Researches into the Embryology of the Oligochaeta.


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With Plates XXX, XXXI.

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Our knowledge of the development of the Oligochaeta is at present based only upon that of a few indigenous forms. Indeed, Lumbricus (including Allolobophora and Allurus), Enchytraeus, Rhynechelmis, and Criodrilus are the only types which have been investigated by modern methods. The present paper is the first of what I hope will be a series of memoirs dealing with exotic forms. In addition to Acanthodrilus multiporus, which is treated of in the present communication, I have a few embryos of Acanthodrilus novae-zelandiae, which will form the subject of a later com-
munication. Mr. W. W. Smith, of Ashburton, New Zealand, to whom I am deeply indebted for these and many other specimens, has kindly promised to collect other cocoons for me. They travel very well in a living condition. I have already had two sets of cocoons belonging to a new genus of aquatic Oligochaeta (Pelodrilus), the anatomy of which I have described in the 'Transactions' of the Edinburgh Royal Society; but unfortunately the tubes in which they were packed were broken in transit. As the cocoons of this species are common and easy to find I have great hopes of getting more.

During August of last year I received a large quantity of cocoons of Acanthodrilus multiporus containing living embryos in various stages of development. The cocoons had been carefully packed in damp moss in a small tin box, which was enclosed in a large biscuit tin, filled with damp moss and covered over with several layers of paper, so as to render it quite air-tight.

Besides the living cocoons I received about two dozen ripe embryos, which had been extracted from the cocoons by Mr. Smith, and preserved with corrosive sublimate.

I shall presently describe the cocoons themselves, but it will be as well to state at once my reason for believing that they belong to the species Acanthodrilus multiporus. It is necessary to do this, as the cocoons were not deposited by the worms in captivity, but were found in the soil upon the margin of a lake. Hence there might appear to be some little doubt as to the species to which the cocoons belong.

Acanthodrilus multiporus was originally described by myself six years ago from material kindly supplied by Professor T. J. Parker, F.R.S. I have since obtained abundant additional material from Mr. Smith.

One of the most prominent features in the structure of this species is the complete duplication of the dorsal blood-vessel; this peculiarity is, it is true, to some extent shared by another New Zealand Acanthodrilus—A. novæ-zelandiæ; but there are numerous other characters which render it quite im-
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possible to confound the two species. Besides, the dorsal vessel is not completely double in Acanthodrilus novæ-zeelandiae. The two tubes, as I have already pointed out (7), in the latter species become fused at the septa; whereas in Acanthodrilus multiporus they retain their distinctness at the septa as elsewhere.

In Acanthodrilus multiporus the prostomium is small, and does not divide the buccal segment; the anterior segments are so much divided into annuli that their limits are almost impossible to map by a superficial inspection of the worm; there are also internal structural differences of importance, particularly in the nephridial system, between the two species.

The transparent cocoons allowed the dorsal vessel to be quite plainly visible, and it showed the complete double character which has just been referred to; the mature embryos extracted from the cocoons showed the other external characters which serve to discriminate the species. As the cocoons were all perfectly similar I have no doubt that they all belong to this species.

Mr. Smith informs me that "the cocoons were found on the edge of a swamp, which is now quite dried up owing to the long drought; in other seasons there are generally several feet of water covering the spot where we obtained them. I obtained a few (some of the more advanced) among the loose shingly soil, from which the water had subsided."

§ The Cocoon.

Our knowledge of the cocoons of earthworms is at present almost confined to the indigenous Lumbricidæ. A very good summary of our knowledge upon this point, together with many new observations, is to be found in Professor Vejdovsky's "Entwickelungsgeschichtliche Untersuchungen," Heft i.

The only exotic form which has been as yet described is Megascolex coeruleus, of which I myself have given an account (8). It is clear that the cocoon of that species, as Vejdovsky has pointed out, departs in no essential particular
of structure from the cocoons of *Lumbricus* and *Allolobophora*.

Neither do the cocoons of *Acanthodrilus multiporosus*. It seems clear, therefore, that the formation of this structure is pretty much the same in all these genera, and that the various glandular structures—such as the atria, with which *Acanthodrilus* is furnished and *Lumbricus* is not—have nothing to do with the manufacturing of the cocoon. No doubt the clitellum alone is concerned in its production.

The cocoons have a length of about half an inch. They are regularly oval in form, and have a slight stalk-like projection at either end, such as occurs in *Lumbricus*.

The colour is yellowish brown; the empty cases have a clear transparent brown colour.

The cocoon is formed of two perfectly distinct membranes which are readily separable after it has been cut open. Vejdovsky has remarked that this is the case also with *Lumbricus*, particularly *L. rubellus*, where the outer layer forms a remarkable projection longer than the cocoon, and to which particles of soil adhere.

The cocoons vary somewhat in size. In a cocoon from which the worm has escaped, a circular orifice at one end marks the place at which the young worm made its exit.

The cocoon never contained more than a single embryo; even in the youngest stages which I examined (fig. 20a) there was but one embryo. As I opened about fifty cocoons, I feel justified in considering that this species may be characterised by the fact that the cocoon only contains a single embryo; it is probable that there are a number of eggs originally enclosed in each capsule, but it is evident that they must disappear early.

Among the *Lumbricidæ* one to three embryos seem to be the rule; but in *Allolobophora fætida* there may be as many as six. I found two embryos in a cocoon of *Megascoleæ* *œœrüleæ* (8).

In fig. 20 are represented the sizes of the embryos of the various stages which I examined; the youngest is of course 1,
while D is a worm ready to leave the cocoon, and showing the principal blood-vessels.

Unfortunately I have very little material belonging to the younger stages; I have only one specimen of stage A, and three or four of B. But considering the length of time which elapsed between the collecting of the cocoons and their arrival at the Zoological Gardens, I may regard myself as extremely lucky in having such a comparatively large series of the younger stages.

Besides the embryos in the cocoons, there were about half a dozen young worms which had been hatched during the voyage.

It seems evident, therefore, that the development of this species may take a considerable time.

The case arrived at the Zoological Gardens on August 11th; it was packed for transmission at latest on June 23rd; a period of seven weeks therefore intervened.

The rate of development also must differ considerably, as Wilson (15) has pointed out in the case of Lumbricus; but the shortest time, so far as I can judge by the evidence afforded by the specimens sent me, can hardly be less than five or six weeks. This is about double the period which Wilson found in two species of Lumbricus. It was always possible to detect an “addled” cocoon by observing whether it did or did not float in water: healthy cocoons with living embryos inside them always sank to the bottom; if the cocoons floated on the surface of the water it was a sign that the embryo was dead.

I have occasionally met with Nematodes in the interior of earthworms’ cocoons, as have other observers. In two cocoons of Acanthodrilus multiporus with partially decayed contents I found not Nematodes, as I at first thought, but several examples of an Enchytræid not yet identified: a curious circumstance was that the majority of these small Annelids were dead,—infected, I suppose, by the decaying matter round them. I saw another example on the moss, which is probably the habitat of the species. This family of
Annelids has not yet to my knowledge been recorded as occurring in New Zealand.

The characters of the albuminous fluid filling the cocoon have been shown by Vejdovsky to vary somewhat in different species. Particularly noteworthy is the fact that in Allurus tetræder this fluid is perfectly clear and transparent; in this there is a resemblance to Rhynchelmis. I have elsewhere pointed out that this earthworm Allurus, largely aquatic in habit, resembles many aquatic genera in the large size of the eggs, and in the shortness of the sperm-ducts, which open on to the exterior in front of the oviducal pore. The coincidence of these three characters in an aquatic Oligocheæte belonging to a group which is so characteristically terrestrial seems to require some explanation, which, however, does not at present appear to be obvious.

In Acanthodrilus multiporusc, as in Lumbricus rubellus, &c., the albuminous fluid filling the cocoon is milky and opaque; it is readily washed out of the cocoon by water, and there was thus no difficulty in extracting the embryos.

§ Development of Nephridia.

Stage A.

The youngest embryo which I have is rather younger than that figured on pl. xviii, fig. 51, of Wilson’s memoir (No. 15).

It has hardly acquired a vermiform shape (see fig. 23), and is 2 mm. in length, being, therefore, rather smaller than the embryo of Allolobophora faetida referred to. The stomodæum had not yet joined the mesenteron, and I could find no proctodæum, which here, as in Lumbricus, is a late formation.

In this embryo the anterior half-dozen pairs of nephridia were fully developed and no doubt functional. They are distinctly paired structures, and lie on either side of the gut or stomodæum as the case may be.

