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EDITED BY

E. RAY LANKESTER, M.A., LL.D., F.R.S.,

Fellow of Exeter College, Oxford, and Jodrell Professor of Zoology in University College, London;

WITH THE CO-OPERATION OF

E. KLEIN, M.D., F.R.S.,

Lecturer on General Anatomy and Physiology in the Medical School of St. Bartholomew's Hospital, London;

H. N. MOSELEY, M.A., LL.D., F.R.S.,

Linacre Professor of Human and Comparative Anatomy in the University of Oxford,

AND

ADAM SEDGWICK, M.A., F.R.S.,

Fellow and Assistant-Lecturer of Trinity College, Cambridge.

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MEMOIRS:

On Certain Points in the Structure of Urochæta, E. P., and Dichogaster, nov. gen., with further Remarks on the Nephridia of Earthworms.

By

Frank E. Beddard, M.A.,
Prosector to the Zoological Society of London, and Lecturer on Biology at Guy's Hospital.

With Plates XXIII and XXIV.

I. The Structure of Urochæta.

M. Perrier's elaborate memoir (22[1]) upon the structure of this worm leaves little to be done in the way of general anatomy. All the principal points which are of importance in the systematic grouping of Earthworms are thoroughly described and figured, with the sole exception of the female reproductive apparatus, which was not present in the examples studied by him. Perrier has also given a most detailed description of the vascular system down to the minutest ramifications, which forms one of the most complete accounts extant of the Annelid circulatory organs. The method of study adopted by M. Perrier was almost entirely that of laborious dissection, and the results which he has obtained by this means are undoubtedly striking. The elucidation of many points in the anatomy of Earthworms demands, however, a recourse to the section-cutting method, which has been adopted by myself in studying this Earthworm. I have, therefore, been able to add some few facts to what is already known, thanks to Perrier's researches, of the anatomy and histology of Urochæta.

[1] The numbers enclosed in brackets refer to the "List of Memoirs" on pp. 279, 280.

§ Integument.

I have elsewhere (4) criticised Perrier's figures of the epidermis, and have now to make some remarks upon the penetration of blood-capillaries into the epidermis.

The vascularity of the epidermis in Annelids was first made known by Lankester (19) in Hirudo; subsequently Bourne (12) showed that in all the Gnathobdellidæ the epidermis was traversed by blood-capillaries. Claparède (13), and later Horst (17) and v. Mojsisovics (21), figured blood-capillaries in the clitellum of Lumbricus, but did not find them in the general epidermis. The first record of the presence of intra-epidermic blood-capillaries in an Earthworm is by myself (5) in Megascolex; subsequently (6) I found the same thing in Perichæta and Perionyx. The figures of Vejdovsky (29), Rosa (25), and Benham (9, No. 3) show that the epidermis of Criodrilus is also vascular. I have now to state that in Urochæta blood-capillaries penetrate between the cells of the epidermis. In the Leeches and in Criodrilus the blood-capillaries form loops in the epidermis, but in Urochæta I could never trace a returning limb of the capillary which entered the epidermis. Judging from Vejdovsky's figures (pl. viii, figs. 16, 17) of Limnodrilus, the blood-capillaries which enter the epidermis of that worm appear to end abruptly in the same way.

Quite recently the brothers Sarasin (27) have described the penetration of blood-capillaries into the epidermis of Perichæta (without referring, I may remark, to my own record of this fact, which may, however, have been inaccessible), which they furthermore observed to open on to the surface of the body, thus putting the blood-vascular system into communication with the exterior. This, if true, is a most remarkable fact. I cannot, however, pending the publication of their more detailed account, accept it. The blood-capillaries of Urochæta reach to the very cuticle, but there they stop. Furthermore, the following appears to be an argument against the free communication of the integumental blood-capillaries with the surrounding medium. These capillaries were perfectly obvious since they were gorged with blood; asuming for the present that they open by means of pores, it would no doubt be the case, as the Sarasins suggest, that capillary attraction would prevent the blood from leaving the body. But when the body of the worm is contracted by the preservative fluid the blood would surely be driven out through the pores. Nor can it safely be said that the contraction of the epidermic cells would be sufficient to occlude the orifice of the blood-capillary; this would be forced open by hydrostatic pressure induced by the far more powerful contractions of the circular and longitudinal muscles. I cannot, therefore, believe that—in Urochæta at any rate—there are any pores which put the hæmal system into communication with the surrounding medium; and in the meantime their resemblance to the integumental blood-capillaries of Limnodrilus is worthy of note.

§ Excretory System.

The nephridial system of Urochæta has been partly described by Perrier (22); according to his account it consists of (1) a large gland, termed "glande à mucosité," occupying the first few segments of the body; (2) a series of "segmental organs," one pair to each segment; (3) a series of remarkable structures only developed in the posterior region of the body, where they are present to the number of a pair to each segment; they coexist in these segments with the ordinary nephridia. I shall consider severally these different organs, which together constitute the excretory system.

Mucous Gland.—The mucous gland is figured and described by Perrier as consisting of a tuft of long, much coiled glandular tubules, which ultimately unite and open on to the exterior by a long muscular duct. The orifices are situated upon the first segment, and are each surrounded by a group of muscular fibrils forming a sphincter. I have already (4) pointed out the presence of this sphincter, which Perrier was unable to definitely prove. Its presence is of course a point of similarity between the mucous gland and the more typical nephridia of the succeeding segments.

The structure of the glandular tubules is compared by Perrier with that of nephridia, and he rightly points out their resemblance, abandoning his earlier belief (24) that these glands were a part of the alimentary system. At the same time Perrier does not consider that their homology with nephridia is definitely proved.

It will be obvious from an inspection of Pl. XXIII, fig. 1, of this paper that the structure of the mucous gland is identical with that of the nephridia. It consists of rows of perforated cells enveloped in a peritoneal sheath, which are so far absolutely indistinguishable from the nephridia of the remaining segments of the body.

There is one point, however, to which Perrier has not directed attention in his memoir, and which conclusively proves that these mucous glands are nephridial; that is, the presence of cœlomic funnels agreeing in their structure with the funnels of the nephridia in the other segments of the body.

The "mucous glands" occupy the first six segments, which contain no nephridia of the normal type; these latter do not commence until after. It is therefore a matter of interest to inquire how far the "mucous glands" represent the missing nephridia. Do they, in fact, simply represent the hypertrophied first pair of nephridia, or are they formed by a fusion of all the nephridia typically present in the space which they occupy? The fact that the external apertures are single would seem to prove the truth of the former supposition. On the other hand, the mucous gland does not only differ from the typical nephridium by its branched character, but also by the presence of several cœlomic funnels.

In my preliminary notice (2) of the mucous gland I have, I now believe erroneously, stated that each gland has four or five funnels. In several instances I have good reason to believe that there are only three present. The funnels are of considerable size, and apparently of a somewhat horse-shoe-shaped form; hence in a continuous series of sections it is not difficult to mistake one funnel for two contiguous but separate funnels. The three funnels of each mucous gland are, however, so widely separated that no mistake of that kind could be made. At the same time I do not wish to state positively that there are only three present; and for the matter of that, the exact number does not appear to me to be of great importance unless it could be proved that each branch opens into the cœlom by a funnel. I shall presently show reasons for believing that this is not the case. Now, two of these funnels are situated at the distal extremity of the gland and correspond in their position to the fourth segment; the third funnel is more anterior in position and corresponds to the fifth segment, so far as one can judge in the absence of definite septa separating these segments. Although there is some appearance of correspondence to the segments in the arrangement of the ciliated funnels, yet it must be admitted that the ciliated funnels are not arranged in a regular, metameric fashion. Taking into consideration the facts (to be referred to more at length below) that the nephridia of some of the posterior segments are furnished with more than a single funnel, and the extent of the first pair of nephridia ("tubiparous glands") of certain Polychæta sedentaria, it is perhaps more likely that the mucous glands represent the nephridia of the first segment alone; on the other hand, there is nothing in the facts, as I read them, which is contrary to the supposition that the mucous gland represents the nephridia of all the segments which it occupies, and that the primitive condition is only shown, and that imperfectly, in the disposition of the ciliated funnels; the concentration of this portion of the nephridial system being due to its specialised function.

Then again, there is a third alternative. Supposing that the mucous gland is the nephridium of the first segment alone, is its branching to be considered as a remnant of what I have elsewhere (1) urged is the primitive condition of the Annelid nephridium, or is the branching, as Dr. Eisig would argue (15), secondary? This raises again the whole question of the derivation of the Annelid excretory system, to which Dr. Eisig's recently published Monograph upon the Capitellidæ is a most weighty contribution.

In the latter part of this paper (p. 260) I discuss some general questions relating to the nephridial system of Earthworms; but it will be convenient to treat here of the arguments which the structure of the mucous gland of Urochæta, and of some other genera, furnish for the derivation of these glands from a continuous network of tubules.

I have already stated that this gland in Urochæta communicates with the cœlom by three funnels; I am not quite certain whether there is not a fourth. In any case there seems to be no doubt that the number of branches is in excess of the number of ciliated funnels. Perrier's figure of the organ (22, pl. xvi, fig. 35) is, so far as I can ascertain, accurate, in that it indicates the convergence of a large number of nephridial tubules to form the long duct of the gland. I have reason, however, to believe that in some cases the tubules unite before their opening into the muscular duct; but this is not a matter of great importance. One of two things must therefore follow: either the tubules again unite before the ciliated funnels, thus forming a network, or a large number (the greater number) of the tubules end blindly without any cœlomic apertures. I can find no evidence of the truth of the first supposition, and must therefore come to the conclusion that the mucous gland is a branched nephridium, of which the greater number of branches end blindly, while a few open into the cœlom by ciliated funnels.

These facts would seem to show that the gland is in some respects degenerate; that it primitively possessed a larger number of ciliated funnels, the greater part of which have been lost. So far this is merely an assumption, which at any rate harmonises with the structure of the organ. Although the nephridia of Earthworms are richly supplied with blood-capillaries, it seems nearly certain (particularly from the investigations of Kühenthal) (20) that a good deal of the waste matter that is excreted by them is not extracted from the blood-capillaries by the cells of the nephridia, but is taken up by the funnels; the large granular peritoneal cells which clothe the intestinal blood-vessels play an important part in this process of elimination.

Now, the very differences between the mucous gland and the other nephridia suggest that it plays a different part in the economy of the animal. A suspicion that this was the case led M. Perrier to term it "glande à mucosité," although he had no evidence to bring forward of a positive nature; this supposition would account for the reduction of the ciliated funnels; the high development of the secreting part of the organ, and the presence of a large vesicle for the storage of the secretion, coupled with the reduction of the cœlomic apertures, is clearly in favour of the view that this gland secretes a substance which is used for some definite purpose.

