal sacs. I could not find any trace in the muscles of the septum, and so cannot agree with Barfurth (**10**), who specially proved its existence in the muscles of the Earthworm. The folding of the septa which results in the formation of these sacs may therefore be caused by the need for an increased amount of glycogen-forming tissue. Vejdovsky refers to structures in Rhynchelmis (**39**) and Claparède in Lumbricus which may be comparable to these septal sacs.

Some time ago I described in the 'Proceedings of the Zoological Society' (**1**) three species of New Zealand Acanthodrili; this account was afterwards supplemented by the description (**4**) of a fourth species or variety. These specimens were kindly collected for me in the vicinity of Dunedin by Professor T. J. Parker, F.R.S. Since then Mr. W. Smith has forwarded to me a large collection of specimens from Ashburton; the majority of these were Acanthodrilus, which is apparently the most prevalent genus in New Zealand; one of them was described by me in a recent number of this Journal (**3**), the others seemed on a rapid inspection to belong to the three species, A. multiporus, A. novæ-zealandiæ, or A. dissimilis. I find, however, that this is not the case, and I therefore proceed to describe the Ashburton species as Acanthodrilus antarcticus and A. Rosæ.

Acanthodrilus antarcticus, n. sp.

The setæ are disposed in four series of pairs, but the two setæ of each pair are not close together as in A. novæ-zealandiæ. Setæ 1 and 2 are closer together than 3 and 4; the distance between 2 and 3 is about equal to that between 3 and 4.

The prostomium does not completely divide the first segment; it does in A. novæ-zealandiæ. The first dorsal pore is between segments V and VI; they are not visible upon the clitellum.

The clitellum, which is distinguishable even in the spirit specimens by its darker colour, occupies segments XIII to XVII.

The atrial pores are, as usual, situated upon the seventeenth and nineteenth segments on prominent papillæ corresponding in position to the setæ $2r$ and $2l$; a longitudinal groove, as in other species, connects the two orifices of each side.

The external characters ally this species rather with Acanthodrilus multiporus than with A. novæ-zealandiæ or A. dissimilis; the distribution of the setæ and the characters of the prostomium are much the same; it differs in the less extent of the clitellum and in the fact that the papillæ upon which the atrial pores are borne are not so prominent as in A. multiporus; the prominent atrial papillæ are specially characteristic of A. multiporus and also of A. annectens.

The internal anatomy of A. antarcticus shows numerous points of resemblance to A. multiporus, though there is no doubt as to its distinctness.

Alimentary Tract.—The pharynx occupies the first four segments; there is a well-developed gizzard in segments VI and VII. In the fourteenth and fifteenth segments the walls of the œsophagus become much thickened; this dilated portion of the œsophagus probably represents the calciferous glands of other Earthworms; in A. multiporus these glands are found further back—in the seventeenth segment.

I have studied the structure of these glands by transverse and longitudinal sections. It appears that they really represent two pairs of glands such as are found, for example, in A. dissimilis, but their apertures into the œsophagus are so large that the glands present the appearance of being little more than glandular dilatations of the œsophagus itself; in transverse sections, however, the epithelium of œsophagus can be here and there detected, and it is totally different from the epithelium of the glands; the cells are much more elongated, and are more deeply stained than the cells of the gland, by the reagent used (alum carmine); both the glandular cells and the epithelial lining of the œsophagus are furnished with long cilia—a character which distinguishes the calciferous glands of this species from those of A. dissimilis, and from certain glands of other Earthworms (e.g. Urochæta), which have been regarded as the homologues of the calciferous glands.

Vascular System.—The dorsal vessel is like that of A. multiporus; it is completely double from end to end of the body; for the most part the two vessels are placed close side by side, but they do not fuse at the points where they traverse the mesenteries; on the gizzard the two dorsal vessels come to be somewhat widely separated. The transverse vessels uniting the dorsal with the ventral vessel form large conspicuously dilated "hearts" in segments x—xiii (inclusive). In all these points Acanthodrilus antarcticus agrees closely with both A. multiporus and A. annectens.

Septa.—The characters of the intersegmental septa appear to offer useful specific characters in this genus; in some species a certain number of the anterior septa are greatly thickened; the number of septa which are thus enlarged, and the degree in which their thickness is increased, differs, for instance, in the present species and in A. multiporus. In A. antarcticus the septa separating segments vii—viii, viii—ix, ix—x, x—xi, xi—xii, are specially thickened, particularly the last four. In A. multiporus the same septa, with the addition of one in front and one behind, are thickened, but not so much as in A. antarcticus.

Genital Organs.—The testes are two pairs of minute bodies in segments x and xi; each is attached to the anterior septum of its segment close to the junction of the septum with the body wall; it is placed exactly opposite to the funnel of the vas deferens.

The ovaries occupy a corresponding position in segment xiii; the funnel of the oviduct having a relation to them similar to that of the funnel of the vas deferens to the testis. The two pairs of atria are situated in the seventeenth and nineteenth segments respectively; each is a much-coiled glandular tube communicating with the exterior by means of a narrower tube with thick muscular walls. The structure of these organs present, in fact, no differences from other species.

Penial setæ are present on both the seventeenth and nineteenth segments as in most other species of Acanthodrilus, but not in A. multiporus; one of these setæ is displayed on fig. 17; it is an immature setæ, showing the cell out of which it has been formed. Close to its base, one on each side, are two other cells which would doubtless have developed two other setæ; these are surrounded by a thick muscular coat which forms a continuous investment of the setæ. I have been unable to procure a fully developed penial setæ for figuring,—the point was broken off in every case. The mature penial setæ are of a deeper yellow colour than the immature ones.

The seminal sacs are two pairs attached to the anterior wall of segments XI and XII; they have the racemose character which is usually seen in this genus. Besides these there are a pair of solid bodies with an oval contour attached to the posterior wall of segments IX and X. A microscopic examination of these showed that they are also seminal sacs; groups of developing seminal cells were contained in the spaces of the meshwork, formed of fibroid tissue; there were also numerous Gregarines, the presence of which is so characteristic of the seminal sacs of Earthworms. There are thus four pairs of seminal sacs of which the anterior two are outgrowths forwards of the septa, separating segments IX—X and X—XI; the posterior two are backwardly directed outgrowths of septa X—XI, XI—XII. This arrangement agrees with that of the seminal sacs of Allolobophora fœtida (Bergh, **12**); there appears to be no median unpaired sac developed such as is found in Lumbricus, Microchæta, and even in certain species of Acanthodrilus (e. g. A. Beddardi, Horst, **24**). In my description of A. Layardi (**7**) I was doubtful about the nature of a pair of bodies attached to the posterior wall of segment X. It is now clear that these structures are in all probability seminal sacs; in A. capensis I have called attention to a pair of problematical structures attached to the posterior septum of segment IX. I am now inclined to think that these may represent the first pair of seminal sacs of A. antarcticus.

It is more usual, however, in this genus to find only two pairs of seminal sacs developed, those of the eleventh and twelfth segments; and these usually differ from the anterior pairs in their racemose character; but there are some indications that the real number of these organs is four pairs, possibly in all the species of the genus. The spermathecæ are two pairs situated in segments VIII and IX; each is furnished with a number of small diverticula.

A. Layardi and A. Beddardi differ from other species of the genus, and from all other Earthworms, by the development of special glandular organs connected with the spermatheca. In the former species the ventral setæ of the eighth segment are replaced by a bundle of long, greatly modified setæ very much like those of the seventeenth and nineteenth segments of that and other species of Acanthodrilus; connected with these is a pair of glandular organs (see Beddard, 7); in A. Beddardi a similar modification of the setæ is met with, but in the ninth as well as in the eighth segment; furthermore, in this species there is only a single gland appended to each bundle of "copulatory setæ" (as they are aptly termed by Horst). At the time when these structures were described by Dr. Horst and myself there was nothing with which they could be compared exactly. Since then Dr. Stolč has published an important memoir upon certain Tubificidæ (38), and figures in Psammoryctes barbatus a pair of glands and a copulatory seta contained in a special sac opening into the duct of the spermatheca just at its external orifice.

This structure appears to me to be quite comparable to the structures annexed to the spermathecæ in the two species of Acanthodrilus. We have in this a remarkable point of similarity between genera otherwise very widely separated. It is well known that in Lumbricus the setæ of the segment upon which the spermathecæ open, as well as of other segments in the neighbourhood of the genital organs, are somewhat modified, but there is not in that genus or in any other such a remarkable specialisation of the setæ as in the instances enumerated above.

Acanthodrilus Dalei, n. sp.

This species is a native of the Falkland Islands, and is specially remarkable on account of its being, apparently, an aquatic species. I owe the specimens to the kindness of Mr. Dale, who informed me that they were found in fresh water; along with them were a number of specimens of another species, which I believe to be identical with A. georgianus. These are the only two species of Earthworms except Allurus, which are known to live in water as well as in earth; at any rate this is the case with A. georgianus and Allurus, which are both terrestrial and aquatic in their habit. This species can be at once distinguished from A. georgianus by its violet red colour; the integument of the former species was invariably decolourised by the alcohol, and appeared therefore of a whitish-brown tint due to the enclosed viscera. All the specimens studied by me were small, the largest not more than one and a half inches in length.

The setæ are paired, the two setæ of the pair being quite close together and not separated by an interval as they are in A. georgianus.

The prostomium, as in A. novæ-zealandiæ, &c., completely divides the buccal segment.

The clitellum was not developed.

The atrial and spermathecal pores are precisely as in other species, i.e. upon the border-line of segments VII—VIII, VIII—IX and upon segments XVII and XVIII. Of the internal characters I am not able to give a complete account, but there are not any great differences from such a species as A. novæ-zealandiæ.

The gizzard is large and well developed, thus contrasting with A. georgianus; it occupies segments VI and VII, and the septum between these two segments is present.

The nephridia are a single pair to each segment, opening in front of the more dorsally placed pair of setæ.

The dorsal vessel is single.

The spermathecæ resemble in every particular those of A. Rosæ (see p. 435); the minute diverticula are borne at the end of a narrow and muscular tube. The identity in shape of the spermathecæ in these two species led me at first to identity this species with A. Rosæ; but it differs very distinctly in the fact that the nephridia do not alternate in position as in A. Rosæ, but open always in front of the dorsal pair of setæ. The two species also differ in the shape of the penial setæ (cf. figs. 14, 19).

The seminal sacs were present in segments IX and XI only. I imagine, however, that in more fully mature specimens there would be two other pairs in segments X and XII; in both cases they had a racemose appearance, and were attached to the posterior wall of their segment.

The two pairs of atria were identical with those of other species; the penial setæ are illustrated in fig. 14.

Acanthodrilus Rosæ,[1] n. sp.

While A. antarcticus might easily be confused, on a superficial view, with A. multiporus, the present species is by no means unlike A. novæ-zealandiæ or A. dissimilis. Indeed the external character of the spirit-preserved specimens hardly permit the species to be distinguished from one or other of the above named, but the internal characters enable A. Rosæ to be recognised as a perfectly distinct and well-marked species; there is no possibility of confounding it with either A. novæ-zealandiæ or A. dissimilis. The largest specimen measured about eight inches in length, the colour of the spirit-preserved specimen is a rich brown, darker upon the clitellar segment, and paler ventrally.

The prostomium completely divides the peristomial segment.