Each nephridium is furnished with a well-developed funnel
which is placed on the anterior side of the intersegmental septum, behind which the nephridium lies. The funnel is ciliated, and the nephridium, where it communicates with it, has a remarkably wide lumen, and is ciliated. The funnel lies close to the nerve-cord, but the external apertures of the nephridia are more dorsal in position; they open in the neighbourhood of the lateral setae.

Fig. 21 represents a single nephridium, which happened to be displayed in a fortunate section for nearly the whole of its course. The nephridia are present to the number of a single pair per segment, but the anterior pair (the “mucous glands” of the adult worm) occupy two segments.

These, however, like the following ones, have a single funnel, which is placed on the anterior side of a septum (see fig. 22), which seems to represent the septum dividing Segments II and III. In this region of the body, however, from the earliest stage the septa have not the regular arrangement that they have posteriorly. The first pair of nephridia open close to the stomodaeal aperture; the funnels necessarily lie behind this point, hence from the very first this anterior pair of nephridia is anomalous, and so far unlike those which follow. It would be very interesting to ascertain whether this difference holds good from the first formation of the nephridia; unfortunately this is one of the many questions in the embryology of Acanthodrilus multiporus which I have no means of solving at present.

Figs. 17 and 18 represent two successive sections which illustrate the position of a nephridium. In fig. 17 the external aperture is seen, which lies dorso-laterally; in fig. 18 the funnel is shown. The first figure shows more of the anterior extremity of the body, owing to the somewhat awkward position in which the worm was embedded. The developing setae of Segments II and III belonging to one of the ventral pairs are seen on the left side (fig. 18); they fix the position of the funnel which is seen to lie between them on the anterior side of a septum. The enormously distended cavity which lies
below the alimentary tract is the ventral blood-vessel; on the opposite side is the brain (br.). The stomodæum is easily recognisable from the mesenteron by the different character of its epithelium; as far as I could ascertain the lumen of the stomodæum was not continuous with that of the mesenteron.

Whether the anterior two segments contain provisional nephridia or not, I am unable to say; this is, unfortunately, another of the many questions in the embryology of Acanthodrilus for the solution of which I do not possess material. I am inclined, however, to think, as will be pointed out later, that the nephridia of the first two segments have no precursors.

Stage B.

The size of embryos belonging to this stage is indicated in fig. 20 B. I have only had three embryos for study, one of which was slightly larger than the others, but not in a more advanced condition of development.

These embryos are completely vermiform in shape, but the anterior end is still considerably the thicker, and dwindles gradually towards the tail end.

Fig. 22 represents a section through the first four segments of an embryo belonging to this stage. The setae are numbered consecutively, the first seta (I) corresponding, of course, to the 2nd segment. The first pair of nephridia seems to occupy three segments, but the irregular arrangement of the muscular bands attaching the pharynx (stomodæum) to the parietes make it a little difficult to be very certain upon the point. Both the funnel (f.) and the external pore (N. p.) were quite obvious at this stage; the funnel lies, as before, in the 2nd or 3rd segment. The external orifice of the nephridium is just within the stomodæum. There is, in fact, no particular change from the conditions characterising the last stage.

Stage C.

Embryos of this stage measure rather more than half an inch in length; they are, of course, completely vermiform in shape.
The nephridia are considerably advanced as compared with those of the earlier stages, but are still very far from showing the characteristics of those of the adult Acanthodrilus.

The first pair occupy the first four segments, which correspond to the extent of the stomodæal invagination; these segments are divided by irregularly running septa, and are only recognisable by the setæ. Apparently, therefore, there is an important difference between this stage and the last in respect of the number of segments occupied by the "mucous gland." This difference is, however, only apparent; it is caused by the concrescence of the "mucous gland" with the following nephridium. I have carefully followed out the first and second pairs of nephridia, and I can nowhere find a break of continuity between them, such as is quite obvious in the two earlier stages. The original distinctness of the two nephridia is still shown by the presence of two funnels, occupying precisely the position of the earlier stages. I detected the external orifice belonging to the posterior nephridium; the whole organ also opens anteriorly as in the earlier stages, but in this stage much further within the buccal cavity. Moreover the actual orifice is now formed by an outgrowth of a tube from the buccal cavity lined with columnar cells, continuous with those which form the lining of that cavity. The shifting backwards of the aperture of the nephridium appears to be related to the shifting backwards of the cerebral ganglia and of the circumoesophageal commissures; the point of opening and the position of those commissures are close together, opposite to the setæ of the 2nd segment. The first nephridium extends back beyond the third setæ, and therefore appears to occupy four segments.

Fig. 16 represents a portion of two segments of an embryo at this stage, showing the body-wall, the ventral blood-vessel, and the intersegmental septa. The nephridia belonging to the segment are not shown in their entirety; only the funnel and the proximal end of a tubule are indicated. The rest of the nephridium forms a compact and dense coil of tubules, with very thin walls and a comparatively wide lumen. Fig. 2 illus-
trates a portion of the nephridium (n.) of two consecutive segments; the anterior nephridium—that at the bottom of the figure—is the end of the "mucous gland." $N$ represents the duct of the nephridium following this; the duct is of greater calibre than the tubule from which it arises, and is always, as is shown in the figure, made up of denser—at any rate more darkly staining—protoplasm in the centre. Very constantly radial strands of this denser layer of protoplasm immediately surrounding the lumen were given off, reaching the periphery. The funnels of the nephridia of worms belonging to stage C have undergone a remarkable change, illustrated in figs. 16 and 19. The funnel is still more or less funnel-shaped—that is to say, it contains a lumen; but the cells composing it have lost their cilia, and have begun to proliferate, forming (see fig. 19) several layers of cells. The section of the nephridium following the funnel has no lumen. The nuclei of the cells are arranged alternately, now on one side, now on the other.

Embryos just before hatching (Stage D).

I always found it possible to tell from an examination of the cocoon whether the contained embryo was nearly or quite ready to make its way out. After washing off the earth the chitinous layers, particularly when the outer one had been peeled off, were sufficiently transparent to show the principal blood-vessels, and even the outline of the worm in parts.

At this stage the worm almost entirely fills the cocoon, there being but little room to spare; what room there is, is occupied by the remains of the albuminous fluid, which has undergone no changes visible to the eye. This fact rendered it somewhat difficult to extract the embryos without injury from the scissors or knife employed in cutting through the cocoon.

The embryo, just before leaving the cocoon, measures about two inches in length. It is of a milky-white colour, and certain of the principal blood-vessels show up very conspicuously.

The dorsal blood-vessels are usually visible from end to end of the body, and they are separated by a very considerable interval. Between them a third trunk may be frequently made
out; this is the supra-intestinal vessel. Anteriorly about four pairs of hearts can be seen, and the ventral vessel is quite evident, running throughout the whole length of the body.

The absence of any pigment in the integument is not so remarkable, since this species appears to have hardly any traces of integumental pigment at any time of its life.

The nephridia have acquired their definitive form, with many external apertures in each segment. The mucous glands form a coiled mass of tubules lying on each side of the pharynx and oesophagus; they are chiefly massed in the segment behind that which contains the pharynx: I presume, therefore, that, had I been able to examine a more complete series of embryos between these and those of stage C, a further fusion of the nephridia to form the mucous gland could have been traced.

The aperture of this complex nephridial gland into the stomodaeum has moved still further back, still retaining its relation to the circumoesophageal comissure, in front of which it opens, and beneath which it passes from the glandular coils. Fig. 9 shows the tube (Nephr.) which leads to the stomodeal orifice close to the latter and in front of the comissure (N). I mentioned, in describing the nephridia of stage C, that the external aperture of the second pair of nephridia, which fuse with the first pair to form the mucous gland, still persist. In stage D there are numerous apertures by which the mucous gland opens on to the exterior; these commence upon the very first segment of the body.

§ Anal Nephridia.