I describe below (p. 258) the structure and relations of the anterior section of the nephridial system in Dichogaster. This worm has an anteriorly situated gland which resembles in many particulars the mucous gland of Urochæta. It consists of a tuft of highly convoluted tubules which have the same structure as nephridia; these tubules open by means of a wider duct; the segments (Nos. 1—3) occupied by this gland contain no other nephridia. The "mucous gland" of Dichogaster differs from that of Urochæta in certain important particulars; in the first place it has no cœlomic funnels; in the second place the duct opens, not on to the exterior of the body, as in Urochæta, but into the buccal cavity; thirdly, it appears to be formed by a single tube much coiled. Apart from these points of difference, the similarity between the two glands is so great that I cannot but regard them as homologous. The fact that the mucous gland of Dichogaster opens into the buccal cavity suggests that its function is analogous to that of a salivary gland; it may be at least admitted that its function is probably different from that of the nephridia in the remaining segments of the body. A comparison between the structure of the mucous gland in the two genera Dichogaster and Urochæta leads to the inference, firstly, that they are homologous, and secondly, that they present two stages in the evolution of the gland. The primitive characters are more completely retained in the mucous gland of Urochæta; it possesses funnels and opens on to the exterior of the body on the first segment; the reduction in the number of the funnels, correlated with the changed uses (?) of the gland, culminates in Dichogaster, where there are no ciliated funnels; at the same time the external aperture comes to be situated in the buccal cavity.

I have elsewhere (7) described a similar gland in Acanthodrilus novæ-zealandiæ which, like that of Dichogaster, opens into the buccal cavity. I could find no ciliated funnels. In this case, as in that of Dichogaster, I discovered (see p. 259) the ciliated funnels of the nephridia elsewhere, and their absence from the mucous gland rests upon observations which are therefore more to be trusted.

Benham (9, No. 2) has recorded a gland in Diachæta which occupies the same position and has the same general appearance as the mucous glands of the types already referred to. He states that it is not a branched gland, but consists only of a single much contorted tube.

In Acanthodrilus annectens (Beddard 8) there are a pair of anterior nephridia exactly like those of A. multiporus; and each opens in the same way into the buccal cavity. I cannot discover very much evidence of this gland being branched; but fig. 14 appears to show that branching of the tubules does occur, though apparently not to any great extent.

There is nothing in the facts so far which is contrary to Eisig's supposition that the branching of the nephridium, whether of the terminal (external apertures) or distal (cœlomic funnels) region, is secondary; on the other hand, these facts may be equally well interpreted on the view that we have here a rudiment of a primitive condition in which the nephridial system formed a continuous network, with many funnels and many external apertures in each segment.

I shall now bring forward further evidence of the truth of this latter view.

Perrier has referred to the presence in Perichæta of a mass of glandular tubes in the anterior segments; these were figured by him in P. Houlleti, and were at first erroneously regarded as connected with the alimentary canal. Later, they were correctly referred to the excretory system. M. Perrier remarks (22, p. 639) "that the segments (in Perichæta) which contain these glands are usually filled by a thick yellow secretion, which the animal evacuates when annoyed." This secretion must be expelled, M. Perrier thinks, by the dorsal pores, since he was unable to discover any excretory canal like that of Urochæta. Now, Urochæta is an extremely small worm, and an anatomist who has proved himself sufficiently skilful, as M. Perrier has done, to dissect out the minute duct of the "mucous gland," embedded as it is among the muscles of the pharynx, would hardly fail to trace the same duct, if it existed, in the comparatively large Perichæta. By the study of transverse and—which are perhaps better for this purpose—longitudinal sections, I can quite confirm Perrier's conclusion as to the absence of an excretory canal like that of Urochæta. I have, however, already (1) shown that the nephridia of these segments open on to the exterior by numerous pores, and that the nephridia of adjacent segments communicate through the septa; this at any rate applies to P. aspergillum. In the few first segments of the body of P. aspergillum (1) the nephridial system is enormously developed; all the cœlomic space available is closely packed with tubules. On dissection this part of the excretory system has, comparatively speaking, a solid appearance; through the rest of the body the nephridia are by no means so conspicuous, and, indeed, they require a microscope for their demonstration.

The massing of the nephridia in a few of the anterior segments and their apparently different function from the nephridia in other parts of the body (if one may so interpret M. Perrier's experiments), renders plausible a comparison of this part of the excretory system with the "mucous gland" of Urochæta. If this comparison be allowed the most important consequences follow; it would seem, in fact, as if the specialisation of this part of the nephridial system ultimately led to the concentration of the numerous excretory pores into one long duct; that in fact the branched mucous gland of Urochæta is traceable to the specialised nephridial mass of the anterior segments of Perichæta; the numerous external pores of the latter being replaced by the single aperture of Urochæta.

I have in a previously published paper pointed out that if the peculiar cutaneous glands of Urochæta correspond to abortive setæ, as they appear to do from a comparison with similar glands in Anachæta (Vejdovsky, 29, pl. vii, fig. 1), the eight setæ per segment of Urochæta are brought about by a reduction of a complete circle of setæ such as exists in Perichæta. On this hypothesis Perichæta is the primitive form, Urochæta comes next, and finally Dichogaster and Acanthodrilus, in which there is no trace of the missing setæ, complete the series. It will be noticed that the evolution of the mucous gland, as I have traced it in the foregoing pages, is in correspondence with this series of facts.

Nephridia.—All the segments of the body in Urochæta from the fifth are furnished with a pair of nephridia.

The external apertures of these are perfectly plain on the exterior of the body.

Perrier has already referred to the fact that the aperture of the nephridium is surrounded by a peculiar cup-like structure, which seems to be composed of radially arranged, short muscular fibres. He has also figured the funnel. I find that with respect to the funnel there is a remarkable difference between the mucous gland and the nephridia of the anterior segments on the one hand and the posterior nephridia. Perrier's figure of the nephridial funnel (22, pl. xvi, fig. 42) evidently represents one of the latter. The funnels of the mucous gland of the nephridia of the anterior segments are in the first place much larger than those of the posterior nephridia; their structure also is different. The funnel itself (Pl. XXIII, fig. 5) is composed of the same columnar ciliated cells with large nuclei, but it does not at once communicate with the narrow tubule; the latter is dilated into a wide cavity of considerable length. This portion of the nephridium is not to be confounded with the funnel although its lumen is of the same size; its walls are tolerably thick and exhibit a faint transverse striation, and contain oval nuclei embedded at intervals. The structure of this part of the nephridium shows that the lumen, although it is extremely wide, is nevertheless intracellular; it is simply a dilatation of the tubule.

This dilatation of the nephridial tubule recalls an analogous dilatation which Bourne (12, figs. 51, 52, 53, 54), has described and figured in Leeches, only in these animals the lumen appears to be intercellular.

I have always observed this dilatation to be filled with what are apparently degenerating corpuscles, the nuclei of which were deeply stained by borax carmine. Bourne has observed similar contents in the corresponding part of the nephridium in Leeches.

In the genus Thamnodrilus (Beddard, 3) the funnels of the anterior nephridia also differ from the funnels of the posterior nephridia.

In a few segments I observed two nephridial funnels, but this branching of the nephridium appears to be rare.

Perrier states that the nephridial funnel is contained in the same segment as the nephridium itself. In a paper upon the structure of an Australian species of Urochæta (4) I pointed out that the funnel, as is usually the case among the Oligochæta, was situated in the segment anterior to that which is occupied by the rest of the nephridium. In Urochæta hystrix I find a justification for Perrier's statement; the nephridia are sometimes entirely contained in one segment and sometimes are not. In the second case the funnel is in the segment in front; the former arrangement seemed to be restricted to the anterior nephridia. Finally, the anterior nephridia agree with the mucous gland, and differ from the posterior nephridia in the small calibre of the duct; in this they agree with the anterior nephridia of Perichæta (see p. 262).

Ovaries and Oviducts.—Perrier's memoir (22) upon Urochæta contains no description of the female reproductive organs, except of the spermathecæ. He remarks "that the female reproductive apparatus seems to be fully developed after the male reproductive organs." This opinion is borne out by my own experience. I have never found the two sets of organs to be completely developed in the same individual. All the specimens that I have examined were either "males" or "females." This functional separation of the sexes, so frequent in hermaphrodite animals, cannot be said to be general among Earthworms. Benham, however, has found (9, No. 2) that Urobenus, Diachæta, and Trigaster agree with Urochæta in this particular; in the two first genera he could only discover the male organs, while in Trigaster the female organs alone were fully developed.

I have investigated the minute structure and the position of the generative organs, both by transverse and longitudinal sections; their position and general relations could only be properly determined by longitudinal sections, owing to the arrangement of the septa in this region of the body. Perrier has already recorded the fact that in the specially thickened septa—the last of which bounds the tenth segment—the middle region is very far behind the lateral margins which are attached to the parietes. Each septum is therefore somewhat thimble-shaped with the concavity forwards, and is largely enclosed by the following septum. This does not only apply to the thick septa, but to a large number of the excessively fine septa which come behind. It is not in fact until the twentieth segment that the intersegmental septum is disposed perpendicularly to the long axis of the body. The ovaries and oviducts are situated anteriorly where the delicate septa are hardly separable. The ovaries and oviducts, as well as the funnels of the vasa deferentia, come to lie opposite to the setæ of segments which in reality are considerably behind those which contain the several organs. In correspondence with the arrangement of the septa the oviducts run forward for some distance before opening on to the exterior. Their position, however, is in reality perfectly normal. The external apertures are upon the fourteenth segments, and the funnels open into the thirteenth.

The vasa deferentia funnels open into the segment in front, i. e. the twelfth.

In two specimens I found the female reproductive apparatus fully developed, and the male organs, with the exception of the vasa deferentia, not fully developed. The vesiculæ seminales in those individuals were very readily visible as outgrowths of the posterior side of the septum which separates segments 13 and 14; the vesicula was in the condition illustrated by Bergh (11) in Lumbricus on pl. xxi, fig. 13, of his memoir. It consisted for the most part of a solid mass of cells, with a narrow lumen extending for a very short way into its thickness.