The setæ are paired; the pairs are, at any rate in the posterior region of the body, equidistant; this region of the body is quadrangular in section, the setæ occupying the four angles.

The clitellum occupies segments XIV—XIX (inclusive) as in A. novæ-zealandiæ.

The position of the atrial pores calls for no special remark as they are identical in position and appearance with those of A. novæ-zealandiæ.

With regard to the internal anatomy there are two principal

[1] Named after Dr. D. Rosa of the "Museo Zoologico," Turin.

points of difference from A. novæ-zealandiæ; firstly, the entire absence of specially thickened septa. I have dissected a tolerably large specimen and compared it with a specimen of A. novæ-zealandiæ of about the same size; there was a very marked discrepancy in the relative thickness of some of the anterior septa; and this difference could not possibly be accounted for by the unequal size of the two individuals. The second anatomical difference between A. Rosæ and A. novæ-zealandiæ is in the form of the spermathecæ; fig. 26, illustrates the four spermathecæ, which, as is so common among Earthworms, have the most varied relations to the septa of the segments containing them, though the situation of the external aperture does not vary at all. Each spermatheca consists of a large pouch with relating thin walls; this communicates with the exterior by a short thick-walled muscular duct; this duct gives rise to a diverticulum which terminates in an enlarged cæcal extremity, the surface of which is furrowed. The difference between the spemathecæ of this species and those of A. novæ-zealandiæ is that in the latter the diverticula are sessile (cf. figs. 24, 25).

The Spermathecæ of Earthworms.—I believe that I was the first to direct attention to the fact that the diverticula of the spermathecæ in Acanthodrilus probably play a different part in the economy of the creature to the spermathecæ themselves. In Acanthodrilus multiporus, in A. novæ-zealandiæ, and in A. dissimilis the spermathecal diverticula were always found—in the sexually mature individuals—to be crammed with spermatozoa; while no spermatozoa could be discovered in the pouch itself.[1] Dr. Horst had remarked before that in Perichæta sumatrana the diverticula of the spermathecæ were filled with an orange-coloured substance which appeared on microscopical investigation to be a mass of spermatozoa. He has more recently (25) found the same thing in Acanthodrilus Beddardi. I have found myself that in Perichæta Houlleti and in P. intermedia the

[1] Dr. Rosa, however, in Acanthodrilus scioanus particularly states that spermatozoa occurred in the pouch as well as in the diverticulum.

diverticula alone contain spermatozoa, while Spencer (**37**, p. 35), has stated that in Megascolides australis "the spermazoa . . . . were confined to the diverticulum." Acanthodrilus Rosæ conforms to the same rule, which there is now some reason for regarding as of general application. It seems probable, therefore, that the diverticula, which are so usually met with in exotic Earthworms, do not merely serve the purpose of increasing the area for the storage of spermatozoa received from another worm during copulation.

In all these instances observed by myself the spermathecæ themselves contained a granular coagulum, which appears to be a product of the glandular epithelium lining the pouch; in Megascolides australis the spermatheca, according to Spencer (**35**), is filled with "a fluid containing granules and masses of nucleate corpuscles."[1] Corresponding to the widely different part taken by the spermatheca and diverticula in the phenomena of reproduction, there appears to be generally some difference in minute structure. I have already pointed out this in Acanthodrilus dissimilis (**1**). Horst (**24**) and Spencer (**37**) have done the same in A. ungulatus and in Megascolides australis respectively. In Acanthodrilus georgianus the difference in the minute structure of the spermatheca and of its diverticula is not only apparent in the sexually mature worm, but also in immature specimens in which the spermathecæ are but little developed. Fig. 27 represents a transverse section through the spermatheca and through the diverticulum of a small unripe individual. Both spermatheca and diverticulum are enveloped in a moderately thick coat of nucleated tissue, derived in all probability, as Bergh (**13**) has pointed out in the case of Lumbricus, from the peritoneum, and destined to form not only the peritoneal sheath but the muscular tissue of the spermatheca; there does not appear to be in Acanthodrilus any more than in Lumbricus

[1] Goehlich has recently stated (**23**) that in Lumbricus in the cold season the spermathecæ contain numerous "blood-corpuscles," the function of which is to devour the spermatozoa that have been left over after the processes of fertilization have ended.

an invagination of the muscular layers of the body wall to form the muscular coats of the spermatheca. The spermatheca itself (fig. 27 *b*), is lined with tall narrow epithelial cells, the nuclei of which are placed near the base of the cells; the diverticulum (fig. 27 *a*) is lined with an epithelium the cells of which are more quadrangular in shape and totally different in general appearance from the cells lining the pouch. In the sexually mature worm the character of the epithelium of the diverticulum alters; the cells become loaded with spherical refracting non-staining granules, and the nucleus, conspicuous through its deep staining, but deformed, is pressed close against the base of the cells; the epithelium at the same time becomes much folded so that the cavity of the diverticulum presents the appearance of subdivision into a series of chambers. While these remarkable changes have taken place in the diverticulum (fig. 28), the epithelium of the spermatheca is but little altered in character though it becomes somewhat folded.

In Acanthodrilus Rosæ the structure of the spermathecæ is quite the same as in A. dissimilis; in both these worms the epithelium of the diverticulum does not appear to be—originally—so different from that of the pouch, though it comes ultimately to present a strikingly different appearance. The pouch itself is lined with tall columnar cells; in the interior of these are formed spherical masses of secreted granules which seem to closely resemble similar products described by Goehlich (**23**) in the spermathecæ of Lumbricus; the epithelium lining the pouch is slightly folded. The diverticulum of A. Rosæ is, as I have already stated, composed of a relatively long tube with muscular walls which terminate in a swollen somewhat lobate cæcal extremity (fig. 24); this latter has a structure quite like that of the diverticulum of A. dissimilis and of Neodrilus (see Beddard, **4**). The epithelium is much folded so as to divide the cavity of the diverticulum; in places the columnar character of the cells can be recognised, but for the most part they are not clearly recognisable for the reason that they have become largely converted into balls of a viscous-looking substance which does not stain. So far as I have been able to follow the formation of these colloid-looking masses, I am inclined to think that they are the product of a fusion between smaller droplets which appear in the interior of the cells. Fig. 29 illustrates the general aspect of a section through the diverticulum with the larger and smaller drops of secretion, and the remains of the columnar cells which are more perfect in parts. The secretion when formed does not seem to be evacuated into the interior of the numerous cæcal pouches which constitute the extremity of the diverticulum, as it is in the spermatheca itself, but to remain where it was formed. In nearly all the viscous drops (figs. 29 *d*, 30 *d*) were embedded bundles of spermatozoa which were always very distinct in my preparations owing to the fact that they were deeply stained by the colouring reagents used (alum carmine and borax carmine). A superficial examination of such a section almost conveyed the idea that the spermatozoa were developed in the diverticulum, so close is their relation to the epithelium; there can be little doubt, however, that the function of these masses formed by the breaking down of the epithelium is to retain the spermatozoa within the pouch until ready for transference to another individual. The spermatopores of Acanthodrilus are not known, and we have no information whatever with regard to the processes of fecundation in that genus. It seems likely on a priori grounds that they will prove to be different from those of Lumbricus, owing to the far greater complication of glandular appendages connected with the reproductive ducts.

In Perichæta intermedia, P. aspergillum, and P. Houlleti the diverticula are of a different structure from the spermatheca; in all these cases the epithelium lining the diverticulum is formed of low quadrangular cells staining deeply; the epithelium of the pouch on the other hand is formed of tall columnar cells of which the nuclei only are stained. These facts would appear to indicate that the cells lining the diverticula are not of a glandular nature. It is worth remarking that the structure of the diverticula in these

Perichæta is like that of the immature Acanthodrilus georgianus; the resemblance is not due to a corresponding immaturity of condition, for the diverticula were in every case crammed with spermatozoa, which, however, only occupied the cavity of the diverticulum, and had no relation whatever with its epithelium.

It seems to be clear from the foregoing description that the diverticula not only perform a different function from the spermathecæ, but that the diverticula of some species (e.g. Perichæta) differ from those of other species (e.g. Acanthodrilus). Now, the presence of diverticula is so very general among Earthworms that they are probably to be looked upon as very ancient organs[1]; their great diversity of form and structure is also an argument leading to the same conclusion. It has been suggested by myself (9) and by Eisig (17) that the diverticulum is the remnant of the glandular part of the nephridium, out of part of which the spermatheca has been developed. This suggestion does not commend itself to me now, for the reason that in no species of Perichæta, or any other worm in which the nephridial system is in an archaic condition, is there any clue to the origin of the diverticula. If it be ultimately proved that the nephridial system of Perichæta, Megascolides, &c., is not archaic but greatly modified, then the above suggestion will have to be reconsidered.

The nature of the spermathecal diverticula can hardly be considered apart from the spermathecæ themselves with which they are so intimately connected. I am not certain, however, that from the developmental point of view the term "diverticulum" is not a misnomer. In the immature spermathecæ of Acanthodrilus georgianus, to which reference has already been made, the connection of the diverticulum with the spermatheca is by an extremely fine cord of cells in which no lumen could be detected; the relative perfection of the distal part of the diverticulum as compared with the proximal

[1] There are very few genera in which they are absent; Lumbricus Allolobophora, Hormogaster, are principal ones.

seems to suggest that the former is developed first. The matter, however, requires renewed study, especially since Bergh (13) has pointed out that in Lumbricus the relations of the spermatheca to the epidermis are very similar, though there can be no doubt that the spermatheca is an invagination of the epidermis.

In many hermaphrodite animals in which there is reciprocal fertilization, there are pouches connected with the oviduct or in its immediate neighbourhood which receive the sperm from another individual; this occurs, for example, among Mollusca and Planarians. In one genus of Earthworms, viz. Eudrilus (see p. 450), the spermathecæ open in common with the oviducts; it may be regarded as absolutely certain that the large pouches in this genus are really spermathecæ, since they contain spermatozoa; and no one has been able to discover any spermathecæ in those other segments of the body where they might be expected to occur. As fully mature examples of Eudrilus have been studied by several observers, it does not seem likely that such spermathecæ exist. An arrangement of this kind might perhaps have been inherited from the Planarian form from which the Oligochæta have been derived.

The question next to be considered is, how far do the spermathecæ of Eudrilus correspond to the spermathecæ of other Oligochæta which have no such connection with the oviduct? It seems perfectly clear that they do correspond to the spermatheca in Teleudrilus, as I point out later in this paper.

Perhaps also the spermatheca of such genera as Lumbriculus which occupy the same segments as the oviducts may have the same history. But this hypothesis hardly seems to fit in with the structure of Acanthodrilus, where the spermathecæ are in segments VIII and IX, and the aperture of the oviducts in segment XIV, and of the majority of Earthworms, where the spermathecæ and oviducts are separated by an equally wide interval.

In Acanthodrilus Rosæ, as already mentioned, the diverticulum consists of a number of small pouches bound up in a common sheath and connected by a thick-walled muscular duct with the spermathecæ just at the point of opening. This duct is lined with a tall columnar ciliated epithelium. The ciliated cells showed the usual refracting band just below the cilia. The cells did not seem to be all ciliated. There were ciliated tracts here and there. As far as I am aware, cilia have never been shown to exist in any part of the spermathecæ of Oligochæta. The statement of Buchholtz that the glandular appendices of the Enchytræidæ are ciliated is believed by Vejdovsky (**39**) to be a mistake, spermatozoa having been taken for cilia. The ciliation of this portion of the spermathecæ is so far favorable to the supposition that the diverticula are mesoblastic structures, that it is only mesoblastic and hypoblastic structures in Earthworms which show any ciliation. It may be that the ciliated canal is the rudiment of an oviduct, and the structure of Eudrilus and Teleudrilus are favorable to this view. It must be admitted, however, that a good many more facts must be discovered before this view can be regarded as in any way established.