The adult Acanthodrilus multiporus is, as I have recently pointed out (9), provided with anal nephridia which open into the hindermost section of the gut; there are also in the same segment integumental nephridiopores, and the tubes leading to the latter could be traced into connection with the tubes leading to the pores that communicate with the interior of the rectum. In these segments there are, moreover, numerous coelomic funnels, which seem to be wanting in the rest of the body of the adult, though, as I have already men-
tioned, they are present (a pair to each segment) in the embryo. The anal nephridia are a secondary development. In stage C there appeared to be no difference between the nephridia of the posterior segments of the body and those lying in front; but in older embryos they were quite distinguishable on account of their greater size: in the earliest stage at which I observed them the openings into the gut had been already formed, but they are less numerous than in the adult worm; I counted three on each side, which seemed to me to be arranged symmetrically. In describing these anal nephridia I suggested that it would in all probability be found that they opened into the proctodæum. I believe now that the section of the gut into which the nephridia open is not proctodæum; it can hardly, therefore, be supposed that their primitive opening was on to the outside of the body, and that the orifices were invaginated along with the proctodæum. These nephridia occupied in all five segments, not the last five of the body, but some little way in front of the end of the body. They are chiefly developed on the septa, beside which their ducts pass on the way to the enteric opening. On the other hand, ducts also lead to the body-wall, and open on to the exterior, as I have already pointed out for the adult. One point in the minute structure of the tube seems to be peculiar. I have not observed the same thing in nephridia from other parts of the body. This, which is illustrated in fig. 6, concerns the relations between the nephridial tubes and their peritoneal covering. Ordinarily, as in A and B, fig. 6, the peritoneal coat (p.) closely invests the nephridial tube (n.); but very frequently, as shown in C and D, the peritoneal coat was widely separated from the nephridial tube by a space containing a coagulable fluid, the presence of which is indicated in the drawing. The existence of this fluid shows that we have not to do here with an effect produced by a reagent. The nephridial tubes illustrated in the figure have not yet acquired a lumen.
§ Perivisceral Fluid and Corpuscles.

The coelomic corpuscles of Annelids—particularly of the Oligocheata—have been so thoroughly investigated by Professor Kükenthal (17), that I have found little to add to his excellent descriptions.

Nevertheless there are some points connected with the numbers and condition of the corpuscles at different stages of development which are worth recording.

The corpuscles themselves may be, as Kükenthal has pointed out, of two kinds—(1) those with secreted granules, and (2) those without such granules. Both kinds are furnished with a nucleus.

In the youngest stages (viz. A and B) only the small lymphoid cells without granules are present; these cells are very darkly stained by borax carmine. Fig. 4 illustrates three such cells isolated by teasing up an embryo of stage B in glycerin, whose tissues had been fixed by osmic acid. These cells show every possible condition of amöeboid movement; in some cases, as shown in the figure referred to, they absolutely bristle with pseudopodia; at the other extreme are roundish or "bipolar" cells. It seemed to me that the intersegmental septa were the principal stations at which these cells originated, of course from the peritoneal layers covering the septa.

In embryos of this age there was no fluid in the coelomic cavities that could be recognised. In stage D the body-cavity was almost completely filled with granular corpuscles, which represent a further development of the small non-granular cells (see fig. 3).

§ Larval Sense-organ.

None of the embryos of Acanthodrilus showed any ciliation over the general body surface; even the youngest embryo was apparently too far advanced in development to show any ciliation, with the exception of a patch at the anterior end, to which I shall refer immediately. As this embryo is older than a Lumbricus embryo in which the ventral ciliated
band has disappeared (cf. Kowalevsky, 18, pl. vii, fig. 26), the fact is not remarkable. In Allolobophora, however (Vejdovsky, 1, pl. xvii, fig. 9; pl. xviii, fig. 9), the ciliation of the ventral surface persists later.

In fig. 18 of Pl. XXXI is represented a longitudinal section through the first few segments of the youngest embryo. Just above the stomodæum and in front of the cerebral ganglia is a group (S) of three or four cells bearing long cilia: as I have not been able to compare these cilia with those which probably, as in other genera, form a band along the ventral surface of the embryo, it is impossible to say if they differ in any way; but by comparing them with the figures given by the various authors who have studied the development of Lumbricus, Allurus, and other Oligoeheta, I should imagine that they will prove to be much longer and stronger cilia. Furthermore, the epiblastic cells which bear them are specialised; they differ from the neighbouring cells in their greater size.

In several Oligoeheta the ventral ciliated band extends on to the dorsal surface of the stomodæum—in Lumbricus trapezoides, for example. Vejdovsky also figures (1, Tab. xvi, fig. 4) cilia upon the dorsal lip of the stomodæal invagination in Allurus tetraeder, and in an earlier embryo (Tab. xvi, figs. 5, 11) of Allolobophora foetida. This embryonic condition is preserved in the adult Æolosoma and in Ctenodrilus (if we are to regard that worm as an Oligoeheta, which cannot be safely done until its genitalia are known): in both these genera the ciliation is limited to the ventral surface as in the embryo Lumbricid, which is an interesting point of similarity. But in none of these cases is there any specialisation of the cells upon the prostomium which bear the cilia; if such a group of cells existed in Lumbricus as I figure in Acanthodrilus multiporus, it could hardly, I think, have been overlooked; so many competent observers have studied Lumbricus with all the improvements of modern methods, that so obvious a structural fact could not well have failed to be noticed by one or other of them. I can discover nothing in the plates of Kowalevsky, Kleinenberg, Vejdovsky, or
Wilson at all like the larval sense-organ of Acanthodrilus, and therefore feel almost certain that it does not exist in the worms investigated by those authors.

A sense-organ of this or any kind does not seem likely to be of the least use to any embryo which undergoes direct development within a cocoon, and is not hatched until mature. At the same time Wilson has described in the embryo of Allolobophora foetida a structure which may, he thinks, have a sensory function. The ventral lip of the stomodæum in that worm becomes expanded and thickened, and is constituted by a mass of elongate fusiform cells, which is strikingly like a taste bud. This body is compared to the larval sense-organs of Clepsine. As it is found in A. foetida only, and not in L. communis and L. terrestris, where its presence is correlated with a tough and jelly-like albumen filling the cocoon, Wilson thinks that the group of cells in question plays a part in the digestion before absorption of this albumen; it is difficult, he thinks, to understand the presence of a sense-organ so highly developed in one worm and its absence from closely allied forms. This structure is figured (15, fig. 82) by Wilson and also by Vejdovsky (1, pl. xv, fig. 5) for the same species. In any case the position of this sense-organ or glandular organ is totally different from that of the larval sense-organ of Acanthodrilus; the one is ventral, the other dorsal. The sense-organ of Acanthodrilus can hardly be a digestive organ of any kind. Whatever it is, it is transitory; I could find no trace of it in later stages. I do not think, however, that it is of any use to the larva; it is difficult to understand that any sense-organ could be, which appears and disappears at so early a period in the development of the embryo. This sense-organ appears to me to be comparable to the larval sense-organ of the Chaetopod larva and of other worm larvac. Such larval sense-organs, as is well known, occur in many free-swimming larvac; they are not limited to the Chaetopoda Polychæta; the Pilidium of Nemertes, for example, possesses such an organ. There is therefore no need, supposing that my comparison be justified,
to bring forward this structure as further evidence of a close affinity between the Polychaeta and the Oligochaeta; but the fact does appear to favour the idea of, at any rate, the former existence of a free-swimming larval stage among the Oligochaeta, though not necessarily to be found in any living genus. It is true that the development of very few genera of this family is known; but the formation of a cocoon is apparently so unusual that we may suppose it to be a very old characteristic of the group, possibly so old as to embrace the ancestors of both Oligochaeta and Hirudinea. The enclosure of eggs within a cocoon does not, it may be admitted, seem favorable to the idea of a free-swimming larva. In only one existing group is there any evidence of a free-swimming Oligochaetous larva. Lankester has described and figured (19, p. 642, pl. xlviii, fig. 4) the young of Acolosoma quaternarium, which is somewhat unlike the adult, and is more extensively ciliated. Vejdovsky (2, p. 165) has remarked upon the resemblance of this larva to that of a Chætopod.

There are several species of Acanthodrilus which are aquatic—for instance, “Mandane stagnalis” of Kinberg; but I do not wish to urge the possibility even of there being a free-swimming larva in any of these. All that I desire to point out is that, so far as we at present know, the development of the group Acanthodrilus is the only type in which the traces of a formerly existent (?) free-swimming stage are to be found. This is so far an argument for the conclusion that Acanthodrilus comes nearer to the ancestral Oligochaete than such a type as Lumbricus does; other facts appear to me to point unmistakably towards the same conclusion.

§ Stomodæum and Proctodæum.

In the youngest embryo the stomodæal invagination is already fully established, but it does not open into the mesenteron; the opening is formed in the next stage in an embryo hardly larger than the youngest, but the aperture of communication (see fig. 24) is narrow. The narrow aperture between the stomodæum and the mesenteron is still further reduced by a
fringe of long cilia shown in the figure referred to. These cilia belong to the endoderm cells, and are only developed upon the first five rows of cells or thereabouts; behind this point there is no ciliation at all, nor is the stomodæum ciliated. The ciliated cells at the neck of the mesenteron do not differ in any way from the other cells of the mesenteron. There is an abrupt break between the cells of the stomodæum and those belonging to the mesenteron, which is quite obvious even when the sections are examined with a low power; the stomodeal epithelium is more stained. The cells of the mesenteron are laden with spherules and are not stained, excepting, of course, their nuclei. The cells of the stomodæum are columnar, but much shorter than the cells of the mesenteron.