In these specimens (Pl. XXIII, fig. 2) there were no testes, but the twelfth segment as well as the thirteenth contained a pair of ovaries. In another individual the gland of the thirteenth segment contained ova in abundance. There were also a few ova in the gland of the twelfth segment. I figure (Pl. XXIII, figs. 3, 4) a small fragment of the glands of segments 12 and 13. In another specimen in which the vesiculæ seminales were in a further advanced condition, the genital gland of the twelfth segment and that of the thirteenth segment appeared to be a testis. These facts are, of course, a confirmation (though indeed a confirmation is hardly wanted) of the accepted view that the ovaries and testes are serially homologous structures. From this point of view the facts are of just as great importance, even if it were shown that the individuals were only abnormal. I am inclined to believe, however, that they are not so, and that in Urochæta the same gland may produce ova or spermatozoa.

In all the four individuals which I investigated by means of longitudinal sections there were a number of bodies resembling mature ova lying in the body-cavity behind the thirteenth segment quite detached from the reproductive glands of that segment. They appeared to be contained in the fourteenth or fifteenth segment, or even to occupy both of these segments. In at any rate one instance these bodies appeared to be contained in a thin-walled muscular sac, to the walls of which were closely applied the transverse vascular trunks. In the other cases they were grouped together, but I did not observe any structure resembling a muscular sac surrounding them.

The maturation of the ova[1] of Urochæta outside the gland in which they are developed is of some interest, even if the supposed muscular sac enveloping them is nothing but a partially detached (by the processes of embedding, &c.) portion of the delicate intersegmental septa. Moreover, the ova themselves differ in some important particulars from the ova of the majority of Earthworms.

Vejdovsky (29), as well as the earlier observers d'Udekem and Claparède, dwells upon the fact that the ova of Earthworms are small and numerous as compared with those of the majority of the aquatic Oligochæta, which are large and few. The greater size of the ova of the "Limicolæ" is due to the fact that they contain very much more abundant yolk. The greater development of yolk in the ova of the "Limicolæ" is, Vejdovsky thinks, due to the different way in which they become mature. In the aquatic Oligochæta the ova detached from the ovary are nourished by the perienteric fluid, while the ova of Earthworms remaining in the ovary are provided with special blood-capillaries. The latter mode of nutrition, as the facts prove, leads to the formation of numerous small ova, the former to the

[1] I found these structures in two specimens of Urochæta, and occupying the same position. I cannot, however, be certain that they are not Gregarines. I am not aware that it is possible in preserved specimens to be absolutely certain about such a point. All that can be said is that the bodies in question are closely similar to the ovarian ova of Phreoryctes, and that I only found them in the situation mentioned. The fact of their not being surrounded by smaller ovarian cells as are the egg masses of Rhynchelmis is not a conclusive argument, since in Earthworms the ova in the receptaculum are not accompanied by such cells.

increase in size of a few ova. Whatever may be the fundamental explanation of this structural dissimilarity, the fact remains that there is a certain difference in the mode of development of the ova in the aquatic and in the terrestrial Oligochæta. At the same time it has to be borne in mind that in many Earthworms the ova when fully developed leave the ovary and make their way to the interior of receptacula ovorum. These chambers must at least be analogous to, if not homologous with, the "egg-sacs" of Stylaria, &c., in which ova also undergo maturation. They differ, however, in being relatively much smaller and thicker walled, and in having their cavity divided up by trabeculæ like the vesiculæ seminales. Vejdovsky does not give a detailed account of the development of the egg-sacs (Eiersäcke) in Stylaria, and their homology with the receptacula ovorum of Earthworms must be left for the present undecided. The question as to homology does not, however, affect the functional similarity of the two structures. The receptacula ovorum of Earthworms are thicker walled, and supplied with abundant blood-capillaries, which give them a reddish appearance. The egg-sacs of Stylaria are thin walled, and have no capillary network, but are supplied by the hypertrophied vascular arch of their segment. This difference may perhaps be responsible for the unequal development of the contained ova in the two cases. The whole question requires further investigation.

Judging from Bergh's (11) figures, the mature ova contained in the ovary of Lumbricus hardly differ in size from those contained in the receptacula ovorum. I have carefully compared the relative sizes of the ovarian ova and those from the receptaculum ovorum in Allurus, and find that the latter are rather larger; but the difference is not sufficiently striking to lead me to the opinion that the ovum undergoes any important increase of bulk during its sojourn in the receptaculum. Indeed, the observations of Dr. A. Collin (14) show that in Criodrilus the ova contained in the receptaculum are smaller than the largest ovarian ova; but this is probably to be explained by supposing that the smaller immature ova ripen in the receptaculum, while the large mature ova pass from the ovary directly into the oviduct.

The mature ova of Allurus and perhaps of Urochæta differ from those of the majority of Earthworms, and agree with those of the "Limicolæ," in the fact that they are of comparatively large size.

The only other Earthworm known to me, in which the ova are of large size, is Allurus. Fig. 22 of Pl. XXIV illustrates the comparative size of the mature ova of a number of Earthworms and of Phreoryctes. It will be seen from that figure that the ova of Allurus are markedly larger than those of Eudrilus, &c., though smaller than the supposed ova of Urochæta. This fact is of particular interest in relation to other points in the structure and economy of Allurus. This worm, although structurally nearer to Allolobophora than to any other Oligochæt, is not terrestrial; at least, not exclusively terrestrial in its habits. I received some specimens from Teneriffe which were collected in company with a number of specimens of Lumbricus and Allolobophora in soil; on the other hand, Mr. Martin Woodward was so good as to forward me a specimen of Allurus, which he discovered in a vessel containing Chara which had been collected for the use of the botanical students at the School of Science, South Kensington. There was no reason to believe that this individual had accidentally found its way into the vessel; it had been in all probability collected in the stream which furnished the Chara. Mr. Benham has lately contributed to 'Nature' a note in which he points out that Allurus is largely aquatic in its habits.[1] It is interesting to find that this particular genus approximates to the "Limicolæ" in its habits; indeed, it is the only instance known to me of an aquatic Earthworm, though of course many of the "Limicolæ" live in damp soil.

[1] Since writing the above I find that Vejdovsky in his paper upon Rhynchelmis ('Zeitschr. f. wiss. Zool.,' 1876) has mentioned the occurrence of Allurus in streams. During a recent visit to the Plymouth Station of the Marine Biological Association I found Allurus in abundance among coarse gravel in the River Plym, near Bickleigh.

Allurus, furthermore, resembles certain of the Limicolous genera in the large size of its ova, and in the fact that the female reproductive pores are behind the male. I have not any evidence that Urochæta can, like Allurus, lead an aquatic life; but the resemblance which it bears to the "Limicolæ" is shown in the possession of bifurcate setæ as well as (perhaps) in the large size of its ova. Perrier discovered the former fact, and I have occasionally observed the same in specimens from British Guiana.

II. Dichogaster Damonis, nov. gen. et sp.

The present section contains some account of the anatomy of a species of Earthworm, which appears to be sufficiently unlike any other type at present known to justify the creation of a new genus for its reception.

I have examined two specimens which I acquired from Mr. R. Damon, of Weymouth. One of these was dissected, the other studied by means of transverse sections.

The worms formed a part of the Godeffroy collection, recently purchased by Mr. Damon, and are labelled "Hypogæon." This name has been applied to several very different species of Earthworms, and in Savigny's original description is characterised by the possession of a single median seta in addition to the eight which are ordinarily found. In this character Hypogæon differs from the present species.

The species was collected in Fiji.

§ External Characters.

The setæ are paired, and lie on the ventral side (fig. 8). The dorsal and lateral pair of setæ are separated from each other by a rather greater interval than that which separates the ventralmost pairs of setæ. The clitellum extends from segments 13—20 inclusive. It is not so markedly developed on the ventral as on the dorsal side; hence the number of segments of which it is composed can be more easily reckoned from the ventral side. The twentieth segment has the whole ventral region enclosed between the lateral pairs of setæ entirely devoid of glandular epithelium, which is only developed on the dorsal region of this segment. The more anterior segments, in like manner, have no development of glandular substance for the greater part of the ventral area. The seventeenth segment bears the apertures of the vasa deferentia, which do not correspond to the ventral setæ, but are more ventrally placed. The apertures are situated on a tumid area which occupies the space lying between the setæ. On the two following segments there are similar areas, but more distinctly marked off from the surrounding integument. Dorsal pores are present, but I could not ascertain where they commenced.

On the eighth segment are the apertures of the single pair of spermathecæ. These are closely approximated in the median ventral line, and open near to the anterior margin, as is so generally the case. The various layers which compose the body wall appear to have much the same structure in this as in other species of worms. Particularly noteworthy is the fact that the longitudinal muscular layer shows the bipinnate arrangement of its fibres which is so characteristic of some, although not of all, species of Lumbricus, and is found also occasionally in other genera. This is illustrated in fig. 6 of Plate XXIII. In the anterior part of the body the fibres of the longitudinal muscular coat do not show any such regularity in their arrangement.

§ Alimentary Canal.

The most salient fact in the structure of the alimentary canal of this Earthworm is the presence of two gizzards (fig. 21); these are situated close together in consecutive segments, and are only separated by a very minute œsophageal portion, the calibre of which is not far short of that of the gizzards themselves; the segments occupied by the gizzards are 7—10, the mesenteries separating these segments from each other are, as is often the case, not obvious. It will be seen, therefore, that each gizzard occupies two segments. The presence of more than a single gizzard is not new among Earthworms; Digaster, Perrier (24), and Didymogaster, Fletcher (16), as their names imply, have two gizzards, but the present genus cannot be confounded with any of these; more than two gizzards occur in other Lumbricidæ, viz. Trigaster (Benham) and Moniligaster (Perrier).

The œsophagus is furnished behind the gizzard with calciferous glands; of these there are three pairs, situated in segments 15, 16, and 17 respectively (fig. 21); the two anterior pairs of these glands are rather larger than the posterior pair and in the specimen studied by me were full of calcareous particles, the product of their activity, which were entirely absent from the smaller pair; the œsophagus contained a large quantity of the calcareous secretion of the calciferous glands.

The posterior pair of calciferous glands is divided by longitudinal furrows into four distinct lobes; its blood supply is derived direct from the dorsal vessel, there being apparently no supra-intestinal trunk; the blood-vessel enters the gland along the short pedicle, which unites it with the walls of the œsophagus. The same appears to be the case with the two anterior pairs, and in all the glands the vascular supply is also in connection with the blood sinus of the œsophageal walls.

§ Generative Organs.

Testes and Vesiculæ Seminales.—I have only been able to study these structures by means of transverse sections; by dissection I could not, owing to the friable condition of the specimen, make out the exact relationship between the component parts of the male generative organs.

The testes (fig. 15, *t.*) are two pairs of small glands situated in segments 10 and 11. The organ is somewhat irregular in shape, and furnished with numerous finger-shaped processes. A dissection even of the immature example which I studied by transverse sections would not have shown the testes, inasmuch as they are completely overgrown and surrounded by the vesiculæ seminales of their respective segments.