On the Classification of the Species of Acanthodrilus.

We are at present acquainted with twenty species of Acanthodrilus,[1] which show a considerable amount of specific variation. The principal points in which the species differ are—(1) Number of segments occupied by clitellum; (2) arrangement of setæ; (3) characters of excretory system; (4) paired or single dorsal vessel; (5) number and characters of the spermathecal appendices. There are also several minor differences, such as the form of the buccal lobe, the presence of one or two gizzards, the alternation in position of the nephridial apertures where there are only one pair per segment, the ornamentation of the penial setæ, &c.

These characters render it possible to arrange the species in several groups, to which, however, I do not think it advisable to give generic names.

[1] Excluding Benham's Trigaster Lankesteri, which Horst thinks should be referred to the genus Acanthodrilus. It is, in my opinion, not yet necessary to make this change.

Affinities of Genus Acanthodrilus.—I have attempted to show elsewhere that in one very important structural character—the nephridial system—the family Perichætidæ represent most nearly the ancestral Oligochæt. The reproductive organs of Perichæta are not, in my opinion, so near to the ancestral condition as those of Eudrilus and Teleudrilus, but still they are nearer to it than those of such genera as Lumbricus and quite as near as those of any other genus at present known. As to other structural peculiarities, the most that can be said is that there is no reason against regarding Perichæta as an ancestral form. The only fact which it appears to me can be urged against this statement is the continuous circle of seta; it is perhaps usual to regard the paired arrangement as primitive, and the continuous circle of seta as derived from this; I am, however, inclined to think that the converse is true, and that the continuous circle of setæ round each segment is the primitive arrangement, the paired condition secondary.

Now, the genus Perichæta is clearly connected with Acanthodrilus through P. Stuarti and Deinodrilus. In P. Stuarti (Bourne, **14**) the Perichætous organisation is retained, but there are two pairs of tubular atria as in Acanthodrilus. I have shown that Deinodrilus agrees with many species of Perichæta in the clitellum; it has two pairs of tubular atria; the setæ are twelve in number in each segment, and are arranged in twelve longitudinal rows; their arrangement is in fact intermediate between that of Perichæta and that of Acanthodrilus. The nephridia of Deinodrilus can be explained on the hypothesis that they have been derived from those of Perichæta.

Affinities of the different Species of Acanthodrilus.

The above facts are, at least, reconcilable with the hypothesis that the eight setæ per segment of Acanthodrilus have been derived by the reduction of a primitively greater number. Now, in most of the species of Acanthodrilus which have a diffuse nephridial system, the individual setæ are, more or less, widely separated and not strictly paired,[1] and, at the same time, the buccal lobe does not divide the first segment, and there are dorsal pores present. In all these characters the species in question agree with Deinodrilus. I should regard these species, therefore, which are placed on the left side of the accompanying figure, as representing the least modified species. A. multiporus belongs to this group, but is indicated in the figure as slightly degenerate, owing to the fact that it has lost the penial setæ. On the right side is a branch which represents A. annectens; higher up, and also on the right-hand side, are a number of species which are rather more modified than A. annectens. All these, however, agree in that the nephridial system is reduced to a single pair in each segment. In A. annectens, the anterior "salivary glands" resemble those of A. multiporus, and for this reason the species is placed nearer to the primitive stock. In all these forms the procephalic lobe does not divide the buccal segment. It seems to me that, from the nature of the procephalic lobe, the condition which characterises many (? all) species of Perichæta, Deinodrilus, and those species of Acanthodrilus which have been as yet referred to is the primitive one; the setæ are, for the most part, separated, but in A. capensis they begin to be approximated, and this appears to be completed in A. communis.

The remaining species I regard as the most modified; the buccal lobe completely divides the buccal segment, and the setæ are strictly paired.

This scheme of classification of the species of Acanthodrilus is, of course, only tentative; the main point, however, which I wish to bring out is, that those species which come nearest to Deinodrilus (i. e. which possess diffuse nephridia, dorsal pores, buccal lobe not dividing buccal segment) have scattered setæ, and present, therefore, a stage in the evolution of strictly paired setæ from a continuous ring. It seems to me, in fact, that, as I pointed out nearly five years ago, the question of the origin

[1] I am not clear about A. scioanus. Rosa (35) does not mention the nephridia, but states of the setæ that they are closely paired.

of the setæ in Oligochæta is bound up with that of the origin of the nephridia, though the connection between the two structures is not quite so close as I then thought it was.

The connection between the three genera, Perichæta, Deinodrilus, and Acanthodrilus is so completely graduated that it seems impossible to avoid the conclusion that they represent a series of stages in the evolution of this group of Earthworms; and if the order of the series is as I have stated there is no doubt that the continuous setæ are primitive and the paired setæ secondary. The only alternative supposition is that Acanthodrilus is the more primitive form and Perichæta the last term in the series.[1]

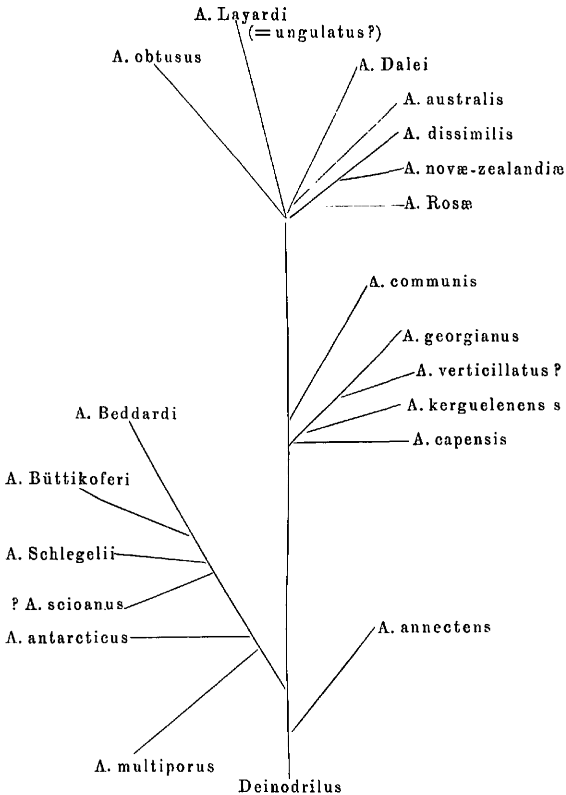
This position is held by Rosa (36), who bases his views upon certain facts in the anatomy of Acanthodrilus which seem to be really primitive; these are (1) the double dorsal vessel found in certain species, i.e. A. multiporus, (2) the presence in A. dissimilis of two pairs of ovaries, (3) the independence of the two pairs of vasa deferentia and their opening by as many distinct apertures, (4) the character of the nephridia of A. multiporus.

The last character I need not discuss again, as I have already argued that Acanthodrilus, although showing affinities to the primitive form, does not come so near it as does Perichæta.

With regard to No. 3, Rosa's facts are (through no fault of his own) incorrect; and in any case the male reproductive organs of Acanthodrilus resemble those of Deinodrilus and Perichæta Stuarti. I have already in this paper (p. 442) expressed the opinion that none of these types are so near to the primitive condition as Eudrilus.

(2) The presence of two pairs of ovaries is not characteristic of A. dissimilis, and it occurs occasionally in Lumbricus and Perionyx, and always (?) in Eudrilus.

[1] My position is of course not seriously affected by regarding Deinodrilus as the form from which both Acanthodrilus and Perichæta have been derived.


A. Layardi
(=ungulatus?)
A. obtusus
A. Dalei
A. australis
A. dissimilis
A. novæ-zealandiæ
A. Rosæ
A. communis
A. georgianus
A. verticillatus?
A. kerguelenens s
A. capensis
A. Beddardi
A. Büttikoferi
A. Schlegelii
? A. scioanus
A. antarcticus
A. annectens
A. multiporus
Deinodrilus

The occasional presence of two pairs of receptacula ovorum in certain species of Perichæta may be regarded as a "set off."

(1) The double dorsal vessel is found in six out of the twenty known species of the genus; but it also occurs in Deinodrilus, in Microchæta, and in Megascolex cæruleus; it is therefore characteristic of at least the two former genera. I am not inclined to regard this character as one of great importance from a classificatory point of view, since two forms so nearly allied as Acanthodrilus dissimilis and A. novæ-zealandiæ differ in this very particular, and, moreover, do not always differ (I have not found a double dorsal vessel in all examples of A. novæ-zealandiæ). The retention of the double dorsal vessel is certainly an embryonic character, comparable to the partial persistence of the left aortic arch in many birds of quite different groups (Raptoressome Struthiones). If it were confined to one group it might be regarded as an important classificatory character in birds and worms.

II. Further Observations upon the Reproductive Organs of Eudrilus, with special reference to the continuity between the Ovaries and their Ducts.

The investigations of Perrier (33), Horst (26), and myself (2), have shown that the reproductive organs of Eudrilus present certain remarkable differences from those of all other Earthworms, excepting the genus Teleudrilus recently described by Rosa (35).

In the male generative system the testes and sperm-sacs appear to be quite normal, that is to say, they differ in no important particular from those of other genera of Earthworms. The efferent ducts and the copulatory apparatus are, however, in many respects peculiar to the genus, being only paralleled in Teleudrilus.

In the first place, the two vasa deferentia of each side are quite independent up to their point of opening into the atrium. The atrium is double, but the two halves are enclosed in a common muscular sheath, and present no external evidence of their separation; distally the cavities of the two atria join to form a common duct, with thick muscular walls and lining of non-glandular epithelium. This duct passes into a penis, which is a projection of the body wall lodged in a pouch-like depression of the integument; a cushion-like thickening of the walls of this latter ("bursa copulatrix," Perrier) bears the orifice of a pair of short cæcal tubes, dilated at the cæcal extremity; these are lined with a cubical epithelium and have thick muscular walls. Sometimes the free extremities of the two tubes unite, and they then form a single horseshoe-shaped tube.

I have elsewhere pointed out that the atrium, into which the vasa deferentia open, is probably equivalent to the "prostates" of other Earthworms, its resemblance in minute structure to the prostate of Acanthodrilus being very close; and the bursa copulatrix is not represented in any other Earthworm, but would seem to be equivalent to the penis sheath of the Tubificidæ; the penis itself in Eudrilus appears to be fixed to the body wall within the bursa copulatrix, and not to be in- or evaginable; its protruded condition, which, so far as my experience goes, is invariable, may, however, be possibly due to contraction, caused by the killing fluid. The "Y-shaped appendage," which opens on to a sensitive (?) pad near to the penis, has puzzled M. Perrier as well as myself. The character of its epithelium seems to negative the possibility of its being a gland. The only structure with which I can compare it is to the sacs of penial setæ which occur in so many Earthworms. I find that the dorsal pairs of setæ upon the segment bearing the male generative pores are absent, the position of the pores being a little behind that which would normally be occupied by the setæ. The structure of the sac is certainly rather different from that which encloses the penial setæ in other Earthworms; but Stolč has figured (**38**, pl. iii, figs. 15, 16), attached to the spermathecæ of Psammoryctes barbatus, a sac containing "copulatory" seta, which has equally thick, many-layered, muscular walls.