The second half of the stomodæum has a muscular investment of fibres of some thickness; this extends for a very short distance on to the mesenteron, and gradually disappears. The peritoneal investment of the stomodæum is much thicker than that of the first part of the mesenteron. The stomodæum occupies the first four segments of the body.

The proctodæum is developed much later; it had not been formed in embryos of stage C. It is of much less extent, and in transverse sections (fig. 10) is seen (p.) to lie dorsally of the mesenteron.

§ Epidermis of Mature Embryo.

In embryos ready to leave the cocoon the epidermis contains some peculiar cells. Here and there in longitudinal sections through the anterior segments the epidermis appears, when examined under a low power, to be perforated; under a high power the arrangement of the epidermic cells at these points presents the following appearance. Above the perforation lies a large round-cell with a conspicuous nucleus, and below this cell is the cavity already spoken of. The cuticle is bulged out above the cell. There is no great regularity in the arrangement of these cells; they occur sometimes anteriorly upon the segment, sometimes posteriorly. The only struc-
tures known to me in an earthworm with which they may possibly be compared are the peculiar integumental cells of *Urochæta*; but these latter lie at the base of the epidermis instead of at the summit as in *Acanthodrilus*. One is usually inclined to regard a modified epidermic cell as a sense-organ, but there is no evidence that the bodies in question have a sensory function. On the other hand, they cannot be compared with the gland-cells of the epidermis. The cavity lying beneath each cell is very curious, and fits with the possibility of their being dioptric media; they are not, however, specially transparent, judging at least from their appearance when preserved. At present I think the nature of the cells must be left unsolved.

§ Gonads.

The development of the gonads in *Lumbricus* has been studied by Bergh (11), who has made known some interesting facts as to the number originally present. The adult *Lumbricus* has two pairs of testes depending from the anterior septum of Segments 10 and 11, and a single pair of ovaries occupying a corresponding position in Segment 13. In the embryo, however, the 12th segment possesses a pair of gonads also, which appear never to advance beyond a very rudimentary stage.

I find in *Acanthodrilus* that there are originally four pairs of gonads present, which are in Segments 10, 11, 12, and 13; but these, instead of being attached to the front wall of their segment, as in *Lumbricus*, are attached to the posterior wall. This is the case with the adult worm, as I have satisfied myself by the dissection of a large specimen. *Acanthodrilus annectens*, therefore, is not the only example known of this anomalous condition. The gonad of the 12th segment in *Acanthodrilus* is, however, at first as fully developed as any of the others; it contains, as they do, large germinal cells, with the peculiar nuclei which characterise these cells. These nuclei (fig. 14) are limited by a distinct and darkly staining membrane, against which are closely
pressed a layer of small darkly staining bodies, the nucleoli, which are thus arranged in a peripheral layer, and are not found in the interior of the nucleus.

The presence of four gonads in the embryo is interesting, inasmuch as one genus of Oligochaeta has always two pairs of testes and two pairs of ovaries. I refer to Phreorictes, where the gonads occupy the same segments as in the embryo Acanthodrilus. The presence of two pairs of egg-sacs in Perichæta aspergillum and other species is evidence in favour of the original presence in that worm also of two pairs of ovaries; and I have elsewhere sought to show that in Eudrilus there are also two pairs of ovaries corresponding to the two pairs of testes. In Lumbriculus it is possible that the same thing occurs, but the genitalia of this worm have not as yet been thoroughly described, though Professor Vej dovsky has promised us an account of them.

The gonads appear at a comparatively early stage in the development of the worm. I first observed them in stage C, but as they are in this stage of, comparatively speaking, large size, they must be apparent even earlier. I could not, however, detect them in stage B. It should be remarked, however, that this stage is evidently separated by a considerable gap from stage C, and I have nothing intermediate between the two.

In stage C the gonad (fig. 12) is placed close to one of the nephridial funnels in which the lumen still persists, and to a certain extent the cilia also; but the duct immediately connected with the funnel has lost the lumen which it possessed in stage B, and has become solid. The gonad is in each case situated ventrally to the funnel. It is formed by a rounded elevation of cells which closely resemble the peritoneal cells covering the septum. I cannot say anything about the condition of the cells forming the gonads, as the histological details were not very clear; this was due to the preservation of the specimen in saturated solution of picric acid, which does not appear to be a good reagent for the preservation of these embryos. It is almost unnecessary to say that the four
gonads were absolutely indistinguishable from each other in their shape and relations to the septum, body-wall, and nephridial funnel; neither were there any ascertainable differences in their minute structure.

In stage D the gonads have become much more evident, and, indeed, they hardly differ in minute structure from those of the newly hatched worm. Figs. 13 and 14 illustrate the gonad and a portion of the genital ducts. In fig. 14 the gonad is shown attached to the front surface of the septum (spt.), and a portion of the genital duct (vas def.) is seen behind the septum. The gonad is frayed out into a number of processes. In fig. 13, which is a few sections further forward, the commencement of the funnel of the generative duct is shown (funn.); the gonad is seen to be partly attached to the funnel. Fig. 15 represents a section through one of the gonads of another individual; the "protova" (g. c.) are peculiar in shape, being prolonged into a stalk; round these lie accessory cells (p. c.), which do not, I imagine, develop into sexual products.

§ Genital Ducts.

The development of the genital ducts in Lumbricus has been studied by Bergh (11), who has arrived at the following results, which I state for the purposes of comparison with Acanthodrilus.

Bergh's results in the main confirm those of Vejdovsky upon certain aquatic genera (2). The first part of the duct to appear is the funnel, but this is not developed until after the young worm has left the cocoon. Previously to this the gonads have been formed, but only nephridia are to be found in the genital segments. When the funnels do put in an appearance they are formed beside the nephridial funnel, but are perfectly distinct from it though in actual contact (Bergh, 11, pl. xxi, figs. 19, 21). The ciliated epithelium of the nephridial funnel is figured by Bergh as totally distinct from the, at first, non-ciliated epithelium of the genital ducts. Although no actual observations were made, Bergh is inclined to confirm Vejdov-
sky's statement that the ducts themselves are formed as outgrowths from the funnel.

In Acanthodrilus multiporus I have found certain points of agreement with these results, but also important points of difference.

In the first place the genital ducts appear much earlier in Acanthodrilus than in Lumbricus. I have first met with the funnels in embryos of rather more than half an inch in length (stage C). They were prominently developed in embryos of an inch in length (still some way from being ready to emerge from the cocoon). In the recently hatched worm the funnels are ciliated, and are furnished with a considerable length of duct. Fig. 1 represents two funnels, those of the 10th and 11th segments, in an embryo of stage D. In this stage I should observe that the funnels corresponding to the four gonads are equally well developed, and it would be impossible to predict that that of the 12th segment was destined to atrophy subsequently. I could, furthermore, detect no difference between the oviducal and spermiducal funnels, such as Bergh mentions and illustrates. The funnels show no signs of ciliation, but are somewhat folded. The gonad, as already mentioned, is in contact with its funnel, and there is a large blood-vessel to the upper side; the cells of the funnel could be easily distinguished from those of the neighbouring regions by the large size of their closely crowded nuclei. The septum was greatly thickened in the neighbourhood of the funnel, but thin just below the funnel itself; at this point it is traversed by a solid cord of cells with large nuclei, surrounded by peritoneal cells with smaller nuclei. The continuity of this rod with the funnel was quite plain; it is the commencement of sperm-duct or oviduct, as the case may be. This rod passes obliquely and without any flexure to the body-wall; there it is continuous with a coiled tube in which a lumen could be in parts detected; the whole structure, in fact, bears an unmistakable resemblance to a nephridial tubule. In the figure referred to
it will be noticed that in the case of the 10th segment the straight rod is prolonged for a very short distance beyond the point where it gives off the coiled tubule \( (\text{nphr.}) \); this appears to indicate a commencing separation between the nephridium and that part of it which is metamorphosed into sperm-duct. Bergh, as well as Vejdovsky, has noticed that the commencing vas deferens is a solid structure which only later acquires a lumen; it might be imagined, therefore, that my supposed nephridium is nothing more than the solid condition of the vas deferens or oviduct; but the connection with it of a coiled tube possessing an intra-cellular lumen and agreeing point for point with the nephridia elsewhere negatives this supposition.

In the 7th, 8th, and 9th segments there are small rudimentary funnels attached to the posterior wall of their segments. These funnels are not ciliated, and consist of but few cells—indeed, the expression "funnel" is hardly applicable to them; each is, however, continuous with a tube passing through the mesentery which is identical in appearance with the tube connected with the funnels of Segments 10—13. This tube is also solid; it has a thick coating of peritoneal cells, and ultimately passes into a coiled tube with an intra-cellular lumen. In the 9th segment the straight part of the tube (see fig. 11) gives off a branch which perforates the body-wall, and nearly, but not quite, reaches the exterior (I traced it into the circular muscular layer). In the segments lying behind the 13th the same arrangement could be observed, but though the septa were perforated by nephridial tubules there was nothing that could be called a funnel upon the opposite side, only a few cells presenting an irregular arrangement.