The fact that the testes are actually surrounded by the vesiculæ during the growth of the latter is, of course, a result of numerous investigations. The adult structure of the Earthworm at present under consideration would prove this point, supposing, that is to say, that there was the least need of proof.

The sac-like vesiculæ seminales completely enclose the testes, and in the case of the anterior pair, at any rate, enclose also a tuft of nephridial tubules, which happen to be closely associated with the testes. In other worms other organs of the body, e. g. the ventral blood-vessel, are enclosed within the cavity of the vesiculæ.

The testes of Dichogaster have apparently the same structure that characterises these organs in other Earthworms. They are attached to the mesentery close to the ventral median line on either side of the nerve-cord ; at the point where they are attached the walls of the vesiculæ come into contact, and are fused with the mesentery.

The structure of the vesiculæ seminales is curious and differs in certain particulars from the vesiculæ of other Earthworms.

In the example which I dissected the eleventh and twelfth segments contained each a pair of racemose structures of small size (fig. 15, *r.'*), appearing on each side of the gut. These presented every resemblance to the vesiculæ seminales of many species of Acanthodrilus. In the tenth segment a mass of developing spermatozoa occupied the ventral region of the segment, and partly obscured the fimbriated apertures of the vasa deferentia. A study of the generative apparatus by means of transverse sections showed that the structure in segment 10 is not a loose mass of developing spermatozoa set free from the vesiculæ of segments 11 and 12, and ready to be extruded through the open funnels of the vasa deferentia. It is really a pair of vesiculæ seminales (fig. 15, *r.*) with a delicate outer wall, and presenting the usual structure. This vesicle, although presumably originally a paired structure, does not show much evidence of being a paired structure in the adult worm; the two halves of the vesicle are almost completely fused in the ventral median line where they enclose the nerve-cord. The ventral blood-vessel is not enclosed within the vesiculæ, but is suspended by a vertical mesentery some little way down between the two vesiculæ, which here become distinctly separate; a portion, however, of the transverse vessel of this segment, as well as (necessarily) a branch on each side, which runs to the testis, are enclosed by the vesiculæ. The vesiculæ send off a narrow lateral band, which seems to become fused with its fellow of the opposite side in the dorsal median line (see fig. 15).

In the eleventh segment is another pair of vesiculæ, for a description of which the foregoing remarks will nearly suffice. The same segment also contains (see fig. 15) the racemose structures already referred to. These are composed of a large number of small spherical acini, which contain bundles of developing spermatophora. The whole structure is firmly attached to the mesentery, which divides its segment from the one in front. I have not been able to make out any connection between this portion of the vesiculæ and the undivided median sac.

Finally, segment 12 contains another pair of these racemose organs, which have apparently no connection with the vesiculæ of the preceding segment.

Vasa Deferentia.—There are two pairs of vasa deferentia funnels situated in segments 10 and 11; they open into the middle of the vesiculæ seminales of these segments, on each side of the nerve-cord and near to it. Their structure calls for no special remark, neither does that of the vasa deferentia, which open, in common with the glandular body, upon the seventeenth segment of the body.

When the worm was opened in dissection the seventeenth, eighteenth, and nineteenth segments were seen to be largely occupied by three pairs of glands, a pair to each segment, of a whitish colour, and meeting above the intestine. The anterior pair of these is very much larger than those which follow, and somewhat contorted; the latter are narrower tubular organs exactly resembling each other (fig. 7).

An examination of these glands by transverse sections shows that they all open on to the exterior at a corresponding point in the three segments; the external apertures of these glands, in fact, correspond in position to the innermost of the ventral pair of setæ. I find, however, that in these three segments, viz. 17, 18, and 19, the ventral pair of setæ are altogether absent, although they are present in the neighbouring segments. The dorsal pair of setæ are as well developed in segments 17, 18, and 19 as in any others.

It is very common to find some modification of the setæ in the segments which bear the male generative pores, such as, for example, the bundles of elongated setæ in Acanthodrilus, but I am not acquainted with any other instance (except Eudrilus) in which the setæ entirely disappear on these segments (figs. 16, 17).

The anterior pair of glands (figs. 7, 16, *pr.*), those which occupy segment 17, and which are distinguished by their greater size and greater opacity, are the real atria; that is to say, it is these glands alone which are connected with the vasa deferentia. These glands have much the same structure as in other Earthworms; the very narrow lumen is surrounded by a layer of columnar cells; outside these is a mass of glandular cells, the exact relations of which the condition of the material does not enable me to state positively. Apparently these cells resemble very closely the corresponding cells in the prostate of Eudrilus. Outside is a delicate sheath containing blood-vessels which send off branches among the gland-cells. The atrium communicates with the exterior by a slender but thick-walled muscular duct; this duct is at first much contorted, but when it enters the body wall is perfectly straight; its course through the latter is oblique, the external orifice being placed nearer to the ventral median line than the point where the tube enters the body wall.

The tubular glands of segments 18 and 19 (figs. 7, 17, *pr.'*) are straight, and not contorted like the glands of segment 17, and their diameter is considerably less; their minute structure, however, seems to be identical, except that the glandular layer is naturally less developed.

Ovaries.—These organs (fig. 15, *o.*) occupy the usual position in segment 13; they are large and conspicuous.

Oviducts.—The oviducts (fig. 15, *od.*) open by a wide, funnel-shaped orifice into the interior of segment 13; their duct perforates the mesentery, dividing this from the succeeding segment. Each opens separately on to the exterior; the external orifices are very closely approximated, and lie within the ventralmost setæ at the same level as the apertures of the atria.

Spermathecæ.—There is only a single pair of these organs present, which are situated in the eighth segment; the external aperture, as already stated, corresponds in position to the ventral pair of setæ. The spermatheca is divided into two parts (fig. 8), a large sac lying posteriorly and opening on to the exterior in common with a mulberry-like structure which represents the diverticulum; as in so many other species of Earthworms, the diverticulum lies anterior to the pouch. The minute structure of these two sections of the spermatheca differs; the pouch itself is lined (fig. 19) with a tall columnar epithelium, which appears to resemble in every particular the lining epithelium of the spermatheca of Lumbricus. Outside this is a comparatively thin layer of muscular tissue permeated by abundant blood-capillaries; the muscular sheath gets much thicker where the pouch narrows to its external opening, and here the character of the lining epithelium alters slightly and becomes indistinguishable from the epidermis of the body surface. The structure of the numerous diverticula differs somewhat; the presence of numerous small diverticula gives to the region of the spermatheca its mulberry-like aspect. They are all, however, enclosed within a common muscular sheath (fig. 20), which is proportionately thicker than in the case of the spermatheca itself, and abundantly vascular. The diverticula are closely packed with bundles of spermatozoa, and the lining epithelium differs from that of the spermatheca itself; the epithelial cells are low and cubical. I have called attention elsewhere (7) to the fact that the diverticula of the spermathecæ in Lumbricidæ are of different minute structure to the spermathecæ, and are usually occupied by the bundles of spermatozoa which are absent from the spermathecæ themselves.

Nephridia.—The excretory system of this worm, as of so many others, differs in different regions of the body. Professor Spencer has called attention, in a paper (28) to which I shall have again to refer, to the fact that the nephridia of Megascolides are different in the anterior and in the posterior regions and of the body; this is also the case with Perichæta (p. 262) and Urochæta (p. 246); and the same condition occurs in many genera (e.g. Microchæta and Thamnodrilus) in which the nephridia consist of paired tubes, each with a single cœlomic funnel and external pore.

With regard to Megascolides, Spencer points out that the nephridia of the anterior segments present more primitive characters than those of the posterior segments, where they first begin to be modified. This statement appears to hold good (as I have already pointed out) in Acanthodrilus, and the facts which I shall bring forward in the present paper show that in Perichæta the nephridial system of the posterior segments is more modified than that of the anterior segments. In Urochæta it is only in the anterior segments that a single nephridium has more than a single ciliated funnel. With regard to such genera as Microchæta and Thamnodrilus, it is difficult to say that the anterior nephridia are in any way more primitive than those of the posterior segments.

In Dichogaster the same generalisation with respect to the nephridia appears to hold good. I am unable, however, to give so complete an account of the nephridia as I could have wished. The first five segments are occupied by a large nephridium, which evidently corresponds to the large anterior nephridium of Acanthodrilus multiporus and A. annectens. I could not find the funnels of this organ (if they are really present), nor could I find any very decided evidence of its being a branched gland. I am rather inclined, however, to believe, from the analogy of Urochæta, that it is branched. This nephridium terminates in a comparatively wide, thick-walled tube, which becomes wider and thinner walled as it approaches the external orifice, which is within the buccal cavity, as in the two species of Acanthodrilus mentioned above. In the segments of the body which follow (I am uncertain how many), the nephridial system is much like that of Acanthodrilus multiporus; that is, it consists of tufts of tubules which open by numerous apertures on the surface of the body. These apertures have no regular arrangement that I could observe; frequently they are situated near to the setæ, but as frequently they open near to the anterior or posterior boundaries of the segment. The apertures are extremely obvious, both in transverse and longitudinal sections, on account of their large size. I have not been able to observe any funnels connected with these nephridia.

In the posterior region of the body the nephridia are different, and, as already mentioned, are in certain respects more modified than those of the anterior segments.

On a dissection of this region of the worm the nephridia appeared to be separable into a number (about six) of pairs of distinct nephridia. In transverse sections the nephridial system was seen to consist of scattered tufts of tubules and of a large pair of nephridia; the arrangement being, in fact, much like that of Megascolides. The calibre of the large nephridia was many times greater than that of the small tufts, or about equal to that of the nephridia of such types as Lumbricus. Each of these large nephridia is furnished with a large ciliated funnel, which lies in the segment in front. I have been quite unable to detect the external apertures of the nephridia of these posterior segments.

The tufts of smaller tubules were not in all cases (if in any) detached from the large nephridia; their apparent distinctness, when seen in a dissection of the worm, is due to the fact that they are for the most part embedded in the centre of a mass of peritoneal cells. These peritoneal cells, which form aggregations round certain parts of the nephridia, are exactly like those which surround the nephridia of Pontodrilus, as well as of Phreoryctes. Perrier was the first who drew attention (23) to the resemblances in this particular between the nephridia of Pontodrilus and those of the "Limicolæ;" and Dichogaster is another instance of an Earthworm which so far approximates in the characters of its nephridia to the "Limicolæ."