In Teleudrilus (Rosa, **35**) the male genital pore is median and unpaired. The bursa copulatrix forms a large sac with very thick muscular walls and narrow lumen; this is continued into another very thick-walled sac, which Rosa terms "bulbo propulsore," and suggests as the equivalent of the "Y-shaped appendages" of Eudrilus; at the junction of this with the bursa open the prostates, whose structure appears to be identical with the corresponding organs in Eudrilus.

Apart from the median unpaired aperture, which is found in no other Oligochæt except Bothrioneuron (Stolč, **38**), there is, as Rosa has pointed out, a general correspondence between the efferent and copulatory apparatus of Teleudrilus and of Eudrilus. The immense thickening of the walls of the bursa have, so to speak, obliterated the distinction between the bursa and the penis, which has therefore disappeared in Teleudrilus. The result is that the copulatory organs of Teleudrilus resemble more closely those of such forms as Perichæta.

The female organs of Eudrilus are chiefly remarkable on account of the continuity of the ovary and oviduct, and the communication between the oviduct and the spermatheca. Teleudrilus is, again, somewhat intermediate in these particulars between Eudrilus and other Earthworms. The discovery of this genus, as Rosa points out, renders less necessary the separation of Eudrilus into a distinct group. At the same time I do not think that Dr. Rosa lays sufficient stress upon some of the peculiarities in the organisation of these two types; and I cannot agree with the way in which he interprets some of the structural features of Eudrilus.

The differences in structure between the female reproductive organs of Teleudrilus and Eudrilus are in reality somewhat greater than would appear from a comparison of Dr. Rosa's paper with my own.

In my paper I described and figured a pair of problematic bodies in the thirteenth segment, which are contained in a thin-walled muscular sac prolonged into a duct. I was unable at that time to find the opening of this duct or to determine definitely the nature of the bodies attached to the wall of the thirteenth segment; I suggested, however, that they might be ovaries because of their position; as they consisted of small round indifferent cells not distinctive in appearance, but not unlike those of the immature gonad, this suggestion was naturally the only one that occurred to me. This supposition was greatly strengthened by Rosa's discovery of a pair of similar structures in Teleudrilus, which are placed in an identical situation, and contain numerous mature or nearly mature ova. Since making myself acquainted with Dr. Rosa's paper I have examined some fresh material, and have found that the bodies situated in the thirteenth segment in Eudrilus contain ripe ova, and are therefore evidently ovaries corresponding to those of Teleudrilus. These bodies in Teleudrilus are contained in a sac, which is continued into a narrow tube, which communicates with the receptaculum ovorum in the fourteenth segment. The wall of the sac and of its narrow prolongation is extremely delicate, but in the narrow tube the cells lining the lumen are aggregated here and there into heaps. All these facts appear to point to the conclusion that the sac and tube which connects it with the receptaculum ovorum are merely specialised portions of the cœlom, in fact a prolongation forward of the receptaculum ovorum which has involved the ovary. Dr. Rosa does not figure the details of the structure of this sac and its duct, but I should imagine that the aggregation of cells in the latter are similar to the aggregations of peritoneal cells which occur in other parts of the cœlom (for example, in the "pericardium" of Deinodrilus (**3**) and Megascolides (**37**)).

Now, the sac which involves the ovary of the thirteenth segment in Eudrilus clearly corresponds to the sac involving the ovary of Teleudrilus. In Teleudrilus this sac, as Rosa points out and figures, contains a portion of a nephridium. I have not found this to be the case with Eudrilus, but this difference does not, of course, invalidate the comparison. Rosa suggests that the duct leading from the sac also corresponds, and that it will be found to open in Eudrilus, as it does in Teleudrilus, into the receptaculum ovorum. It must be admitted that this suggestion, based upon the very imperfect description which I was able to give of this part of the reproductive system, is not unreasonable.

I am, however, now able to state that the duct in question has no relations with the receptaculum of segment XIV, but opens into the spermatheca just opposite to the opening of the oviduct of segment XIV, and is lined throughout with a cubical epithelium, quite continuous with that which forms the inner layer of the spermathecal duct.

I now pass to the consideration of the organ in the fourteenth segment which I have termed "ovary," but which Rosa considers to be nothing more than a receptaculum ovorum homologous with that of other Earthworms.

Rosa found that the oviducts of Teleudrilus open separately from the spermatheca on a line with the dorsal pair of setæ; the spermathecæ open into an atrium, which itself opens on to the median ventral line of the body; the oviducts, however, agree with those of Eudrilus in having a thick muscular layer and in their continuity with the receptaculum; it appears, however, from the figure which Rosa gives (35, pl. ix, fig. 5) that the oviduct opens by a funnel into the cœlomic sac which connects the ovary and the receptaculum, and only just enters the latter; its relations to the receptaculum are, in fact, much like those of Lumbricus, except that the greater part of the funnel, which in Lumbricus depends freely into the interior of segment XIII, is here enclosed by the forward extension of the receptaculum. This receptaculum has its cavity subdivided by numerous trabeculæ, a condition which is also met with in the receptacula of other Earthworms. The contents of the receptaculum consisted of mature ova and numerous smaller cells probably serving for their nutrition. Rosa suggests that this may also be the case with Eudrilus, that the "developing ova" described by myself in that worm might be merely such cells. Dr. Rosa has not, however, quoted my paper in the 'Journal of Anatomy' (6), which deals with the minute structure of the ovary of Eudrilus. I have there figured structures which seem to me to be only possible of interpretation on the view that they are developing ova. If, then, the "ovary" of the fourteenth segment of Eudrilus be nothing more than a receptaculum, it is anomalous by reason of the fact that the ova may undergo there their whole course of development. Nothing of the kind has ever, to my knowledge, been described in any other Earthworm; indeed, Teleudrilus is the only instance of an Earthworm known to me[1] in which the receptaculum contains anything more than mature, or very nearly mature, ova. It is true that Goehlich has recently described bodies in the receptaculum of Lumbricus which bear a certain resemblance to germ-cells; but he is inclined to doubt their identity with such. Nevertheless, an analogy with the male organs might be regarded as an argument on Rosa's side.

The passage of the ova from the gonad into the receptaculum in Teleudrilus is of course rendered possible by the cœlomic sac which connects the two, though why they should not be drawn in passing into the open mouth of the oviduct is not easy to understand; in other Earthworms, such as, for example, Lumbricus, it is very difficult to see why the ova should get into the receptaculum instead of all finding their way to the exterior through the oviduct. In Eudrilus it is still more difficult to understand how this is carried out, if the organ of the fourteenth segment, which I regard as the ovary, be really a receptaculum to which the developing germ-cells are transferred. In the first place, as I have already pointed out, mature and immature ova are found in both the ovary and the supposed receptaculum; but, leaving this aside for the present, it does not seem possible that the ova could be conveyed directly, as they must be in Lumbricus, from the ovary which is enclosed in a muscular sac to the recep-

[1] Except in the Perichæta described for the first time in the present paper (p. 471).

taculum which appears to have no cœlomic aperture. On the other hand, it seems improbable that the ova from the ovary of segment XIII pass down into the spermathecal duct, and then pass up the oviduct into the supposed receptaculum. I am not able to state positively whether there are cilia in the oviduct of segment XIII, though I believe that there are not; but the spermathecal duct is certainly without cilia, as is also the distal half of the oviduct of segment XIV. The proximal half of this oviduct is abundantly furnished with long cilia; but, if the movement of the cilia is such as to further the exit of ova from the ovary of the fourteenth segment, they would prevent the entrance of ova into the same organ; but even supposing that the cilia by occasional cessation of their movement offered but little obstacle to the entrance of ova into the ovary of segment XIV, the passage of ova from the ovary of segment XIII into this would necessitate very complicated changes in the direction of the peristaltic action of the various parts of the female reproductive system.

But the force of any arguments that might be used to explain the passage of ova from the ovary of segment XIII to the supposed receptaculum of segment XIV, is greatly weakened by the fact that *ova in all stages of growth occur in both these organs.*

Another difficulty in the way of supposing that the cellular mass with developing ova in segment XIV is really an ovary is its position.

The ovaries of segment XIII correspond exactly in position with the testes, but not to the problematical organ in the fourteenth segment. The difference, however, even when most accentuated, is not a great one, and I should not have referred to it had it not been mentioned by Rosa; moreover, in some specimens the organ of the fourteenth segment appeared to correspond to that of the testes and ovaries. It must be remembered that (1) the ovary of segment XIV becomes very closely attached to the spermatheca, and (2) that the septum separating segments 13 and 14 is, in the region of the genital organs, largely deficient; the growth of the spermatheca might therefore easily have shifted the ovary from its original position.

I am inclined therefore to adhere to my original opinion that the mass of cells containing developing ova which is attached to the anterior wall of segment XIV is really an ovary; but I agree so far with Dr. Rosa—and indeed I have already put forward this view—that the walls which enclose the ova, and from which partitions grow inwards subdividing its cavity, are very probably to be regarded as the receptaculum ovorum. The receptaculum ovorum has here grown round the ovary just as the sperm-sacs frequently enclose the testis.

Returning now to the oviduct which is connected with the ovary of the thirteenth segment and which also communicates with the duct of the spermatheca, is this structure homologous with the tube which in Teleudrilus connects the ovary with the receptaculum? The homology cannot be a complete one, so far as can be determined from the minute structure and relation of the parts in question. The said tube in Teleudrilus is a cœlomic sac, perhaps produced by a growth from the receptaculum ovorum of segment XIV, perhaps an independent outgrowth of the wall of segment XIII which has become fused with the former. The tube in Eudrilus is probably a compound structure. The part which immediately surrounds the ovary is no doubt to be looked upon as a cœlomic sac corresponding to that of Teleudrilus. This sac passes without any break into a tube with a lining of cubical epithelium opening into the spermatheca. I am inclined to think therefore that this tube may be also cœlomic in origin, but the aperture into the spermatheca may be formed by an outgrowth of the epidermal involution (?) out of which the latter has been formed.

This is, of course, merely a supposition, and the matter cannot be decided until the development of this very interesting Oligochæt has been worked out.

The oviduct of the thirteenth segment differs in certain important particulars from the oviducts of segment XIV. In the first place it is a straight tube; secondly, it is completely continuous with the sac investing the ovary; there is no conspicuous break in the epithelium to mark the position of what might be regarded as the funnel; thirdly, the epithelium lining the oviduct is formed of inconspicuous cubical cells which are not ciliated. The oviducts of segment XIV, on the other hand, form a pair of much-coiled tubes, which are not so completely continuous with the perigonadial sac; the columnar ciliated cells lining the oviduct end abruptly in its interior and thus form a distinct funnel.