It seems to me impossible to avoid the conclusion that these structures correspond from segment to segment, and that therefore the funnels of the sperm-ducts and oviducts, as well as the commencement of the ducts themselves, are formed out of a section of the nephridia of their segments. In describing the development of the nephridia I have mentioned that the nephridial funnels and the tube which is immediately connected with them very soon become
solid and lose their cilia; this condition is seen in the newly hatched worm, where, however, there is hardly a trace of the funnels. It is, therefore, perhaps surprising to find that four out of these funnels commence to grow again and a second time acquire cilia, serving as the funnels of the genital ducts in the adult worm. This led me to suspect that the funnels might possibly be new structures, and that the original nephridial funnel might be present and connected with the nephridial tubule which I have described as the commencing sperm-duct or oviduct. I should remark, however, first of all that the loss of cilia in a cell (Protozoa) is not necessarily a prelude to degeneration; on the contrary, it is sometimes followed by a specially marked activity of division. Besides, the solidification of that portion of the nephridial duct which is connected with it might be looked upon in the same light, as it is undoubtedly at first furnished with a wide lumen which is ciliated. But the outgrowth of a tube from this, which I have figured (fig. 11) as nearly reaching the exterior, is hardly an indication that the structure in question is really degenerating. There seems to be no doubt, however, that, with the exception of those in Segments 10—13, the original nephridial funnels do ultimately disappear, or are represented by the merest traces.

On the hypothesis that the structures which I have identified with the nephridial funnels of Segments 10, 11, 12, and 13, are really new structures, and not the persistent funnels, some traces of the latter should be forthcoming. I could not, however, detect any such traces. Yielding this point for the moment, it would be sufficient as an argument for the time being if there were no clear connection between the large funnels of the genital segments and the nephridial tubule; this connection, however, is quite unmistakable.

It seems, therefore, difficult to explain the connection of the funnels of the genital ducts with nephridia except on the hypothesis, supported by other facts, that the funnels in question are the persistent and enlarged nephridial funnels. I do admit, however, that this is by no means necessarily a proof
that the distal sections of the genital ducts are formed out of these nephridia.

There are some facts, nevertheless, which are in favour of this view.

In the young worm that has just escaped from the cocoon the genital ducts are more advanced in development, though still imperfect. This statement, however, only applies to the ducts of the 10th, 11th, and 13th segments; those of the 12th, though not much smaller than they were during the last stage, are, by comparison with those of the remaining genital segments, rudimentary.

The latter have become ciliated. The epithelium is here, arranged several layers deep. Each funnel communicates with a short duct, which has acquired a lumen plainly intra-cellular; the duct passes somewhat obliquely to the body-wall, but without any windings, and penetrates for a short distance into the longitudinal muscular layer. It is particularly noticeable that at this stage it is impossible to distinguish, except by their position, the sperm-ducts from the oviducts.

Where the sperm-duct or oviduct comes into contact with the parietal peritoneum it is in close relation with a part of the nephridium; but, as far as I can make out, there is no actual communication between nephridium and genital duct. The most careful search failed to reveal any nephridial funnel in Segments 10, 11, 12, and 13, other than the genital funnels, nor did the nephridial tubules in these segments approach very nearly to the septum, as if there were such a funnel present which I had overlooked.

On the other hand, in the 8th and 9th segments, at any rate, a nephridial tubule (solid, with no lumen) passed up from the body-wall to the septum, and, perforating it, terminated on the opposite side in a group of cells, which is no doubt a rudimentary funnel. Careful measurements showed that the position of this nephridial tube and funnel in the 8th and 9th segments is precisely the same as that occupied by the genital duct and funnel in each of the four following segments. This looks very much as if the solid rod communicating with the
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genital funnels in the earlier stage were really metamorphosed into the proximal part of the genital duct; at any rate, there was no trace in the young worm of these solid rods, except in the segments in front of and behind the genital segments, other than the straight genital duct.

The temporary occlusion of the lumen during the development of the vasa deferentia and oviducts marks the change in their function from excretory tube to efferent ducts of the genital products. It is, however, also shown that the nephridial tubes are destined to undergo this physiological change, though in a less degree; in a less degree because the funnel, which possesses an obvious lumen in the youngest stages (Pl. XXXI, fig. 18), never seems to recur to this condition, any more than does the immediately following section of the tubule. It has appeared to me, however, that in the adult worm part of the nephridia had regained the lumen temporarily obliterated. In any case the occlusion and reopening of the lumen does occur with the genital ducts. This phenomenon seems to be connected with the growth of the tubes; although remarkable, it is not without parallel. Balfour (3) discovered that in Elasmobranchs the oesophagus during development became solid, and then reacquired a lumen. "The solidification of the oesophagus," he remarks (3, p. 218), "belongs to a class of facts which are curious rather than interesting, and are mainly worth recording from the possibility of their turning out to have some unsuspected morphological bearings."

More recently (16) Dr. Milnes-Marshall and Mr. Bles have observed precisely the same phenomenon in the developing frog. The solid oesophagus is "a constant feature in tadpoles of from 7½ mm. to about 10½ mm. in length."

These observers have not referred to a paper by de Meuron (14), in which a similar temporary closure of the oesophagus is described in the chick.1

1 I am indebted for this reference to Professor Howes.
§ Homology between Genital Ducts and Nephridia in the Oligochaeta.

The homology between genital ducts and nephridia has been a question of interest in Annelid morphology for some years. But the evidence in favour of the homology, as regards the Oligochaeta, has hitherto rested upon comparatively few facts; indeed, some of the arguments that have been used were based upon inaccurate observation. Claparède pointed to the absence of nephridia in the genital segments of the aquatic genera as evidence that the genital ducts were the slightly altered nephridia. Vejdovsky, however, discovered that the nephridia are at first present in the genital segments of these worms, but that on the maturation of the genital products and the development of special efferent ducts they disappear. Some years ago Lankester (20) put forward the ingenious suggestion that in earthworms (Lumbricus was at that time the only type known anatomically) the genital ducts represented the sole remaining traces of a set of ventral nephridia corresponding to the persistent dorsal nephridia. This view subsequently received a good deal of support from the researches of Perrier into the anatomy of earthworms. Perrier discovered that in some genera the dorsal set of nephridia were retained while the apertures of the genital organs were related to the ventral setae, showing, therefore, an interesting reversal of the conditions in Lumbricus. Later (6) Perrier found that in Plutellus the nephridia actually alternated from segment to segment, which of course was a further confirmation of the view that originally two pairs of nephridia existed in each segment of the body in earthworms. Mr. Benham’s discovery (4) of a form—Brachydrilus—actually possessing two pairs of nephridia in each segment would have clinched the matter had it been made a little earlier, but would at the same time have necessitated some alteration in the hypothesis as formulated by Lankester, for in Brachydrilus the genital segments also contain two pairs of
nephridia. However, my own discovery of numerous external pores in each segment of Acanthodrilus multiporus did away with some of the difficulties which had been raised by Perrier. The whole subject has been recently treated in an exhaustive fashion by Dr. Eisig in his magnificent treatise upon the anatomy and physiology of the Capitellidæ; his own observations upon the Capitellidæ led him to confirm the view that nephridia and genital ducts in the Oligochaeta are homologous. As I disagree with Dr. Eisig's view that the Capitellidæ are near akin to the Oligochaeta, I should regard his very important observations as only furnishing an argument from analogy comparable to Mr. Sedgwick's discovery of the complete homology between the genital ducts and nephridia in Peripatus.

The study of the embryology of Lumbricus has thrown considerable doubts upon the justice of the view that the genital ducts have a relation to the nephridia. Dr. Bergh, who is one of the latest investigators of the group, has not positively denied any such homology (except in the case of the spermathecae), but his observations have shown the complete independence in development of the sperm-ducts and oviducts from the nephridia. The former arise in the first place at a considerably later date than the latter, and have no relation to them; the septa which bear the funnels of the reproductive ducts are also perforated by a nephridium ending in the usual fashion in a funnel. Dr. Bergh, however, admits that the proved presence of more than a single pair of nephridia in a single segment of Annelids does away with the force of any arguments which his facts might be supposed to lend against the view that the genital ducts are modified nephridia.