III. Further Remarks on the Nephridia of Earthworms.

The Nephridia of Perichæta aspergillum.—With regard to the nephridia of Perichæta aspergillum, I am able to make some additions to my former papers upon this genus (1). The most important point which I was then able to prove is that the nephridiopores, instead of being present to the number of only one pair in each segment, are extremely numerous. I stated (1, p. 401) that there were often four or five nephridiopores lying between two setæ, making, therefore, a total of from one to two hundred in each segment. I have figured and described these nephridiopores as forming a continuous row round the middle of each segment. After discovering that in Dichogaster the nephridiopores are not limited to the spaces between the setæ of a segment (v. suprà, p. 259), I carefully re-examined Perichæta aspergillum with reference to this point; the result of this re-examination is to show that P. aspergillum resembles Dichogaster. The nephridiopores are scattered irregularly over every part of the body, and are not by any means confined to the area lying between the setæ of a given segment.

Ciliated Funnels.—Another fact of some little importance which I am able to add to my former paper upon Perichæta, is the description of ciliated funnels. In the posterior region of the body the funnels were extremely obvious although small; the small size of the ciliated funnel corresponds to the small calibre of the excretory tubules. These structures were obvious, for the reason that, as a general rule but by no means always, they are borne at the extremity of a very straight tubule (fig. 10). The structure of the funnels is illustrated in fig. 10. There is nothing specially remarkable about them except their small size. The presence of ciliated funnels has been already described in the genus Perichæta by Rosa (26), who found in P. armata a pair of ciliated funnels in every segment. Dr. Benham informs me that he has noticed in a species of Perichæta from the Philippines numerous funnels in each segment, corresponding to the numerous nephridia, which he has already briefly referred to (9, No. 1, p. 256) as existing in that species (which has apparently not yet been identified).

In P. aspergillum I have satisfied myself that there are a number of funnels in each segment; this, however, only applies to the segments behind the clitellum. In the anterior segments, the nephridia of which alone were described in my former paper, I am still unable, after a renewed search, to discover any evidence of the presence of ciliated funnels.

It has been stated that the ciliated funnels are of small size, but they are not all of the same size; some (fig. 10 *a*) are distinctly larger than others (fig. 10 *b*). I shall have occasion to point out directly that the nephridial tubules of these posterior segments are partly of greater calibre than those of the anterior segments; it is possible in the posterior segments to distinguish these wider tubules from the minute tubules which resemble those of the anterior segments. This accounts for the difference in size between the funnels. The larger funnels are connected with the larger tubules. It occasionally happens that the larger funnels are borne upon tubules, which immediately perforate the septum and join the nephridial tufts of the segment behind.

Comparison of the Nephridia of the Anterior with those of the Posterior Segments.

In my paper already quoted upon the nephridia of Perichæta aspergillum I have described the perforation of the intersegmental septa by tubules which connect the nephridial systems of adjacent segments. In some of the anterior segments of this Perichæta, particularly those which contain the spermathecæ, the nephridial system consists of an enormous mass of tubules which almost completely fills the available part of the cœlom. So closely are the excretory tubules packed that I have found it impossible to distinguish a series of separate nephridia corresponding to the numerous external pores. This fact, together with the perforation of the septum by tubules, led me to the impression that there must be in this region of the body a continuous nephridial network independent of the segments.

It occurred to me while making these observations, and it has occurred to me lately after discovering the ciliated funnels of P. aspergillum, that the supposed connection between the nephridial system of two adjacent segments might be really nothing more than the normal perforation of the septa by tubules, terminating on the anterior side of the septum in ciliated funnels.

This supposition, however, appears to be negatived by the following considerations: In the first place I succeeded in many cases in tracing a given tubule through the septum until it became lost in the excretory mass of the segment in front. Secondly, in the posterior region of the body the ciliated funnels are usually not borne upon the anterior face of the mesenteries in the way that is so general among Earthworms, though this sometimes happens. In most cases the long straight tube bearing the funnels rises up from a tuft of tubules, and does not perforate the septum, but ends in the same segment. Thirdly, it occasionally happens, both in the anterior and in the posterior region of the body, that a mesentery was perforated at one spot by a number of tubules running close together in irregular windings. Such masses of nephridial tubules did not pass between the individual muscular fibres of the septum, but the continuity of the tissues of the septum was broken at the point where they traversed it. A conspicuous gap was thus formed, which was entirely occupied by the nephridial tubules and peritoneal cells coating them. In these cases it appeared to me that the bundle of tubules passing through the septum was not formed by the coils of a single tube, but that it really represents a number of separate tubes running side by side. On the assumption that the perforation of the intersegmental septa by nephridial tubes is not evidence of an intercommunication of the nephridia of successive segments, one would have expected to find a number of funnels dependent from the septum at this point. I could not, however, detect these structures, and in the posterior region of the body, as already stated, the funnels are rarely attached to the septa.

The probability of my statements being correct is also largely increased by the discovery of Professor Spencer (28), that in Megascolides australis there is a continuous network of nephridial tubules uninterrupted by the septa.

The observation of the nephridial tubules within the thickness of the septum is not always easy. In some cases, however, they are accompanied by a tolerably thick coating of peritoneal cells, when they can be readily detected. I have found that in the anterior region of the body it is easier to trace the tubules from segment to segment in transverse sections. In the case of the larger tubules of the posterior segments the branches connecting the tufts of adjacent segments are not difficult to make out.

In the posterior region of the body the nephridia are not so well developed as they are anteriorly. The nephridial tubules are, however, much like those of the anterior segments (unless there are really no funnels in the anterior segments), but they are closely attached to the body wall, and particularly to the septa. They do not occupy a large portion of the body-cavity. I have ascertained by sections, as well as by an examination of stripped-off pieces of cuticle, that the nephridiopores have the same irregular distribution that they have in the anterior segments. Furthermore, there is, as has been mentioned, an intercommunication between the nephridial tufts of successive segments. I have observed frequently a connection, by tubules traversing the septum, between two nephridia adherent to opposite sides of the same septum. At the same time it appears to be certain that in the nephridia of these segments there is no longer an intimate connection between all the nephridial tubules of the same segment. An examination of a series of sections shows that there are tufts of tubules which are quite isolated from neighbouring tufts. On the other hand, there is—as has just been said—frequently no break between nephridial tufts of adjacent segments. These facts appear to me to be of some importance with regard to the views which I have elsewhere (1) advanced as to the origin of the Oligochæt excretory system. We have here, as it appears to me, a commencing separation of the continuous excretory network into isolated nephridia. This breaking up has at first no relation to the segmentation of the body. The nephridial tufts have no regular arrangement within the segment, and their apertures are dotted about irregularly over its surface, and the separation into separate nephridia does not follow the lines of the intersegmental septa. The excretory system, in fact, appears to retain, longer than many other organs of the body, traces of the primitive unsegmental condition.

For the most part the nephridia of the posterior segments have the same appearance as those of the anterior segments, that is to say, they consist of tufts of tubules having an excessively fine bore. There are, however, tubules of greater calibre which appear to be wanting in the anterior segments. In this particular there is a resemblance between P. aspergillum and Megascolides (Spencer). In that genus the posterior segments of the body contain nephridial tubules which are much larger than others in the same segments, and than all in the anterior segments of the body. There is also the further resemblance that the tufts of larger tubules are connected with funnels which project into the segment in front. In Perichæta, however, the smaller nephridial tufts also possess funnels, which they apparently do not in Megascolides. Until the publication of Professor Spencer's illustrated account of Megascolides it is impossible to say how far this resemblance in the specialisation of the nephridia goes. The difference in size is not very marked in P. aspergillum, not nearly so much so as in P. armata.

In my paper upon Perichæta aspergillum I have not figured the cuticular pores of the nephridia, and so I have thought it worth while to introduce into the present paper illustrations of their structures. Fig. 23 of Plate XXIV represents a portion of the cuticle of P. aspergillum, showing the cuticular ingrowths which surround the proximal region of the seta (*a*), and the very delicate cuticular tube (*b*) which lines the extremity of the duct of the nephridium. When these structures are viewed from above the aperture, whether of the seta or of the nephridium, they appear to be surrounded by a thickened layer of the cuticular membrane. This is, I believe, only an optical effect due to the inturned edges of the cuticle. It seems, however, to define very plainly the orifice. The very great size of the seta orifice, as compared with that of the nephridiopore, will be evident from an examination of the figure cited. The cuticular pore of the nephridium is further remarkable for the fact that its edges are usually much crinkled, which is probably due to the contraction of the epidermic cells by the preservative reagent. The cuticular pores which lead into the seta sacs never show these crinkled edges, probably for the reason that they remain distended by the seta.

Having ascertained that these cuticular pores belong to the nephridial system, I have examined the cuticle of another species of Perichæta of which I possess examples not sufficiently well preserved to show the modifications of the epidermal cells round the nephridiopore. I find that they are present in Perichæta Houlleti, and I consider myself therefore at liberty to infer that in this species (and, indeed, probably in all Perichæta in which the nephridia have a "tufted" character) the structure of the nephridial system is much the same as that of P. aspergillum.

In Acanthodrilus and Dichogaster the external orifices of the nephridial system are larger than those of Perichæta and (judging from Spencer's description) of Megascolides;

their greater size renders them very plainly visible in transverse and longitudinal sections of the body wall and upon fragments of the cuticle. The cells surrounding the orifice are tall, thin cells, not bulged like those of Perichæta and Megascolides.

The Nephridia of Perichæta armata (F. E. B.).—I owe the material, upon the study of which the present description is based, to the kindness of Mr. W. L. Sclater, of the Indian Museum, Calcutta.

The species was first described by myself, and has been recently in some respects more fully characterised by Rosa (26).

There is, however, one point in which Rosa's description differs from my own. I stated that the nephridia, at least in the anterior region of the body, consisted of numerous tufts of tubules, resembling in this particular the nephridia of the greater number of species of Perichæta. The characters of the nephridia in the specimens examined by me was such that I should have presumed—in the light of my own subsequent investigations—that the number of nephridiopores in each segment would be greater than two.

On the contrary, Rosa's description of those organs shows that he considers them to be like those of Lumbricus, i. e. a single pair to each segment. He describes, and I can confirm the accuracy of his description, the presence in each segment of a pair of coiled nephridia, each of which opens into the segment in front by a ciliated funnel. Rosa was unable to find the external pores. So far I can fully bear out the statements made by Rosa; but this description of the nephridial system of P. armata is not exhaustive. It consists also of numerous tufts of minute tubules which are scattered about irregularly in the segments. These tubules are not obvious on a dissection of the worm, but they are quite easily seen in transverse sections.