The structural differences between the two pairs of oviducts which have thus been briefly enumerated appear to be perfectly constant. I have suggested in an earlier paper (2) that these differences may be due to the immature condition of the oviducts and the perigonadial sac of segment XIII. Since I have discovered mature ova in the ovaries of segment XIII I am no longer disposed to believe that this is the case, but I now think that the differences described above are real differences. They appear to indicate a commencing disappearance in the oviduct of segment XIII. In Teleudrilus this pair of oviducts has completely vanished, and only the ovarian sacs remain; these have come to be connected with the ovarian sacs of segment XIV. This connection may perhaps account for the disappearance of the ovaries of the fourteenth segment, if they are really not represented in Teleudrilus; but Rosa's figures do not seem to me perfectly satisfactory upon this point. In most Earthworms all trace of the perigonadial sinus round the ovary has vanished, but in Lumbricus—as Rosa points out, quoting Hering—the ovary is prolonged into a delicate tube which may be a last remnant of this perigonadial sac. The receptaculum ovorum in these Earthworms often retains a partial connection with the oviduct in such forms as Acanthodrilus georgianus and A. scioanus (Rosa, 35) this connection is lost, and in many Earthworms the receptaculum itself is no longer to be found.

This series of changes in the female reproductive organs in a number of types is not, of course, meant to express my views on the evolution of the genera of Earthworms. I merely give instances which occur to me as representing a number of stages; these may evidently from their nature have taken place simultaneously along a number of different lines of descent; they are not sufficiently complicated to lead to the assumption that they can only have occurred once.

The different structure of the first from the second pair of oviducts, together with the relations of the anterior ovarian sac in Teleudrilus, suggests another view, which is: that the anterior pair of oviducts in Eudrilus are of a different nature from the second pair and from those of other Earthworms, and represent a pair of cœlomic sacs opening by a pore on to the exterior. In this case the relationship between these oviducts and the second pair would be analogous to that which the oviducts of Teleosteans bear to those of Elasmobranchs, &c., among Vertebrates.

While the structure of the adult compels me to regard this as a possible alternative, I do not think that the study of the development of the parts in question will be at all likely to confirm this view.

There is therefore, I submit, no doubt that there are in Eudrilus two pairs of ovaries and two pairs of oviducts which are continuous with the ovaries and which open in common with the spermatheca by a common aperture one on each side of the body. The fact that both pairs of oviducts open by one pore, with which is also connected a receptaculum seminis and a glandular appendix, suggests a comparison with the corresponding organs in the Planarians, from which group I am disposed (following Lang) to derive the Annelids. If this resemblance be a real one, it follows that the female reproductive organs of Eudrilus present the most archaic form which has yet been met with in the Oligochæta; and that this is an ancient type of Oliochæt is also confirmed by the structure of the efferent part of the male organs of generation as I have attempted to show elsewhere. On the other hand, the nephridial system and the setæ must be regarded, if my view that a diffuse and irregular nephridial system and a complete circle of setæ in each segment is the primitive condition be accepted, as greatly modified. We know, however, that within the limits of a single genus (Perichæta, Acanthodrilus), the nephridial system may become reduced to one pair of nephridia per somite, so that it is not necessary to assume that Eudrilus represents more nearly than any living form the ancestral Oligochæt. I believe, however, that it does in respect of the reproductive organs.[1]

The diffuse condition of the ovaries in many Planarians (which have already come to exhibit a regular segmental arrangement in Gunda), connected by a series of ducts with a single median pore[2] furnished with various accessory pouches, seems to me to be just recognisable in the female reproductive apparatus of Eudrilus.

I would not, however, venture to assert that the continuity of ovary and oviduct is a direct inheritance from the Planarian. It seems to me to be rather a secondary modification comparable to the formation of the "pericardium" in Deinodrilus, and to be the first step in the subdivision and partial obliteration of the cœlom which culminates (as far as Annelids are concerned) in the Leeches, and in the Crustacea[3] and Mollusca. In saying this I do not mean to imply a belief in the old distinction between ovaries independent of their duct and tubular ovaries, which has been urged with such ability by the brothers Hertwig in their "Cœlomtheorie."

[1] Lang has figured (**30**, pl. 26, fig. 4) an ovary of Cycloporus papillosus which shows a remarkable resemblance to the ovary (of the fourteenth segment) in Eudrilus in being subdivided into a series of chambers.

[2] The two symmetrical pores of Eudrilus are not opposed to the above statement, for we know that in Perichæta there may be a single median pore, or two pores placed side by side, and there are other instances among Earthworms.

[3] See an abstract of a paper on the cœlom of Arthropods and Molluscs by Professor Lankester in 'Nature' (1887), and Mr. Sedgwick "On the Development of Peripatus," 'Quart. Journ. Micr. Sci.,' vol. xxvii.

V. On Certain Points in the Anatomy of Perichæta, with Description of a New Species.

(1) Blood-glands.

The observations of Kükenthal (**28**) have gone some way towards showing that the peritoneal cells in Annelids play an important part in excretion. The so-called "chloragogen cells" of the intestine—which were regarded by earlier writers as representing a liver, and were on that account termed hepatic cells—are not, according to Kükenthal, an integral part of the intestine, but arise from the lymph; these cells attach themselves to the intestinal and other blood-vessels; the cells are at first clear but afterwards become loaded with yellow brown granules; the cells in this condition give a very distinctive appearance to the intestine in the Oligochæta. Later on these cells become again detached, and float freely for a time in the cœlom; finally they break down and the secreted granules liberated by this process are evacuated by the nephridia. The nephridia therefore in Annelids play to a certain extent a secondary part in the elimination of waste matter; in this capacity they serve merely as the conduits through which this waste matter, drawn from the blood by the chloragogen cells, reaches the exterior. It would appear therefore that the chloragogen cells do not, as they are commonly stated to do, form a layer covering the intestine, but their relation is to the blood-plexus or sinus which surrounds the intestine. The fact that these cells are generally pear-shaped, attached to the surface of the gut by a slender stalk devoid of granules, has probably given rise to the idea that they were unicellular secreting glands, pouring their secretion into the lumen of the gut. As to the connection between the chloragogen cells and the blood system, this was originally pointed out by Claparède (**15**, p. 227), who remarks, "The general opinion is that the pigmented cells form a hepatic layer on the intestines. M. d'Udekem describes them as unicellular glands of two kinds opening directly into the intestine. I have already expressed doubts as to the correctness of this view, which a more detailed study has only strengthened. These cells cover not only the intestine but also the dorsal vessel, and this is so in all species (Hoffmeister knew that this was the case in Tubifex rivulorum). They are often more closely packed upon that vessel than upon the intestines. They appear to be more intimately attached to the vessel than to the digestive tube, because in certain species they are seen to cover that vessel, not only in that part of its course where it lies upon the intestine, but also where it lies upon the œsophagus.

"In Lumbriculus variegatus, Grube, for example, the pigmented cells which do not cover the intestine until the sixth segment, are seen to cover the dorsal vessel from the fourth onwards. . . . The intimate relationship of these supposed hepatic cells to the vascular apparatus is also very evident in the true Lumbricidæ."

Further on Claparède remarks that these cells "probably get rid of their contents into the perivisceral cavity." Professor Lankester pointed out, in the case of certain "Limicolæ," that the abundance of granules in the perivisceral fluid often depends on the condition of the glandular coating of the intestine of the dorsal vessel, and that this glandular coating may have "a most important connection with the production of the corpuscles of the perivisceral fluid, and may serve to place this fluid in organic relation with the liquid of the closed vascular system of the intestine and contents of the digestive tract."

Vejdovsky (**39**, p. 112) has expressed the opinion that the chloragogen cells "with dark granular concretions most probably become free, and are absorbed by the cœlomic fluid, the small particles being removed to the exterior by the nephridia." He has therefore, in the time of publication, the priority over Kükenthal in putting forward these views.

It is evident therefore that these authors had some suspicion of the real nature of the part played by the chloragogen cells, which has been so admirably cleared up by Kükenthal.

An interesting contribution to this subject by Dr. Grobben has recently appeared (**22**, p. 450). This author had described in many Mollusca (**21**, p. 369), ramified glandular bodies arising from the pericardium, containing concretions in their cells. In his second communication (**22**) he suggests that the diverticula of the dorsal vessel in the Lumbriculidæ which are covered with chloragogen cells are homologous structures; in both groups (Mollusca and Annelids) the pericardial gland is a special development of the peritoneum in connection with vascular enlargements (the pericardium of Mollusca is of course cœlomic).

In Perichæta Houlleti, in P. aspergillum, and in Acanthodrilus Rosæ there are certain organs which are, I believe, referable to the same category.

These organs were first described by Perrier (**33**, p. 100), in Perichæta Houlleti, as glands ("glandes en grappe") opening into the œsophagus in segments VI and VII, close to the septum which separates these segments. These "glandes en grappe" were stated by Perrier to consist of numerous acini connected with a branching system of ductules, which unite to form a thin-walled duct of considerable calibre. The acini are composed of very small nucleated cells.

I have myself briefly described the glands in some examples of P. Houlleti, which were kindly collected for me in the Bahamas by Mr. W. F. R. Weldon. In my specimens there were three pairs of these organs, situated in segments V, VI, and VII; they appeared to be connected by a longitudinal duct on each side (= the "pyriform glands" of Perrier) and to open into the pharynx. I am now convinced that the interpretation which Perrier and I myself placed upon these structures are entirely wrong, and that they are not salivary glands at all. They certainly do suggest such structures, but a more careful examination of their minute structure, particularly in P. aspergillum—of which I have well-preserved examples—shows that the supposed ducts are only blood-vessels.

Fig. 9 illustrates a small portion of one of these glands in P. Houlleti, which was teased out and examined in glycerine. Each "acinus" is a spherical body, consisting usually of a dense mass of small nucleated cells, enveloped in a thin fibrous sheath; sometimes the centre of the acinus was hollow and contained a blood-clot (fig. 9 *a*); most of the acini (? all) were connected with two blood-vessels, generally, but not always, empty of blood. The walls of these are tolerably thick, and there is a continuous lining of cells, which gives them a certain resemblance to ducts. These blood-vessels form a series of branching tubes, the acini being simply dilatations, in which the lining epithelium has undergone so vigorous a growth as almost to obliterate the cavity.

In Perichæta aspergillum (probably also in P. Houlleti, though my material is not sufficiently well preserved to allow me to speak with certainty) these acini are closely packed together (fig. 8) and surrounded with a sheath of chloragogen cells; these cells also form a branching network, variable in the amount of its development between the individual vessels and the large dilatation. A compact organ, or rather a series of organs, is thus formed, which consists of a capillary network, with numerous large dilatations and a coating of modified peritoneal cells. These organs show a metameric arrangement, which is perhaps rather more conspicuous in P. Houlleti than in P. aspergillum.

The occurrence of identical organs in Acanthodrilus is interesting, as it tends to strengthen the evidence of near relationship between these two genera. It is very possible, however, that they will be found to occur elsewhere.

It is well known that in the nephridia of Lumbricus the capillaries are here and there dilated, the dilatation being filled with free nuclei. These structures are comparable to those which have been just described in the anterior segments of Perichæta, but they are scattered here and there among the coils of the nephridium, and are not compacted into large masses, as in the "blood-glands." The dilatation occurring on the capillaries of the nephridia are also of smaller size than those which make up the "blood-glands," though in the latter small dilatations, just like those of the nephridia, are also found.

The fact that these dilatations are always crowded with small cells, which seem to be just like the free corpuscles of the blood, suggests that they may be the seat of formation of the latter.

On the other hand, the immense mass of cells contained in the anteriorly situated blood-glands is altogether out of proportion to the very scanty number of free corpuscles present in the blood. Moreover, Vedjovsky (**39**) has pointed out that certain valve-like structures, which are found along the principal vessels, are probably the source of the corpuscles, which would appear to be from Lankester's investigations little more than the nuclei of such cells.