Dr. Otto Lehmann (27), who has lately reinvestigated the question from the point of view of the development of Lumbricus and Allolobophora, entirely confirms Bergh as to the perfect independence of the vasa deferentia and oviducts from nephridia; but he states that the nephridia of the genital segments become degenerate on the appearance of the vasa
deferentia (p. 332: “Hier finden sich beim jungen Tiere in den Genitalsegmenten anfangs nur Segmentalorgane, die mit der Entwicklung der Geschlechtsorgane degenerieren”). This is a matter that requires confirmation, since Bergh distinctly states that there is no such degeneration. Lehmann gives no figures of the development of these organs. The paper concludes with a brief summary of the arguments for and against the view that the genital ducts and nephridia are corresponding structures. The arguments against lose some of their weight by reason of the statement that no instance is known of the presence of numerous nephridia in a single segment in the Oligochaeta (!). This paper was published two years after I found that Acanthodrilus multiporus is furnished with multiple nephridia, and communicated the discovery to the Royal Society.

Dr. Benham, in discussing this question (5), also admits the probable homology, which he regards as fairly evident in the case of the oviduct. As to the sperm-duct, it is suggested that the modification which the nephridium has undergone is—(a) a fusion of a series of nephridia, (b) a disappearance of a part of nephridia, (c) a shifting of the position of the pore. “In the somites in which the ciliated rosettes are, the external extremity of the nephridium has disappeared; in the somites carrying the male pore the funnel region of the nephridium is absent, whilst in the intervening somites both these regions have aborted, and a fusion of these various parts has taken place to form the more or less elongated duct.”

Professor W. B. Spencer (22) writes decidedly against any homology between genital ducts and nephridia. The first objection which he puts forward is the inter-cellular duct of the vasa deferentia and oviducts, and the intra-cellular duct of the nephridia. This objection would of course apply equally well to the homology between the nephridia of Oligochaeta and those of many Polychaeta; and, as a matter of fact, I show in this paper that an intra-cellular duct is, in the case of oviduct and vas deferens, actually converted into an intercellular duct. Another difficulty is “the presence of the perfectly
distinct ducts running side by side in Megascolides.” Another objection urged by Mr. Spencer is one which I also urged myself; it is that in Perichæta, which has a primitive excretory system, the genital ducts are fully as specialised as in other types where the nephridia are greatly modified. He concludes that in all Terricolæ the genital ducts have no connection with the nephridia, and are not to be regarded as nephridia specially modified to serve the purpose of conveying genital products to the exterior.

M. Perrier had found that in Anteus the sperm-ducts are actually represented by nephridia, a condition analogous to that of Æolosoma to be mentioned immediately. But in view of the possibility that in Anteus the sperm-ducts run embedded in the body-wall as in Acanthodrilus, and may therefore have been invisible on dissection only, it must be considered that this instance requires further study before the facts can be definitely accepted as a contribution to the question of the homologies between genital ducts and nephridia. Besides, in Rhinodrilus, which comes extremely close to Anteus, if it be not actually congeneric, vasa deferentia of the ordinary type are unquestionably present.

An important contribution to the question of the homologies of the genital duct with the nephridia is contained in a memoir upon the genital organs of Æolosoma by Dr. Štolic (23). As Dr. Štolic has favoured me with an English abstract of his paper I give a fairly full account of it, as there must be comparatively few persons who can read the original.

The testis is situated in the 5th segment, the ovary in the 6th; the gonads appear to be unpaired, and are situated between the ventral blood-vessel and the ventral body-wall. The spermaticæ vary in number from one pair to three, and are in Segments 3, 4, and 5. There is a tendency for only one spermaticæ in each of these segments to be developed. The clitellum is developed only on the ventral side of the sexual segments. On the median ventral surface of the 6th segment is the unpaired oviducal pore; as a pair of nephridia also exist in this segment, it is not plain that the
pore represents the rudiment of nephridia. There are no special sperm-ducts present; only the nephridia of the 6th segment seem to be slightly enlarged. Dr. Štolic observed the spermatozoa to pass out of the body by all the nephridia, especially by those of the 6th segment, which are figured in his paper as slightly different from the rest. During the sexual period the nephridia in certain segments disappear either wholly or in part. There appears to be no formation of genital setæ; these at least are not figured.

M. Roule has discovered something of the same kind in *Enchytraeoides minimus* (26). In this worm the first eight segments contain no nephridia at any time; those of the 9th, 10th, and 11th segments appearing only to disappear when the sexual organs are developed. The 12th segment possesses no nephridia, and it is not until much later that the sperm-ducts arise where the nephridia should have been; they are not preceded by nephridia, but may be regarded perhaps as equivalent to a pair of nephridia somewhat delayed in their development. Inasmuch, however, as there is no conversion of undoubted nephridia into undoubted genital ducts, the homology in this case could only be regarded as probable.

My own facts, which have been described in some detail above, seem to show that in *Acanthodrilus multiporus*, at any rate, the funnels and a portion of the actual ducts themselves of the vasa deferentia and oviducts are formed out of the nephridia. Balfour's suggestion ('Comp. Embr.,' vol. ii, p. 617) that "in the generative segments of the Oligochaeta the excretory organs had at first both an excretory and a generative function, and that, as a secondary result of this double function, each of them has become split into two parts, a generative and an excretory," is thus confirmed in a way, which is to me most unexpected. We have in each segment to begin with a single pair of nephridia; in the genital segments a portion of these nephridia is used to form the genital ducts, the rest retaining its excretory function.

I have not had material which permitted me to trace the growth of the vasa deferentia to their point of opening on to
the exterior in Segment 18. I imagine, however, that there is little doubt but that they continue to grow backward until this point is reached.

I do not think that Benham's suggestion of a fusion with portions of nephridia lying in Segments 12—18 will prove to be correct. In any case I have seen no evidence of the commencement of any such process, which ought to be apparent in my latest stages; on the other hand, I have evidence as to the growth of the blind end of the developing sperm-duct into the body-wall for a certain distance.

It is important to remember that this subdivision of the excretory organ into a genital and excretory portion does not commence until after the excretory organ has acquired more or less the complicated structure that it has in the adult; the distinctively paired character of the embryonic nephridia has been to some extent lost by the development of numerous external pores in each segment. This fact must be duly borne in mind in attempting to account for the apparent differences in the development of the genital ducts in *Lumbricus*, where all observers agree that there is no actual connection with the nephridia. I have described in *Perichæta* the existence in each segment not only of numerous nephridiopores, but of numerous funnels also. *Acanthodrilus multiporus* agrees with *Perichæta* in having numerous nephridiopores in each segment, not so numerous perhaps as in *Perichæta*, but still considerably more than an opening to each seta; but I have never succeeded in finding a corresponding number of funnels except in the case of the "anal nephridia" described above (see also No. 9); the persistent rudiment of the larval funnels is all that appears to exist in the anterior segments of the body, and even that may sometimes vanish. I am inclined, therefore, to think that Spencer was after all right in believing the acquisition of numerous funnels to be secondary, and to be derived from a condition where there were no funnels.

Now it seems impossible to doubt that the genital ducts in *Acanthodrilus* are perfectly homologous with those of
Lumbricus; the converse supposition is incredible, although the development appears to be so different. In Lumbricus the pronephridia become the persistent nephridia after but little change; there is no “flame-cell,” as in Rhynchelemis (Vejdovsky); in Acanthodrilus multiporus the pronephridia are converted into the nephridia by the degeneration of the funnel and by the multiplication of the external pores; it is after this has occurred that the genital ducts are split off. I can only reconcile this mode of development with that shown in Lumbricus by the supposition that the persistent nephridia in that type are not the exact equivalents of the paired nephridia of the young Acanthodrilus, but that the breaking up of the nephridium is slurred over, only showing traces of its former existence in the funnels and the proximal portion of the genital ducts. In this case the apparent simplicity of the nephridia in Lumbricus, and their apparent correspondence with an early stage in the development of the nephridia of Acanthodrilus will be delusive. If, on the other hand, it be proved that the nephridia of Lumbricus have never advanced beyond the stage which characterises the embryo Acanthodrilus, some explanation will have to be offered of the different modes of development of the genital ducts in the two types.

The whole matter is evidently not ripe for solution at present, and the problems involved grow more difficult as fresh facts are accumulated.

§ Remarks upon the Nephridia in the Oligochaeta.

The facts recorded in this paper have an obvious bearing upon the question of the evolution of the excretory organs in the Oligochaeta. But before discussing how far these facts affect current theories upon the matter, it will be useful to clear the ground by briefly describing the structure and development of the nephridia in other Oligochaeta.