The nephridial system of Perichæta armata differs in important particulars from the nephridial system of any species of Perichæta; it differs from that of P. aspergillum (see p. 265) and an undescribed species briefly referred to by

Benham (9, No. 1) in the presence in each segment of a pair of large nephridia, opening by a funnel into the segment in front, in addition to the tufts of minute tubules present in these types. In one or two species from Australia, described by Mr. Fletcher (16), only the large pair of nephridia are present. The minute tufts of tubules are unrepresented.

There is, however, a close resemblance between the nephridia of P. armata and those of Megascolides australis, which have been briefly described in a note published in 'Nature' of June 28th, 1888, by Professor Baldwin Spencer. I have not yet had the opportunity of seeing Professor Spencer's detailed memoir upon this most interesting genus of Earthworms, but the note referred to is an abstract of the more important results of his investigation of the nephridial system.

It appears that in the anterior segments of Megascolides there are abundant scattered tufts of minute nephridial tubules, which are connected by a network lying within the peritoneum and extending from segment to segment. In the posterior segments of the body there are in addition a pair of coiled nephridial tubes of a very much greater calibre than the minute tubules. Each of these opens by a funnel into the segment in front, and they are connected by a continuous longitudinal duct which runs from segment to segment. These larger nephridia, as well as the longitudinal duct, are also in connection with the system of minute tubules; the latter have no ciliated funnels but open externally by numerous pores.

In P. armata I have not actually traced the nephridial tubules through the body wall to their point of opening on to the exterior. I have, however, found upon the cuticle the nephridiopores, which were abundant in each segment, and agreed in all particulars with those of P. aspergillum (see p. 265), so that I cannot admit any doubt as to the resemblance in this particular between the nephridia of P. armata and those of P. aspergillum. I have also been unable to detect any ciliated funnels except those belonging to the large pair of nephridia. In all these points, therefore, there is an agreement with Megascolides. But the nephridial tufts of P. armata appear to be at any rate largely isolated from each other and from the pair of large nephridia; and I have not found a longitudinal duct passing from the large nephridia of successive segments and connecting them. Neither can I discover evidence of any nephridial network uniting the tufts of minute tubules of successive segments. In all these points the nephridia of P. armata are different from those of Megascolides. I shall refer again to the nephridia of P. armata and to Professor Spencer's description of Megascolides (see below.

Comparison of the Nephridia of Perichæta, Megascolides, Acanthodrilus multiporus, Deinodrilus, Dichogaster.

Before attempting to draw any conclusions as to the path of development of the excretory system in Earthworms, it will be convenient to briefly review the facts already known concerning the nephridia of those genera in which there is a greater or less development of a network with numerous external pores in each segment.

It appears to be possible to separate those genera into two groups: the first group contains Perichæta and Megascolides; the second, the remaining genera enumerated above. I am at present uncertain as to the relations of Typhæus, which has not yet been properly investigated.

The principal character which distinguishes the nephridia of these two groups is the size of the tubules.

In Perichæta, and apparently also in Megascolides, the greater part of the nephridial system (the whole of it in the anterior segments of the body) is made of tubules having an excessively fine lumen; the entire diameter of the tubules is not inconsiderable, but the perforation of the cells which form the duct is much less than the thickness of its walls. Besides the network of fine tubules, both these genera possess coils of tubules of a much greater diameter which are more or less closely connected with the network of fine tubules; that is to say, they form a more or less independent nephridium opening internally in Megascolides and Perichæta armata by a single funnel.

In Deinodrilus, Acanthodrilus, and Dichogaster, the general nephridial network is made up of tubules, the lumen of which is greater than in Perichæta; the diameter of the cells is not greater, but the lumen occupies a greater proportion of the cell. These tubules resemble in fact very closely the finer portion of the nephridium of Lumbricus. In Deinodrilus (at any rate in those segments of the body which I have investigated—some of the more posterior ones) the nephridial network appears to be entirely made up of tubules of this kind. In the other two genera, however, part of the nephridial network is composed of tubules of a much greater calibre, equal in size to the larger tubules of P. armata, or of such Earthworms (e. g. Allurus, Pontodrilus, Eudrilus, Acanthodrilus novæ-zealandiæ) as possess but a single pair of nephridia in each segment of the body. In Acanthodrilus multiporus the larger tubules are not independent of the smaller tubules, and the network opens into the cœlom by numerous funnels, as in Perichæta aspergillum. In Dichogaster, in the anterior segments, this specialisation of the network is not seen; in the posterior segments, on the other hand, there is not much beyond the coil of large nephridial tubules, which have to a great extent the characters of a single nephridium, such as that of Lumbricus, &c., and open into the cœlom by a single funnel borne at the end of a duct which traverses the intersegmental septum.

We have therefore a parallel series in the nephridia of these two groups which may be expressed in the following Table:

A. Nephridia forming a network, consisting of excessively fine canals, continuous from segment to segment.	B. Nephridia forming a network consisting of wider canals, discontinuous at the septa.
(1) ?	(1) No further specialisation. Deinodrilus.[1]
(2) Nephridial network of posterior segments, partly composed of tubules of greater calibre. Numerous cœlomic funnels. Perichæta aspergillum.	(2) Nephridial network, partly composed of tubules of greater calibre. Numerous cœlomic funnels. Acanthodrilus multiporus.
(3) Larger nephridial tubules increased in size and forming a nephridium nearly independent of the finer tubes, and opening by a single cœlomic funnel. P. armata, Megascolides.	(3) Nephridial network of posterior segments, chiefly composed of larger tubules, opening by a single cœlomic funnel. Dichogaster.

The nephridia of Acanthodrilus multiporus, of Dichogaster, and of Deinodrilus, are formed of tubules which, as said, are on the whole of greater calibre than those of Perichæta. The measurements may be approximately determined by a comparison of figs. 11–14. At the same time the nephridia of these types present other differences from Perichæta. The network is much reduced in extent and in two ways. First, only a limited area of each segment is occupied by the nephridia. They are by no means so abundantly developed as in Perichæta, not nearly so abundantly developed as in the anterior segments of Perichæta aspergillum. Secondly, the intercommunication from segment to segment has disappeared in Acanthodrilus and Dichogaster, and has almost disappeared in Deinodrilus. In the last-mentioned genus the nephridia are attached to the anterior wall of their segment, and are, for the most part, entirely restricted to this situation. In one or two instances, however, a small tuft of tubules was attached to the posterior wall of a segment; and in these cases (which are not at all

[1] The apparent absence of cœlomic funnels in this genus may perhaps be a secondary modification.

numerous) the tuft of tubules attached to the posterior wall was in communication through the septum with the nephridium of the segment behind. This seems to me to indicate that the nephridial system of Deinodrilus is in a more archaic condition than that of either Acanthodrilus or Dichogaster. In Deinodrilus the primitive disposition of the excretory system of Perichæta has been so far retained that there is still an intersegmental communication here and there. The metameric arrangement of the nephridial system is not so complete as in Acanthodrilus and Dichogaster, though, for the matter of that, neither of these forms have an excretory system perfectly metameric in its disposition.

Another point of difference between the excretory system of Perichæta on the one hand, and that of Acanthodrilus, Deinodrilus, and Dichogaster, is in the form of the external orifices.

Professor Spencer (28) described the external orifices of the nephridia of Megascolides in the following words: "The external opening itself is formed of cells of the epidermis, so modified as to present very much the external appearance of a taste-bulb; that is, they form a sphere with the cells thicker in their middle parts, and the two ends attached to the poles of the sphere, the duct passing right up through the centre."

This description applies very closely to the modified epidermic cells which surround the nephridiopores of Perichæta. When I first observed these cells in Perichæta I thought for a moment that they really belonged to sense organs. The cells are so much swollen in their middle parts that the duct which forms up between them is of an excessively fine bore; for this reason it is not always easy to detect upon fragments of the cuticle the actual orifice.

The Evolution of the Excretory Organs in Earthworms.

I shall now proceed to deduce, from the facts described in the present paper and in Professor Spencer's account of Megascolides, what I believe to have been the course of development of the nephridial system of Earthworms.

In my paper upon Perichæta (1) I pointed out that the facts therein described were in favour of the assumption that the presence of a single pair of nephridia per segment (e. g. in Lumbricus) was the last stage of a reduction of an excretory system like that of Perichæta; and that the excretory system of Perichæta was distinctly comparable to that of the Platyhelminths. With regard to the first point, Professor Spencer's observations are, as he has pointed out, decidedly confirmatory of that view. Indeed, the nephridial system of Megascolides appears to me to be hardly intelligible on the hypothesis that Lumbricus represents the primitive condition.

Dr. Hugo Eisig's magnificent monograph of the Capitellidæ (15), which has just been published, contains a very detailed discussion of the nephridial question. It must be confessed that the structure of the nephridia in the Capitellidæ might be equally well explained on the hypothesis that the ancestral condition of the Annelid nephridial system is represented by a pair of distinct nephridia in each segment. And this is the position which Dr. Eisig takes up. The branching, whether of the distal or proximal end of the nephridium, and the connection between nephridia of the same segment, as well as the multiplication of the latter, he regards as secondary. It appears to me that this position may be safely yielded without affecting the strength of the converse view which is maintained in the present paper. I believe it to be unnecessary to assume that the Oligochæta and the Polychæta have been derived from the same Annelid stock: I hold that the ancestral form from which they diverged was intermediate between the Platyhelminths and Annelids. There is no difficulty in drawing a sharp line of division between the Oligochæta and the Polychæta. The peculiarities of the reproductive system will be the basis of this distinction. The investigations of Korschelt, Meyer, and Weldon upon Dinophilus have gone a long way towards demonstrating that this worm stands at the base of the Polychæt series. Now, the nephridia of Dinophilus are in their minute structure comparable to those of the Platyhelminths; in most species they form a single pair of branched organs terminating in numerous "flame-cells." In D. gyrociliatus, according to Meyer, each single nephridium is broken up into a series metamerically arranged, and each opening by a separate external pore. This I believe to be the way in which the Polychæt nephridia have arisen.

There is no known form which seems to me to represent an intermediate stage between the Oligochæta and the Platyhelminths. On the whole, it must be admitted that certain of the aquatic Oligochæta, such as the Naidomorpha, stand at the base of the Oligochæt series. The fact that the nephridia of these Annelids are paired is a difficulty in regarding Perichæta as representing in the structure of its nephridia an ancestral form. It must be remembered, however, that our knowledge of the aquatic Oligochæta, though no doubt fairly advanced as regards indigenous forms, is very small as regards exotic genera. Also there are traces (in Anachæta, Vejdovsky (29) (Pl. VII, fig. 14) of what I believe to be the primitive condition. It may be that the (presumed) reduction of the nephridia in these aquatic forms has some relation to their small size, and, in consequence, to the reduced size of the cœlomic cavities.