I would not, however, venture to assert that this is not a function of the bodies in question.

The close packing of the cells in the capillaries of the blood-gland, which seems occasionally (and perhaps only temporarily) to produce an actual occlusion of the lumen, and the general arrangement of the capillaries, would naturally tend to slow the circulation in this part of the vascular system; and it is also possible that the cellular mass which forms the greater part of the spherical dilatation along the capillaries may play an active part in the elimination of waste matter from the blood, the waste matter being then temporarily stored up in the chloragogen cells. Perhaps both these functions go on side by side.

In any case I am inclined to compare these organs with the "pericardial glands" of other Annelids and other Invertebrates.

(2) Capsulogenous Glands.

In three species of Perichæta, viz. P. Houlleti, P. aspergillum, and P. mirabilis, there are a number of small glands opening on to the exterior in the neighbourhood of the reproductive pores; the histological structure of these has not been investigated, and they have been, to a certain extent, confused with other structures, with which they do not appear to have anything in common.

Perrier, in his description of Perichæta Houlleti, has stated that the spermathecæ (of which there are three pairs) are each furnished with two diverticula; one is a moderately long tube of equal diameter throughout, and bent upon itself like a "Pan's pipes;" the other is a pear-shaped body attached by a long stalk to the duct of the spermatheca. I have found that in this species there are sometimes a pair of these structures (fig. 6), of which one may lie in the cavity of the segment, anterior to that in which the spermatheca lies; this increases the resemblance of the structures in question to diverticula. These bodies are of a perfectly different structure from diverticula; each consists of a mass of granular cells which are prolonged and form collectively the stalk of the organ,—it is in fact merely a bundle of unicellular glands, which pour their secretion into the duct of the spermatheca.

In P. aspergillum, Perrier has directed attention to a number of small white glands which open on to the exterior, round the orifices of the spermathecæ and vasa deferentia. These glands (figs. 3, 4, 5) are identical with those just referred to in P. Houlleti.

In Perichæta mirabilis, the same glands are found and their orifices are exceedingly conspicuous. I observed four apertures. There are three apertures in one segment—two lateral and one median, and a single median aperture in the following segment. I neglected to note the exact position of the segment occupied by these pores, but the anterior, at least, also contains a pair of spermathecæ. The apertures of the glands are, as remarked, extremely conspicuous, and might easily be taken for spermathecal openings; in fact, the uselessness of external characters only, as a guide to zoological affinities, is strikingly exemplified by this case. With each pore communicates several bundles of unicellular glands, which converge at the point of opening, or sometimes earlier.

So far as I am aware, these peculiar glands are confined to the genus Perichæta.[1]

[1] Perrier has described in P. affinis what are apparently similar glands; in that species they are connected with the genital papillæ which occupy segments 17 and 19; it is possible that the papillæ in Perichæta are often connected with such glands.

Their arrangement in the three species mentioned above seems to indicate that they will, when better known, serve as a means of discriminating the species of this genus, which are already very numerous.

The restriction of these glands to the neighbourhood of the spermatheca and vasa deferentia pores, is an indication that they are concerned with the reproductive functions.

The descriptions of the cocoon and embryos in exotic Lumbricidæ, although limited to Megascolex cœruleus (Beddard, **8**), and Megascolides australis (Spencer, **37**), seem to indicate that there is no great difference between these types and our indigenous Lumbricidæ. The cocoon membrane is now generally admitted to be a product of the clitellar glands; the albuminous fluid in which the ova are embedded seems to be formed by the capsulogenous glands ("Eiweissdrüsen") in the Lumbricidæ, and in such forms as Rhynchelmis. Spencer has, however, suggested that this substance in the cocoon of Megascolides is, probably, in part at least, cœlomic fluid. I confess myself unable to agree with Professor Spencer as to the likelihood of the cœlomic fluid being used for such a purpose, though, at the same time, it is very possible that, during the formation of the cocoon, some cœlomic fluid might be accidentally squeezed out of the dorsal pores and included within the cocoon. Spencer's statements, in fact, do not really imply more than this, as I read them.

As no capsulogenous glands have been found in Megascolex and Megascolides, some other origin for the albuminous fluid in the cocoon must be sought for.

The only organs which can be supposed to secrete this fluid in the two genera are the atria (= prostates) and the spermathecæ.

Now, the function of the atria seems to be probably that of compacting together the spermatozoa so that they can be easily transferred to another individual during copulation, and they are well developed with additional glands in the Tubificidæ, whose cocoons appear to be without any albumen (Vejdovsky,

39, p. 149); again, in the Naidomorpha, and, to a less extent, in the Enchytræidæ there is a glandular atrium; and here the ova are laid singly, each enveloped in its own cocoon and closely filling it, so that but little room is left for any albumen.

Vejdovsky (**39**, p. 153) agrees with Lankester that the central axis of the spermatophore is formed by the secretion of the prostates ("Cementdrüsen") in the Tubificidæ; in Clitellio where these glands are unrepresented, the epithelium of the atrium seems to be unusually thick and glandular, and may perform the same function.

The fact that the atria in Earthworms (e. g. in Acanthodrilus, Typhœus, some species of Perichæta) are commonly furnished with penial seta, or, if not, can be protruded so as to form a temporary penis (some species of Perichæta, Teleudrilus), seems to suggest that their function is a similar one, viz. to glue together the spermatozoa in bundles and to convey them to another individual.

This function does not seem to be compatible with that of forming albumen for the nourishment of the embryos in the cocoon.

Again, the position of the atrial pores for the most part behind the clitellum or just within it, is not the most favorable for such a purpose, assuming that the cocoon, when formed, is passed over the head of the worm, as it is in Rhynchelmis (Vejdovsky, **40**).

Unless, therefore, the cœlomic fluid be ultimately proved to be the source of the cocoon albumen, the only organs in Megascolides and Megascolex which can prepare this fluid are the spermathecæ. In an earlier part of this paper, (p. 435), I have commented upon the fact that in Earthworms whose spermathecæ possess diverticula the spermatozoa are always found in the diverticula and not in the spermatheca.[1] It is true that I have myself omitted to describe any such diverticula to the spermatheca of Megas-

[1] I have referred to Rosa's statement that in Acanthodrilus scioanus there are spermatozoa in the spermathecæ; but this is one exception, and indeed it may conceivably often occur and yet be accidental.

colex. I did not, however, investigate these structures by means of sections, and remembering (1) that in Acanthodrilus multiporus the diverticula are embedded in the body wall, and not visible on a dissection, and (2) that in no other species of Perichæta or Megascolex are diverticula wanting, it seems to be probable that these structures will be ultimately proved to exist in Megascolex cœruleus.

I have found in Acanthodrilus that the spermatheca contains (in preserved specimens) a hard coagulated mass, showing no structure, which gives the ordinary albumen reactions. I am disposed, therefore, to think that the function of the spermathecæ in Acanthodrilus, and other genera where diverticula are present, is to prepare the albumen for the nourishment of the embryos in the cocoon, the diverticula being the real sperm reservoirs.

The connection between the spermetheca and the albumen gland in Sutroa (Eisen, **18**) is suggestive in view of this possibility.

I had written to this point when Michaelsen's most recent memoir (**32**) came into my hands through the kindness of the author. In his description of Cryptodrilus purpureus Michaelsen records the interesting fact that there are five spermathecæ occupying as many segments and opening in the ventral median line. Each pouch is furnished with a pair of diverticula, one on each side. "These cylindrical diverticula contain sperm after fecundation. The wide middle sac is filled with a granular mass which is feebly coloured by picro-carmine (nutritive matter for filling the cocoon)" (**32**, p. 5). The suggestion made in the above quotation is not supported by any further discussion.

I do not think that the question of the function of the spermathecæ can be at present definitely settled, but the hypothesis advanced in the present paper is at least not contradicted by our experience.

It occurred to me that the remarkable glands in Perichæta, of which some description has just been given, might serve as capsulogenous glands. There are some facts which seem to me to favour this supposition, and some which are opposed to it.

In describing the spermathecæ of Acanthodrilus (p. 435) it has been pointed out that the spermatozoa become embedded in granular masses which are formed by the metamorphosis of the lining epithelium of the spermathecal diverticula. I take it that the spermatophores of Acanthodrilus consist of little more than a number of these balls of granular substance containing spermatozoa compacted together. In no species of Perichæta that I have been able to examine (and I have studied mature specimens of a good many species) is there any such modification of the epithelium of the diverticula, although the spermatozoa are only found in the diverticula. It is possible, therefore, that here the diverticula have not yet assumed, or have lost, the function which their homologues in the Acanthodrilidæ perform.

In this case, therefore, the formation of the spermatophores may be partly due to the epithelium of the spermathecæ; hence the need for capsulogenous glands, which is satisfied by the abundant glandular development in the neighbourhood of the spermathecæ.

The spermathecæ of Perichæta on this hypothesis lie midway between Acanthodrilus and Lumbricus.

Against regarding these glands of Perichæta as capsulogenous glands is perhaps their development in the neighbourhood of the atria as well as more anteriorly. This rather suggests that they may secrete a fluid serving to attach together the worms during copulation.

At any rate, the presence of capsulogenous glands in Lumbricus and Brachydrilus is correlated with the absence of diverticula. This statement does not apply to Microchæta, but as only four specimens of that worm have been dissected it is still far from certain that it does not possess any capsulogenous glands.

In Lumbricus and its allies the disappearance of the diverticula has resulted in the formation of special glands—the capsulogenous glands; in Brachydrilus and Microchæta it seems to me to be possible that the spermathecæ have disappeared and the diverticula remained to discharge their functions. The structure of these small pouches, their large number per somite, and their variability in number, are facts which are quite in accord with such a view.

Criodrilus is a form which is difficult to fit in with this hypothesis, but the total absence of any trace of spermathecæ at all is sufficiently puzzling without going any further.[1]

Perichæta intermedia, n. sp.

The genus Perichæta, of which there are a larger number of species known than of any other genus, forms one of the best-marked types among Earthworms; so much so, indeed, that its affinities with other genera are by no means clear. I have recently, however, described in this Journal (3) a remarkable type—Deinodrilus—which is to some extent a connecting link between Perichæta and Acanthodrilus, though it is perhaps, on the whole, nearer to the latter.

I have now to describe a species, like Deinodrilus, from New Zealand, which, although it must certainly be placed in the genus Perichæta, shows affinities to Acanthodrilus.

I have given this worm the specific name of "intermedia," in order to indicate its intermediate characters, but I am not quite certain as to its distinctness from an Australian form recently described by Mr. Fletcher as Perichæta Bakeri (19), with which it appears to agree in some structural peculiarities. In Mr. Fletcher's paper, which is apparently preliminary to a more exhaustive account of the anatomy of Australian Earthworms, no special stress is laid upon the more important characters of P. Bakeri, in which it seems to resemble the present species, and to differ markedly from other Perichætæ.

[1] The absence of capsulogenous glands in some Lumbriculidæ is perhaps to be accounted for, as is their absence in Tubifex, i.e. by the fact that the cocoon contains no albumen. Hormogaster, Urochæta, Thamnodrilus, and some other genera have no capsulogenous glands and no diverticula. But this is only negative evidence, and these genera are clearly not so well known as Perichæta and Acanthodrilus.

In any case, therefore, it seems to be desirable to draw the attention of zoologists to this Earthworm, as it seems to connect the genus Perichæta with other forms.