Lumbricus and Allolobophora.—We owe our knowledge of the development of the excretory system in these types principally to Kleinenberg (24), Vejdovsky (1, 2), Bergh (12),
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and Wilson (15). I leave out of consideration the larval excretory organs, which consist of epiblastic cells in the neighbourhood of the mouth, known as "Schluckzellen," for they appear to have no relation to the excretory system of the adult.

In the young embryo there are a pair of provisional excretory organs, "pronephridia" they have been termed by Vejdovsky. They have also been termed the head kidney. These organs appear in very young larvae (younger than the earliest stage of Acanthodrilus described by me) as a pair of delicate ciliated tubes lying on the dorso-lateral walls of the archenteron, and, according to Wilson, who could find neither external nor internal orifice, actually embedded in the walls of the archenteron. Lehmann (21) found no aperture into the coelom; the canal runs along nearly the whole length of the very young embryo, and opens by a pore at about the middle of its length. In later stages only the anterior portion appears to be present; it runs from the head-cavity backwards and opens on to the 4th segment; in this embryo were three pairs of definitive nephridia. The head kidney runs in the body-cavity; anteriorly it terminates in a single large cell traversed by several canals.

Vejdovsky’s account is different; according to him the aperture is anterior in position, and lies (cf. his tab. xix, fig. 15, pr.) just behind the brain upon the 1st segment of the body; therefore it occupies two segments, and the permanent nephridia, which develop before the pronephridium disappears, only commence in the 3rd segment. The position of the external pore, it should be observed, does not correspond with that of the permanent nephridia.

In Rhynchelmis, again, there is a pronephridium of the same kind on each side of the body, i. e. a single pair which occupy the first two or three segments; these, however, are figured as opening below and to the side of the cerebral ganglia (cf. Vejdovsky’s tab. xii, figs. 12, 13, 15, pr. or pn.).

In Criodrilus Bergh (12) finds that the pronephridia open posteriorly on the sides of the body; they end blindly in front
in the head-cavity. Otherwise their structure appears to be that of the pronephridia of Lumbricus and the other types studied.

The differences between Criodrilus and the other types are remarkable, and not at all easy to understand.

But, apart from this genus, there is considerable evidence in favour of regarding the pronephridia as homologous (homodynamous) with the permanent nephridia. The permanent nephridia only commence after the pronephridia. The difference in form of the pronephridia may be correlated with their early appearance, and with the needs of the larva. The fact that they occupy two segments is more puzzling. Vejdovsky explains it for Rhynchelmis (1, p. 290) by the incomplete formation of the septa at the date of the appearance of the pronephridia; they are thus able to extend further back, being interfered with by the formation of the intersegmental partitions.

In the aquatic Oligocheta—in many of them, at least—a number of pairs of nephridia after the first pair also disappear, which is further evidence for regarding the whole series of nephridia, including the first pair, as homodynamous.

In Rhynchelmis the pronephrial stage is marked by the formation of a closed cell with a single flagellum; this afterwards develops into the funnel; there is no such change in Lumbricus. The pronephridia are directly converted into the permanent nephridia.

The correspondence between the pronephridia of the 1st segment ("head kidney") and the succeeding nephridia is strengthened by the observations recorded in the present contribution. In the youngest embryo at my disposal a pair of nephridia lie in the first two segments, and open on to the exterior just within the mouth-cavity. These nephridia do not degenerate as development advances, but become more complicated, and remain as the mucous glands. Now the embryo in which these nephridia are in the simplest stage of development, resembling in almost every particular the nephridia which follow, is apparently not older than embryos of Lumbricus with functional head kidneys. In both cases, it
may be remarked, the nephridia occupy two segments; but the position of the funnel, as well as of the external pore, is different. In the development of Acanthodrilus multi- porus I have pointed out that the apertures of the mucous glands gradually shift backwards with the brain until they are placed well within the buccal cavity, instead of only just within it: it is quite possible that in an earlier stage still they are outside of it. If the aperture belongs to the prostomium it is perhaps inevitable that with the ingrowth of the stomodæum they should come ultimately to lie within the buccal cavity. The prostomium of these embryos, as of the embryo Lumbricus, is inconspicuous; but fig. 22 looks very much as if the aperture of the first pair of nephridia is in reality upon the prostomium. In this case the apparent difference in position between the nephridiopores of the first pair and of those which follow can be understood.

I think that there can be no doubt as to the homology between these nephridia and the provisional first pair of Lumbricus; and they are certainly not different from the nephridia which follow, except that they occupy two segments. I have referred to the difficulty of comparing the first pair of pronephridia to those which follow, by reason of the fact that they occupy two segments in Lumbricus; and also to Vejdovsky's suggestion that they are able to extend backwards through the incompleteness of the septa. The same explanation will suit Acanthodrilus perfectly well, so far as these facts are concerned.

Later on a complication ensues in the fusion of the first and second nephridia, the compound organ having two funnels.1

1 In connection with this I may refer to the mucous gland of Urochæta; I described that organ as extending through several segments (which Perrier first pointed out), and as furnished with several funnels. Dr. Rosa has lately pointed out (28) certain discrepancies between my descriptions and figures. On again looking into the matter I find that Rosa is right, and that the mucous gland opens on to the anterior margin of the first setigerous segment; and that an interval of a segment occurs between the pore of the mucous gland and that of the first nephridium, i.e. the latter is upon the third setigerous
The connection thus formed between the first and second nephridia recalls the statements of Hatchek with regard to the development of the nephridia in Polygordius. I have lately pointed out that in a Eudrilid Libyodrilus (10) such a connection is soon established between successive nephridia; but in all these cases the paired nephridia are developed first, and the connection is brought about later. There are, however, plenty of analogies which might support the view that there has been an acceleration in the development of the nephridia, the connecting duct being developed later and later until it ceased to appear at all.

However, it is in any case evident that the "pepto-nephridia" of Acanthodrilus are compound structures representing the two pairs of nephridia of the first three segments. It is quite possible that the corresponding organs in other earthworms have a similar history. It is very noticeable that in earthworms which have no pepto-nephridium the nephridia do not commence before the third segment;¹ in Lumbricus this is the case, and in Urobenus, Acanthodrilus, and Rhinodrilus. Microchæta appears to be an exception; but the segmentation of this form is not yet definitely made out.

In these worms, therefore, I should expect to find a "head kidney" lying in the first two segments of the larva, while in forms which have a pepto-nephridium I should expect that this organ will prove to be a permanent "head kidney" plus the following one or two nephridia.

The next important fact of general interest to be noticed about the development of the nephridia in this Acanthodrilus is their paired condition in the embryo.

The facts that I have been able to make out in the ontogeny segment. Dr. Rosa has suggested that I have accidentally referred to the mucous gland a funnel which should belong to the following nephridium. I would point out, in reply, that it is very possible that the development of the first pair of nephridia in Urochæta is like that of Acanthodrilus; in this case the existence of more than one funnel would be not surprising.

¹ Later, of course, in such forms as Pontodrilus, but never before that segment.
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of the nephridia are apparently at variance with the views which I have up to the present maintained with regard to the phylogenetic development of these organs in the Oligochaeta.

There can be no possibility of doubt that in Acanthodrilus multiporus the embryo is at first furnished with paired nephridia—one pair to each segment,—with the funnels opening into the segment in front of that in which the main part of the nephridium lies. This seems to indicate that Oligochaeta with paired nephridia are in this respect more primitive than such forms as Acanthodrilus multiporus and Perichæta, where the nephridia are furnished with numerous irregularly arranged external pores.

I suggested originally that the diffuse condition of the nephridia in the latter types was the more primitive, and that the paired arrangement could be derived from this by reduction. Professor Spencer strengthened this view, though differing from myself in certain details. Dr. W. B. Benham has also argued in favour of the primitive nature of the excretory organs in Perichæta. Others have, however, declined to accept this theory of the evolution of the excretory organs in the Oligochaeta. Dr. Eisig has treated the question at great length in his work upon the Capitellidae, naturally basing his arguments principally upon the Capitellidae themselves. These worms were the first in which the presence of many nephridia in a single segment was made known (by Dr. Eisig). Since the many nephridia per segment of the adult worm are preceded by a single pair in each segment, it appears reasonable to conclude that the former is the more primitive condition.

Dr. R. S. Bergh, who has recently contributed a series of valuable memoirs to the settlement of these questions, has nothing to say in favour of the position taken up by Spencer and myself. Indeed, the facts in the development of Lumbricus, which he has done so much towards elucidating, would hardly allow him to be of our opinion. Dr. Bergh begs to be excused from refuting all the arguments used by us, for the reason that they carry their own refutation. In so far as concerns the longitudinal duct of Polygordius
and *Lumbricus* Dr. Bergh is very possibly right, but I must object to his curt dismissal of the arguments to be derived from the "network" of *Perichæta* with the remark, "Gewisse anatomische Verhältnisse (Existenz eines 'nephridialen Netzwerkes' bei *Perichæta* und bei einigen anderen hochdifferenzirten Regenwürmern), die ohne Weiteres, als "ursprünglich Einrichtungen gedeutet werden." In the first place, "einen" ought to be replaced by "vielen," and in the second place, to state that *Perichæta* and those other forms in which the "plectonephric" condition occurs are highly differentiated is, at least, begging the question. Finally, neither Spencer nor I assumed the primitive character of the nephridia in these types "ohne Weiteres."