It will be of no advantage to endeavour to combat Dr. Eisig's arguments against regarding the nephridia of Acanthodrilus multiporus as representing an archaic condition, principally for the reason that at the time when he wrote he was able to say that only one or two genera exhibited the dysmetameric condition, the vast majority having a metameric condition of the nephridia.

We are now, however, acquainted with the following genera in which the nephridia are often or always dysmetameric :— Perichæta, Acanthodrilus, Typhæus, Deinodrilus, Dichogaster, Megascolex (?), Megascolides, Notoscolex, while traces of the same are to be seen in Urochæta. The argument of the rarity of the occurrence of the dysmetameric nephridia cannot any longer have any weight, and his detailed criticisms, though powerful at the time, are now, through the progress of discovery, of less weight. His other arguments depend chiefly upon the fact that this condition is only found among the Polychæta in the Capitellidæ. Regarding, as he does, the Capitellidæ as nearly akin to the Oligochæta, and in fact forming the intermediate link between them and the Polychæta, this argument is a powerful one. I find myself, however, unable to accept this position. The peculiarities of the reproductive system in the Oligochæta, coupled with the entire absence of parapodia and external gills, distinguish them from the Polychæta. Dr. Eisig compares the peculiar modification of the integument which surrounds the genital pores with the clitellum of the Oligochæta. I would myself rather compare it with the modified integument which surrounds the aperture of the vas deferens in Allurus and Allolobophora; but I do not think that the possibility of this comparison is necessarily a mark of near affinity. The comparison between the nephridia of the Capitellidæ and those of Acanthodrilus does not really show a very close resemblance; the structure of these organs is so peculiar, as Eisig has shown, that it renders a detailed comparison difficult, as does also the fact that they are often preceded by a provisional set. Indeed, I cannot help agreeing with Dr. Eisig that their modifications in the Capitellidæ are secondary, though I would maintain that this is not the case with Urochæta, Acanthodrilus, &c.

The nearest approach to the primitive condition of the excretory system in the Oligochæta is, in my opinion, seen in Perichæta aspergillum; in the anterior segments the resemblance to the Platyhelminth excretory system is closest. There is here a continuous network of tubules, with numerous external pores. The network is not interrupted by the septa, and the external pores are not in any way related to the segmentation of the body. If funnels are really absent, as appears to be the case, then the termination of the tubules in single cells will be an additional point of resemblance to the Platyhelminths; if, on the contrary, funnels are really present, they must be small and inconspicuous and not much advanced beyond the single flame-cell.[1]

In the posterior segments part of the nephridial network consists of tubules of a greater calibre, and these, as well as the smaller tubules (which are exactly similar to those of the anterior segments), are provided with funnels. The external apertures are still extremely numerous, and irregularly distributed over the surface of the body. The network of tubules is beginning to break up into more or less isolated tufts; but the separation of the continuous network into isolated nephridia has no discernible relation to the segmentation; the tufts of tubules have no regular arrangement within the segment, and the septa do not as yet form barriers between the excretory tubes of different segments.

In the posterior segments, therefore, the primitive characters of the nephridial system are just beginning to disappear. If the posterior segments resembled the anterior segments the nephridial system of P. aspergillum would exhibit the presumed ancestral condition.

From this point the modification of the excretory system has, as I think, proceeded along two slightly divergent paths; the ultimate point reached, however—the reduction of the nephridial system to a pair of isolated nephridia in each segment—is the same in both cases. The facts known appear to

[1] I have already (1) discussed the "funnel" of the Annelid nephridium and its relation to the Platyhelminth flame-cell. Since that paper was written Vejdovsky has published ('Zool. Anzeiger,' Bd. x) an account of the nephridia of certain Oligochæta. The "provisional" nephridia, which are preceded at the anterior extremity of the body by a "larval" set, terminate in a flame-cell. These nephridia entirely disappear in the first two or three segments; behind this they become converted into the permanent nephridia; the flame-cell divides and gives rise to a funnel.

me to necessitate this view of the gradual reduction of the excretory system; it is difficult to harmonise the facts with the hypothesis of one continuous line of development.

It is obvious that any theory of the development of the nephridia must allow for the reduction of the nephridial network in Perichæta aspergillum to a single pair of nephridia, such as is found in P. novæ-zealandiæ,[1] and also in the genus Perionyx, which is in all respects a very near ally of Perichæta; and this reduction must not involve the various stages represented by Deinodrilus, Acanthodrilus, and Dichogaster, though these are intermediate between P. aspergillum and P. novæ-zealandiæ.

The intermediate stage between P. aspergillum and P. novæ-zealandiæ is represented by P. armata. In this Perichæta the nephridia of the posterior segment are, as Spencer pointed out in the case of Megascolides, separable into two categories; firstly, there are the tufts of minute tubules; secondly, a pair of convoluted nephridial tubes, with a ciliated funnel borne upon the extremity of a tube which has traversed the septum, and lying in the segment anterior to that which contains the nephridium; these latter are of the same calibre as the nephridia of P. novæ-zealandiæ, and indeed of most Earthworms in which there is but a single pair of nephridia per segment. I believe that these have originated from the somewhat larger nephridial tubules of such a form as P. aspergillum; the minute nephridia form tufts which are largely, if not entirely, isolated from each other and from the large nephridia; they are comparatively inconspicuous, and seem to be in course of disappearance. Megascolides offers an analogous stage in the development of a single pair of nephridia out of the nephridial network. I quite agree with Spencer that the single pair of nephridia of certain Earthworms (e.g. Perichæta novæ-zealandiæ and Perionyx) have arisen by a gradual increase in

[1] This is an apparently new species of Perichæta, which I hope to describe shortly; it possesses a single pair of nephridia per somite, as in Lumbricus.

calibre of a part of the nephridial network in each segment to form a pair of nephridia, and by the gradual disappearance of the rest.

The second way in which I conceive the gradual reduction of the network to a single pair of nephridia to have been brought about is as follows:

The network became arranged metamerically by the isolation of the networks of successive segments at the septa; at the same time the tubules themselves acquired a greater calibre. This stage is nearly reached in Deinodrilus, where the nephridial system forms a continuous series of tufts attached to the anterior wall of each segment; but here and there in Deinodrilus the nephridia are connected through the septa with feebly-developed tufts of tubules lying on the posterior side of the segment in front.

In Acanthodrilus multiporus this stage is exemplified; all trace of the intercommunication between the nephridial systems of successive segments through the septa is lost, and the tubules are uniformly of greater calibre than those of Perichæta; at the same time they are more decidedly related to the setæ of their segments. From this point the paired nephridia of other species of Earthworms have been derived either by a great increase in the calibre of the tubules coupled with the disappearance of part of the network and all the external orifices, except a pair to each segment (Dichogaster seems to be a stage further advanced than Acanthodrilus in the direction of those worms with a single pair of nephridia in each segment),[1] or by the breaking up of the network into separate nephridia. Brachydrilus (Benham, **10**) offers an intermediate condition in this reduction; the nephridial network has been broken up so as to form two separate pairs of nephridia in each segment. One pair then disappears, and the typical condition of the Earthworm excretory system is arrived at.

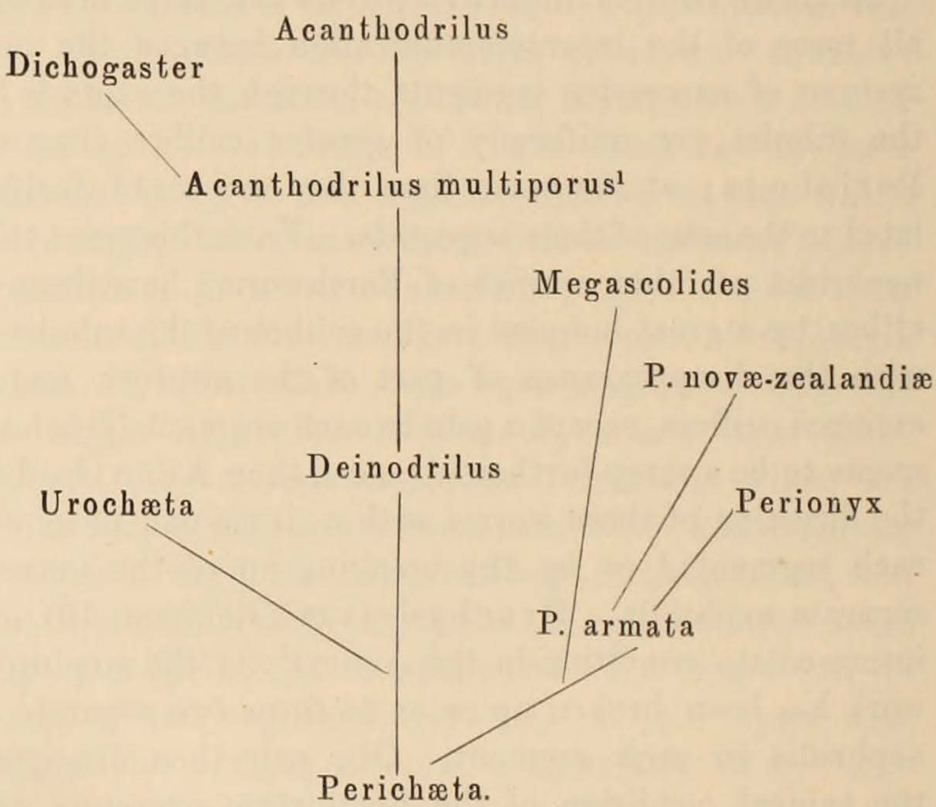
I am disposed therefore to believe that the paired

[1] I have elsewhere (8) called attention to other points in which Deinodrilus is intermediate between Perichæta and Acanthodrilus.

nephridia of certain other Earthworms (e.g. Acanthodrilus novæ-zealandiæ) have been derived through the gradual increase in calibre of the tubules forming the primitive network, which has become isolated into metamerically disposed tufts of tubules, corresponding more or less to the setæ; these separate nephridia have become ultimately reduced to a pair in each segment.

In the first case, therefore, the single pair of nephridia have been derived directly from a part of the primitive network; in the second case the primitive network has become converted into a single pair of nephridia in each segment by a more gradual series of changes.

The annexed scheme shows the relationship between certain genera of Earthworms, as indicated by their excretory system.



This scheme, as will be seen, only refers to the genera which

[1] It is possible that this species is really a distinct generic type. It has no paired setæ like the other species of the genus. If so, A. annectens (Beddard, 8) should probably be referred to the same genus.

have been specially treated of in the present paper. I do not feel able at present to extend the diagram so as to embrace all the known genera, or even the greater number.

I would point out, however, that the above scheme, though meant only to express the probable course of the development of the excretory system, does not do violence to the relationships in other structural characters between the different genera.