The most remarkable structural peculiarities of P. intermedia concern the excretory and reproductive organs.

The genus Perionyx was distinguished by Perrier (33) from Perichæta, chiefly for the reason that each segment is furnished with a pair of nephridia. These organs in Perichæta usually consist of innumerable tufts of extremely fine tubules, which, as I have shown, form a network communicating with the exterior by many pores, and with the cœlom by numerous ciliated funnels, in each segment. Although Perrier did not observe the microscopical characteristics of the nephridia of Perichæta, he did point out such obvious differences between the nephridia of this genus and of other Earthworms as could be discerned on a dissection of the worm; and these differences led him to separate Perionyx, which agrees with Lumbricus and many other genera in having a single pair of distinct nephridia in each segment of the body. Perichæta intermedia and, according to Fletcher's description, P. Bakeri, agree with Perionyx, and differ from other Perichæta in their nephridia.

The second point of interest in the structure of the two last-named species of Perichæta is in the form of the "prostate," or atrium, as it is better termed. In nearly all the species of this genus the atria form branched glandular structures, being frequently divided by furrows into variously sized lobes. The branched character of the atrium is but little marked in P. Newcombei (see Beddard, 4) as compared with many other species. In P. intermedia the atria are precisely like those of Acanthodrilus and Typhœus; they are long tubular organs much coiled upon themselves; their cavity is simple, not branched, and the histological structure of their walls is quite indistinguishable from Acanthodrilus (see Beddard, 3). I imagine, from Mr. Fletcher's description of P. Bakeri, that the atria of this species of Perichæta are like those of P. intermedia. A very interesting Perichæta has been lately described by Bourne (14); this species, P. Stuarti, appears to possess two pairs of tubular atria, and therefore resembles Acanthodrilus very closely indeed.

Perichæta intermedia is a moderately large species, being stout in proportion to its length; its general aspect is very different from that which is characteristic of Perichæta; the setæ are not at all conspicuous, and the worm has a smooth, somewhat glandular appearance. This seems to be due to the absence of a ridge in the middle of each segment for the implantation of the setæ.

The buccal lobe does not divide the peristomial segment.

The clitellum was not developed in either of my two specimens.

The colour of the spirit preserved was of a reddish brown, paler ventrally. During life, according to Mr. W. W. Smith, from whom I received the specimen, the colour is "bluish green."

The setæ form a nearly complete ring round each segment, only failing for a short space in the mid-dorsal and mid-ventral lines.

There are no dorsal pores.

In the neighbourhood of the male genital pores are a number of papilla.

The male genital pores are a pair of slit-like orifices on the eighteenth segment, on a line with the setæ, which are almost absent in the space between the two orifices, there being apparently only one seta on the inner side of the pore.

The oviducal pores are paired, and upon the fourteenth segment; this is unusual, but is occasionally met with in the genus Perichæta. The common arrangement is a single median pore.

The nephridiopores are quite obvious upon most of the segments and lateral in position.

Alimentary Canal.—The gizzard is situated in the fifth segment; it is very small and the muscular walls not very thick.

The œsophagus is furnished with separate calciferous glands in segments X and XI. These glands are not, as is so often the case, connected with the lumen of the œsophagus by a narrow duct; they present the appearance of swellings of the œsophagus and resemble very closely the calciferous glands of Microchæta (Beddard, Benham). Though probably formed as two paired outgrowths of the œsophagus no trace of a paired arrangement is visible in the adult worm.

The nephridia, as already stated, are paired; the funnels, as is nearly always the case, open into the segment anterior to that which bears the external orifice. I reserve for the present details as to the structure of the nephridia.

Genital Organs.—The sperm-sacs are in segments IX, X, XI, and XII. The vasa deferentia open into segments X and XI; the two vasa deferentia unite to form a single tube, the relations of which with the atrium I have not been able to make out with certainty. I believe, however, that it does not open on to the exterior independently of the atrium; there are no conspicuous penial setæ, but it appeared to me, in one specimen which I investigated by means of sections, that one or two of the setæ in the immediate neighbourhood of the genital pore were rather larger than the others.

The ovary is in segment XIII, and the oviduct opens into the same segment; there is nothing unusual about either of these organs. The ovary, as in most Earthworms, is not a compact organ, but is prolonged into numerous filiform processes.

The egg-sacs (receptacula ovorum) are very conspicuous structures; they lie upon the posterior surface of the septum separating segments XIII and XIV, and on either side of the intestine.

These organs are larger than is generally the case, and have a racemose appearance; in both these points they present an interesting resemblance to sperm-sacs; furthermore they contain numerous Gregarines.

In one specimen, the genital region of which I investigated by transverse sections, the structure of the egg-sacs was a little different from that of other Earthworms which I have had the opportunity of studying. The walls (see fig. 12) are tolerably thick and appear to be made up of fibres. Interspersed among them are nuclei which are extraordinarily numerous; the blood supply was not very great, but this may be due to accidental causes. The presence of egg-sacs in Perichæta has been noted in but few species. Bergh (**13**, p. 318, footnote) remarks upon the presence of two pairs of egg-sacs in P. Hasselti; the first pair are situated in the ovarian segment above the ovary; the second pair in the following segment occupying a corresponding position. He also quotes Perrier's (**33**, p. 116) observation of a pair of apparently similar structures lying above the ovaries in P. robusta. In P. aspergillum there are two pairs of egg-sacs lying in segments XIII and XIV; like Bergh, I could find no ova in these egg-sacs, nor any connection with the oviduct. As, however, in Perichæta intermedia there is a similar absence of connection with the oviducal funnel and yet the egg-sacs are full of ova, I cannot agree with Bergh in regarding the egg-sacs of P. Hasselti as functionless (as egg-sacs).

Bergh states that the ova of Lumbricus, although surrounded while in the ovary by a follicular layer of flattened cells, leave the ovary in a completely naked condition. So far as I am aware this statement is borne out by other observers, who have figured or described the ova in the egg-sacs as without a follicular layer. This appears also to be the case with Criodrilus (Collin, **16**) and Microchæta (Benham, **11**, pl. viii, fig. 10).

In Perichæta intermedia the egg-sacs were filled with mature ova, all of which were surrounded with a perfectly distinct follicular epithelium composed of flattened nucleated cells.

In addition to this follicular epithelium—between which and the ovum is a distinct vitelline membrane—many of the ova were also furnished with a small number (four or five) of germinal cells attached to one pole (see fig. 12). This is an interesting resemblance to certain of the lower Oligochæta, in the majority of which the ova are detached from the ovary and fall into the egg-sacs in company with a number of germinal cells, which probably serve for the nutrition of the ovum. My specimens were not sufficiently well preserved to enable me to make out how far there is an actual contact between the protoplasm of the ovum and of the nutritive cells.

There are four pairs of spermathecæ occupying segments V—VIII; each is furnished with a single supplementary pouch of small size; this was conspicuous by reason of its yellow colour, and, as in P. sumatrana, was crowded with spermatozoa.

The septum to which the egg-sacs are attached is one of the specially thickened septa, of which there are six dividing segments, VIII—XV. The egg-sacs are attached close to the œsophagus, and where the œsophagus perforates the septum there is a space left, through which the egg-sac is prolonged, opening into the interior of the thirteenth segment and coming into very close relations with the funnel of the oviduct; the passage of ova into the egg-sac is facilitated by this, and by the fact that the two thick mesenteries which bound segment XIII are closely approximated, so that the actual cavity of the segment is much reduced. The part of the egg-sac nearest to its attachment forms a spacious cavity, undivided by trabeculæ. I have noticed in this part masses of ovarian tissue containing germinal cells and eggs in all stages of development. This fact appears to be contrary to the opinion advanced above, that the ovary of segment XIV in Eudrilus is really an ovary; but the egg-sacs of Perichæta contained only very small fragments of ovarian tissue, besides the developing ova, while the organ in Eudrilus was quite full of germinal cells in all stages of development.

Nervous System.

In figs. 2, 10 are illustrated the way in which the nerves arising from the ganglia are distributed to the body wall in Perichæta intermedia and in P. aspergillum.

In both species, as Vejdovsky has mentioned for Dendrobœna (39, p. 85), the nerve courses in the interior of the body wall between the longitudinal and the circular muscular coat. I am not certain whether the two nerves meet dorsally, but they certainly do ventrally (see fig. 2, 2 *a*). These nerves give off innumerable branches, for the most part from the upper surface of the nerve-trunk, i.e. towards the epidermis. These nerve-branches consist, like the nerve from which they arise, of numerous delicate fibres, which have usually a somewhat wavy aspect. Among them are many nuclei which may belong to the nerve-fibres or to their sheath. As these nuclei were found on the smallest branches close to their connection with the epidermis it seems to be more likely that they are the nuclei of the nerve-fibres.

The bundles of nerve-fibrils pass in every direction, as is shown in fig. 1, and appear to anastomose with each other, though I could not detect any ganglion-cells connected with them. These nerve-branches finally terminate in connection with (?) the cells of the epidermis; bundles of fibrils could be observed passing up into the epidermis, which were quite as large as the branches immediately arising from the main nervous trunk. I only observed the presence of this intramuscular nervous plexus in the immediate neighbourhood of the setæ.

Subneural Blood-vessel.

The subneural blood-vessel, which does not appear to be present in any genera of Oligochæta which have been referred to Claparède's division of the Limicolæ, is also wanting in some Earthworms. Perrier has denied its existence in Pontodrilus and Perichæta, and Benham states that it is also absent in Michrochæta. It is therefore of some little importance to note that this blood-vessel is not invariably absent in the genus Perichæta (see fig. 7).

I have found it in the following species:

Perichæta, sp. (from the Philippines),
P. aspergillum,

but it is absent in P. armata.[1]

[1] I may also mention that the two latter species have no typhlosole, but that there is a rudimentary typhlosole in Perichæta, sp. (? affinis).

I may also take this opportunity of remarking that there is a subneural blood-vessel in Thamnodrilus.

Summary.

The more important new facts contained in the present paper are the following:

(1) Description of Acanthodrilus antarcticus, A. Rosæ, A. Dalei, nn. spp.

(2) The ciliation of the spermathecal appendix iu A. Rosæ.

(3) The presence in Eudrilus of two pairs of ovaries, connected by oviducts with a single aperture on each side; the oviducts are continuous with the ovaries.

(4) The description of Perichæta intermedia, n. sp., which differs from most species of Perichæta in having a single pair of nephridia in each segment, and in having a tubular atrium like that of Acanthodrilus.

(5) The presence of functional egg-sacs in the same species, in which the ova undergo their development surrounded by a follicular epithelium and with a mass of germinal cells attached to one pole, as in certain "Limicolæ," &c.

(6) The presence of a peripheral nerve plexus in Perichæta, specially developed in the neighbourhood of the setæ.

(7) The presence of a subintestinal blood-vessel in Acanthodrilus.

(8) The presence of a subneural blood-vessel in Perichæta.

(9) Description of the minute structure of the spermathecæ and the spermathecal appendices in Perichæta and Acanthodrilus; spermatozoa are only found in the appendices, the epithelium of which has largely undergone degeneration into a viscous substance, in which the spermatozoa are embedded.

(10) Description of some epidermic glands in Perichæta, which are possibly equivalent to the capsulogenous glands of Lumbricus.