At the same time I freely admit that the observations recorded in the present paper, added to those of Bergh, Kleinenberg, and Wilson, have shaken considerably the position which I have taken up in regard to the phylogenetic development of the nephridia in the Oligochæta.

They seem to show that paired nephridia in this group are earlier than the irregular network. It must be remembered, however, that the permanent nephridia of *Lumbricus* cannot be the precise equivalents of the nephridia of the embryo *Acanthodrilus*; the reason for this is that the permanent nephridia of *Lumbricus* are developed out of the pronephridia. It is true that in *Lumbricus* there appears to be no break in continuity; the pronephridia are converted into nephridia by a gradual series of changes. In *Rhynchelmis*, however, the pronephridial stage is marked by the single "flame-cell" which afterwards, by division, develops into the funnel. In *Acanthodrilus* there is a break between the pronephridia and the permanent nephridia; this is marked not only by the disappearance of the funnels, but also by the occlusion of the lumen of the tubules. This would seem to imply a temporary cessation of function or at least an alteration of function in the nephridia.

It is interesting to notice that the enormous development of perivisceral corpuscles loaded with secreted granules occurs
after the early stages in which the funnel is present and functional; whether there is any connection between these two facts I do not know. To a certain extent, therefore, the nephridial system of the adult worm is a new formation, for which, however, the nephridia of the embryo furnish the material. It is not a simple increase in size and complication of structure which converts the nephridia of the embryo into those of the adult. There is first of all a temporary cessation of function (?) in a part of the nephridium—the portion nearest to the funnel—which is produced by the disappearance of the lumen; this part of the nephridium, as well as other parts, then grows actively, and a fresh series of apertures to the exterior are formed. There is quite as much change from the nephridia of the earlier stages to those of later stages as from the "pronephridia" (Vejdovsky, 1) of Lumbricus to the definitive nephridia. I have pointed out in this paper that the mode of development of the genital ducts in Acanthodrilus, as compared with Lumbricus, seems to show that the paired nephridia of the larval Acanthodrilus cannot be regarded as the exact equivalents of the permanent nephridia of Lumbricus. It seems, therefore, still possible to believe that, as regards earthworms at any rate, a more diffuse arrangement of the nephridia has preceded the paired regular arrangement; at the same time it appears to be necessary to assume that originally the paired arrangement existed, and that the diffuse condition of the nephridia was a subsequent modification of this. But in my opinion it must still be proved that the paired nephridia of Eudrilus, and other earthworms whose development is unknown, are homologous with the paired nephridia of the larval Acanthodrilus.

§ Summary of the more Important New Facts contained in this Paper.

(1) Nephridia.—In the youngest embryos these are paired tubes opening on to the exterior by the lateral setae, and each
provided with a funnel which opens at the segment in front. They are present in all the segments of the body, but there is only one pair of nephridia to the first two segments. These latter open on to the exterior at the commencement of the stomodæum. Later the second pair of nephridia, and afterwards one or two other pairs, become connected with the first pair, and collectively constitute the "mucous gland;" the stomodæal opening of this gland has moved further within the stomodæum. The funnels of the nephridia, except those belonging to Segments 11—14, become rudimentary, and numerous secondary external apertures are formed. The anal nephridia are a comparatively late formation; they appear to open into the mesenteron, not into the proctodæum.

(2) Gonads.—There are four pairs of gonads, which up to a certain point develop equally; later the gonad of Segment 12 degenerates.

(3) Genital Ducts.—Four pairs of genital ducts are developed; they are formed out of the nephridial funnels and a short section of the following tube: the genital ducts belonging to the 12th segment degenerate.

(4) The young embryo is furnished with an unpaired sense-organ consisting of a few large ciliated epidermic cells to one side of the stomodæal aperture; this is not recognisable in later stages.

(5) In the epidermis of the very advanced embryo there are peculiar cells which may possibly be sense-organs; the cells lie immediately beneath the cuticle, and are separated by a space from the basal membrane of the epidermis.
List of Principal Memoirs consulted.

1. VEJDYSKY, F.—"Entwicklungsgeschichtliche Untersuchungen," Hefte 1 and 2, Prague, 1888, 1890.
EXPLANATION OF PLATES XXX and XXXI,


Fig. 1.—Longitudinal section through a portion of two genital segments of an advanced embryo.

Fig. 2.—Longitudinal section through part of Segments 2 and 3 of an embryo of “Stage C.” N. Nephridia. Np. Duct of posterior (upper in the figure) nephridium. Ep. Epidermis. M. Circular muscular layer. M'. Longitudinal muscle layer.

Fig. 3.—Coelomic corpuscles of an advanced embryo in various stages.

Fig. 4.—Coelomic corpuscles of an embryo of “Stage A,” more highly magnified.

Fig. 5.—Transverse section through ventral blood-vessel of newly-hatched worm, illustrating the way in which the hearts communicate with that vessel.
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v. b. Ventral blood-vessel. m. Mesentery, by which it is attached to oesophagus. v. Valves in hearts.

Fig. 6.—Section through a portion of anal nephridia. A, B. Two tubes, one cut transversely, the other longitudinally, in which the peritoneum (p.) is slowly adherent to the nephridial cells (n.). C, D. Two other tubes, in which the peritoneum (p.) is separated by a space containing a coagulable fluid from the nephridium itself (n.). In every case the nephridial tubules have not yet acquired a lumen.

Fig. 7.—Transverse section through two nephridial tubules to illustrate the specialisation of the protoplasm of the cells into a central and peripheral portion.

Fig. 8.—Transverse section through longitudinal muscle-layer of newly-hatched worm. b. Muscular fibres imbedded in a faintly granular matrix. These are closer together, and have a columnar arrangement in that part of the longitudinal muscular layer which lies nearest to the circular muscles. a. Cavities in the gelatinous connective-tissue matrix.

Fig. 9.—Section through part of buccal cavity of advanced embryo. Ep. Epithelium of buccal cavity. N. Circum-oesophageal nerve-ring. neph. Duct of "mucous gland."

Fig. 10.—Transverse section through posterior region of the body of an advanced embryo. Nephr. Anal nephridia. Nephr'. Their ducts leading to exterior of body; the apertures into the alimentary canal are not shown.

Fig. 11.—Longitudinal section through a portion of the 9th segment. Ep. Epidermis. M. Circular muscle-layer. M'. Longitudinal muscular layer. s. Septum. f. Rudimentary funnel of nephridium, which lies behind the septum. At n a duct leads towards the exterior.

Fig. 12.—Gonad (gon.) and nephridial funnel (funn.) of one of the genital segments of an embryo of Stage C.

Fig. 13.—Gonad (gon.) and funnel (funn.) of newly-hatched worm.

Fig. 14.—Gonad (gon.) and commencing vas deferens (vas. def.) of the same individual. Spt. Septum.

Fig. 15.—Gonad of an embryo of Stage D. g. c. Germinal cells. p. c. Peritoneal cells.

Fig. 16.—Longitudinal section through a portion of the anteriorly-placed segments of an embryo of Stage C, showing nephridial funnel.

Fig. 17.—Two anterior segments of an embryo of Stage A, showing the nephridia. The segments are numbered. neph. External orifice. f. Funnel.

Fig. 18.—Anterior end of body of same embryo. s. Larval sense-organ. br. Brain. Stom. Stomodaeum. Mes. Mesenteron.

Fig. 19.—A portion of Fig. 16, enlarged to illustrate the structure of nephridial funnel, which has lost its cilia and is commencing to degenerate.
Fig. 20.—Embryos of the various stages described in the text, of the natural size.

Fig. 21.—Nephridium of Stage A, displayed for nearly its whole course. 
  \( f \). Funnel. \( s \). Seta sac.

Fig. 22.—Section through head end of embryo of Stage B. \( N.p \). External orifice of mucous gland. \( f \). Funnel of the same. \( p.h \). Pharynx. The segments are numbered, the figures being opposite to the setæ.

Fig. 23.—Embryo of Stage A.

Fig. 24.—Longitudinal section through function of stomodæum and mesenteron in embryo of Stage C. \( f \). Peritoneal cells. \( c \). Cilia, covering a few cells of the mesenteron.