(11) Description of certain organs in Perichæta and Acan-

thodrilus which probably correspond to the "pericardial glands" of Lumbriculus. These consist of a network of capillaries with numerous spherical dilations crowded with cells; the whole network forms a compact series of organs clothed with chloragogen cells; they are found in the anterior segments only, and exhibit a more or less perfectly metameric arrangement.

(12) Description of a series of paired sacs attached to the septa of Acanthodrilus georgianus, which appear to be special glycogenic organs.

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EXPLANATION OF PLATES XXIX and XXX,

Illustrating Mr. Frank E. Beddard's paper "Contributions to the Anatomy of Earthworms, with Descriptions of Some New Species."

Fig. 1.—Transverse section through body wall of Perichæta intermedia. *ep.* Epidermis. *n.* Nerve. (n^2. in Fig. 2) n'. Branches of the same. *bl.* Blood-vessels.

Fig. 2.—Diagrammatic transverse section of a portion of the body wall of the same species, to illustrate course of nerve-trunks. *n.* Nerve. n'. Portion lying between transverse and longitudinal muscles. *b.* Point at which nerve branches; the branch passing to the left (below the ganglionated cord), fuses with the corresponding nerve of the left side. *v. d.* Vas deferens. *a.* Fragment of fourth longitudinal muscle-mass, separated by nerve.

Fig. 2 (*a*).—Disposition of nerve (*n*) at its point of bifurcation (*b*) within the bodv wall in another segment.

Fig. 3.—" Capsulogenous " glands of Perichæta aspergillum, magnified about 20 diam. *o.* External orifice.

Fig. 4.—Section through body wall of Perichæta, sp., to show "capsulogenous" glands (*gl.*). *a.* External orifice.

Fig. 5.—Transverse section through body wall of Perichæta aspergillum. *e.* Epidermis. *t.* Transverse. *l.* Longitudinal muscular coat. *b.* A "capsulogenous" gland, the section passing through the blind extremity. *a.* Duct of another in longitudinal, *a'* in transverse section.

Fig. 6.—Spermatheca of Perichæta Houlleti. *d.* Diverticulum. *a.* Capsulogenous glands.

Fig. 7.—Transverse section through nerve-cord (*n*) and median ventral portion of body wall of Perichæta affinis (?). *v.* Subnervian blood-vessel.

Fig. 8.—Section through one of the "blood-glands" of Perichæta aspergillum. *v.* Blood-vessels. *bl. bl'.* Dilatations of same. *m.* Muscular fibres. *p.* Peritoneal epithelium.

Fig. 9.—Portion of network of one of the blood-glands of Perichæta Houlleti. *b.* Blood-vessels. *a.* Dilatation.

Fig. 10.—Section through nerve-cord and a pair of lateral nerves in Perichæta aspergillum. *n.* Nerve-cord. *b.* Body wall.

Fig. 11.—Female reproductive organs of Eudrilus. *s.* Septum between segments XIII and XIV. *s'.* Septum between segments XII and XIII. *sp.* Spermatheca. *gl.* Glandular body. *o.* Ovaries with their ducts.

Fig. 12.—A portion of egg-sac of Perichæta intermedia. *c.* Walls of sacculi. *a.* Nutritive cells. *b.* Follicular epithelium surrounding ovum.

Fig. 13.—A portion of ovary of Eudrilus. *a—d.* Ova in various stages of development.

Fig. 14.—Penial seta of Acanthodrilus Dalei.

Fig. 15.—Penial setæ of A. georgianus.

Fig. 16.—Extremity of same seta more highly magnified.

Fig. 17.—Penial seta of A. antarcticus.

Fig. 18.—Extremity of penial seta of A. capensis.

Fig. 19.—Penial setæ of A. Rosæ.

Fig. 20.—Anterior segments of A. Rosæ.

Fig. 21.—Anterior segments of A. multiporus.

Fig. 22.—Anterior segments of A. georgianus.

Fig. 23.—Spermatheca of A. Dalei. *a.* Glandular part of diverticulum.

Fig. 24.—Spermatheca of A. Rosæ. *a.* Glandular part of diverticulum.

Fig. 25.—Spermatheca of A. novæ-zealandiæ. *a.* Glandular part of diverticulum.

Fig. 26.—Spermatheca of A. Rosæ in situ. *a.* Spermathecal pouch. *b.* Diverticula. *c.* Their long muscular duct. *n.* Nerve-cord.

Fig. 27.—Transverse section through spermatheca of sexually immature A. georgianus. *b.* Pouch. *a.* Diverticulum. *bl.* Blood-vessels.

Fig. 28.—Diverticulum of spermatheca of the same species more mature.

Fig. 29.—Diverticulum of spermatheca of A. Rosæ. *a.* Colloid masses formed between cells *b*, *d*, containing spermatozoa.

Fig. 30.—Constituent cells of diverticulum of the same species more highly magnified. I, in longitudinal; II, in transverse section. Lettering as in last figure.

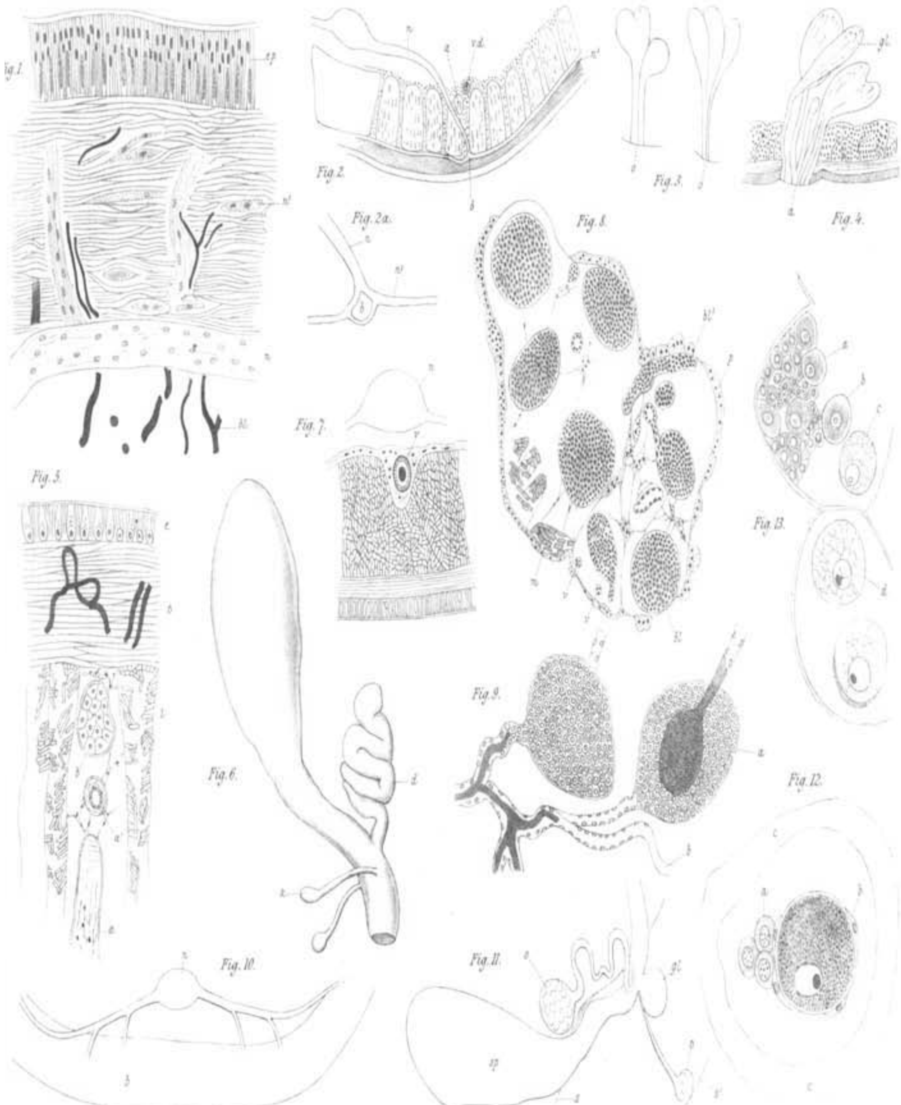
Fig. 31.—Septal organs (*a*) of A. georgianus.

Fig. 32.—One of the septal organs more highly magnified. *s.* Septum. *x.* Septal organ. *bl.* Blood-vessel.

Fig. 33.—Transverse section through gizzard of A. georgianus.

Fig. 34.—Section of muscular portion of spermathecal diverticula to show ciliated epithelium.

Fig. 35.—Wall of median unpaired sperm-sac of A. georgianus.



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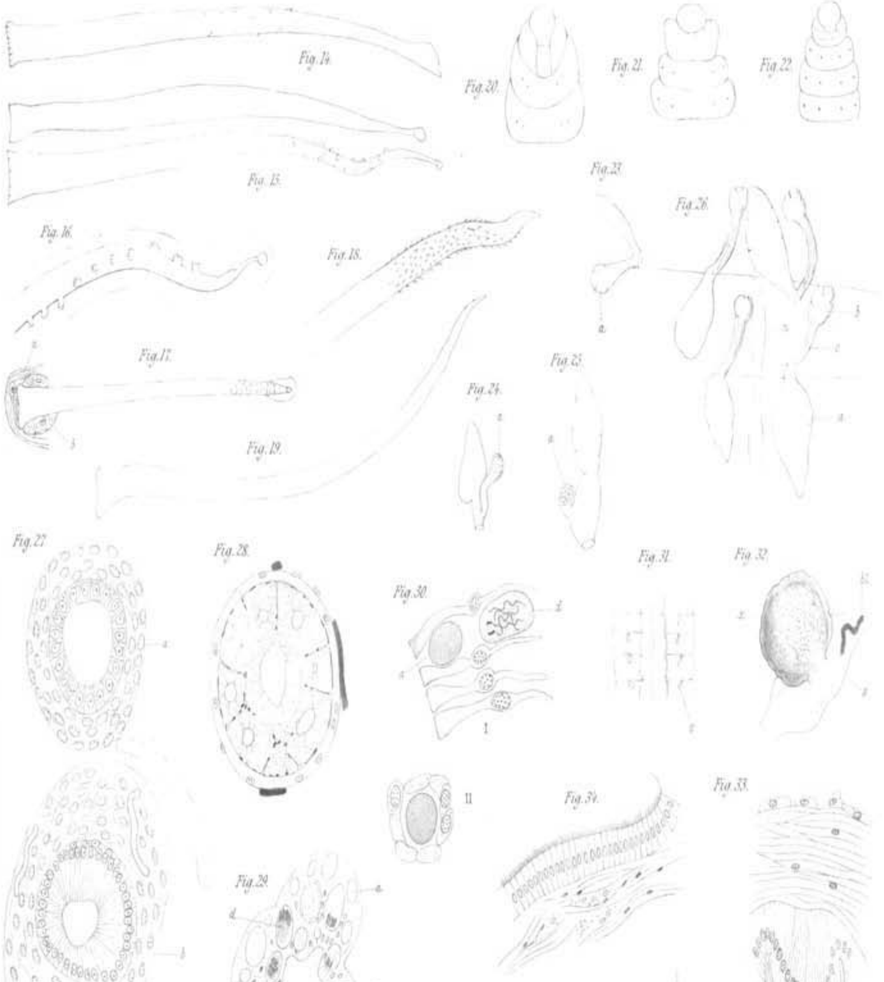

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