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EXPLANATION OF PLATES XXIII & XXIV,

Illustrating Mr. Frank E. Beddard's paper "On Certain Points in the Structure of Urochæta, E. P., and Dichogaster, n. g., with further Remarks on the Nephridia of Earthworms."

PLATE XXIII.

Fig. 1.—Semi-diagrammatic longitudinal section through anterior extremity of Urochæta corethrura. The aperture of the mucous gland at *o* is correctly drawn as regards its position relative to the setæ, but it should be more ventral in position. *n.* Ventral nerve-cord. *f.* Funnels of mucous gland (3). *g.* Gizzard. *s.* Setæ. *c.* Supra-œsophageal ganglion. *al.* Cavity of anterior end of the alimentary tract.

Fig. 2.—Longitudinal section through genital segments of the same species. The vesiculæ seminales are not represented. *t.* Testis. *o.* Ovary. *ov.* Oviduct pore. *v. d.* Vas deferens. The segments are numbered.

Figs. 3 and 4.—Contents of genital glands of the same specimen. Both testes and ovaries have produced ova in this individual.

Fig. 5.—A funnel of the mucous gland of Urochæta.

Fig. 6.—Transverse section through body wall of Dichogaster Damonis. *e.* Epidermis. *m.* Circular muscles. *l.* Longitudinal muscles. *p.* Peritoneum.

Fig. 7.—Dichogaster. Segments in the neighbourhood of the male reproductive pores. *v. d.* Vasa deferentia. *pr.* Atria. *pr'.* Glands in 18th and 19th segments, similar in structure to the atria, but unconnected with the vasa deferentia.

Fig. 8.—Dichogaster. Ventral external view of segments in the neighbourhood of the male reproductive pores, to show pores upon the 17th, 18th, and 19th segments.

Fig. 9.—Fragment of nephridium of ditto, with glandular peritoneal cells (*a*).

Fig. 10.—Perichæta aspergillum. Nephridial funnels, *a* smaller, *b* larger. In *a* one of the two funnels, that to the right, is seen in longitudinal section.

Fig. 11.—Perichæta armata. Large nephridia of posterior segments. *a.* From a glycerine preparation, which showed very clearly the boundaries between the successive "drain-pipe" cells.

PLATE XXIV.

FIG. 12.—Perichæta aspergillum. Nephridial tube. *a*, with larger, *b*, with smaller lumen.

FIG. 13.—Deinodrilus Benhami. Nephridial tubes from posterior segment.

FIG. 14.—Acanthodrilus multiporus. Nephridial tubes. *a*, with small lumen; *b*, with wider lumen; *c*, represents the greatest size to which the nephridial tubes of this species reach.

Figs. 11—14 are all carefully drawn to scale with camera lucida.

FIG. 15.—Dichogaster. General view of genital segments dissected. The upper wall of the seminal reservoirs is removed on the left side to show the funnels and testes. *r*. Seminal reservoirs. *r'*. Seminal reservoirs of a racemose appearance. *t*. Testes. *f*. Funnel of vasa deferentia. *o*. Ovary. *od*. Oviduct.

FIG. 16.—Transverse section of body of the same worm at the line of the atria (*pr*.). *v. d*. Vasa deferentia joining the muscular portion of atria.

FIG. 17.—Corresponding section through nineteenth segment. *pr'*. Glandular body.

FIG. 18.—Spermatheca with appendix, *a*.

FIG. 19.—Transverse section through wall of spermatheca.

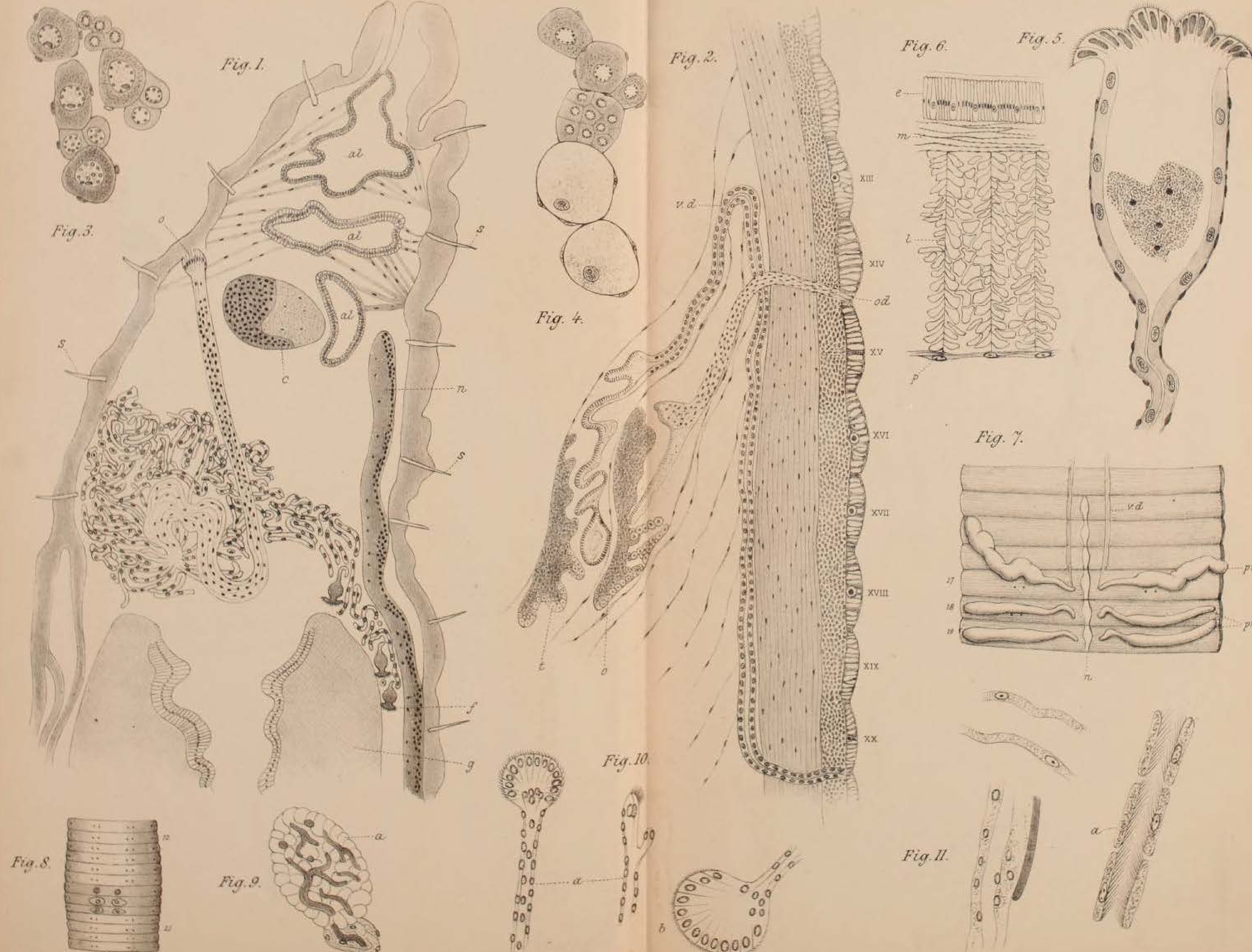
FIG. 20.—Transverse section through appendix of spermatheca.

FIG. 21.—Anterior region of alimentary canal, to show two gizzards, *g*., and calciferous glands, *Ca*.

FIG. 22.—Ova of different species of Oligochæta, to illustrate their relative sizes. Drawn to scale. *a*. Of Urochæta corethrura, from cœlom. *a'*. Largest ova from ovary. *b*. Of Phreoryctes Smithii, from ovary. *c*. Of Allurus. *c*. From receptaculum ovorum. *c'*. From ovary. *d*. Of Eudrilus, from ovary. *e*. Of Acanthodrilus, from ovary.

FIG. 23.—Fragment of cuticle of Perichæta aspergillum. *a*. Orifices of setæ. *b*. Nephridiopores.

FIG. 24.—Perichæta aspergillum. Diagram to illustrate nephridia of posterior segments. *o*. Nephridiopore. *f*. Funnel.



F. E. Beddard del.

F Huth, Lith^{r} Edin^{r}

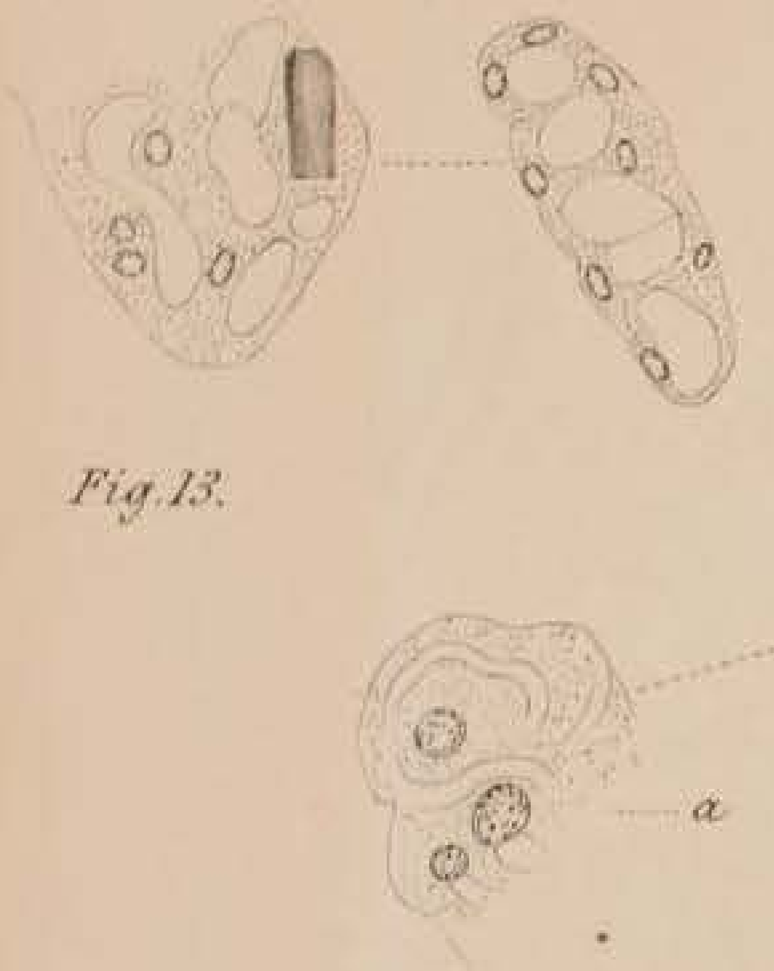


Fig. 13.

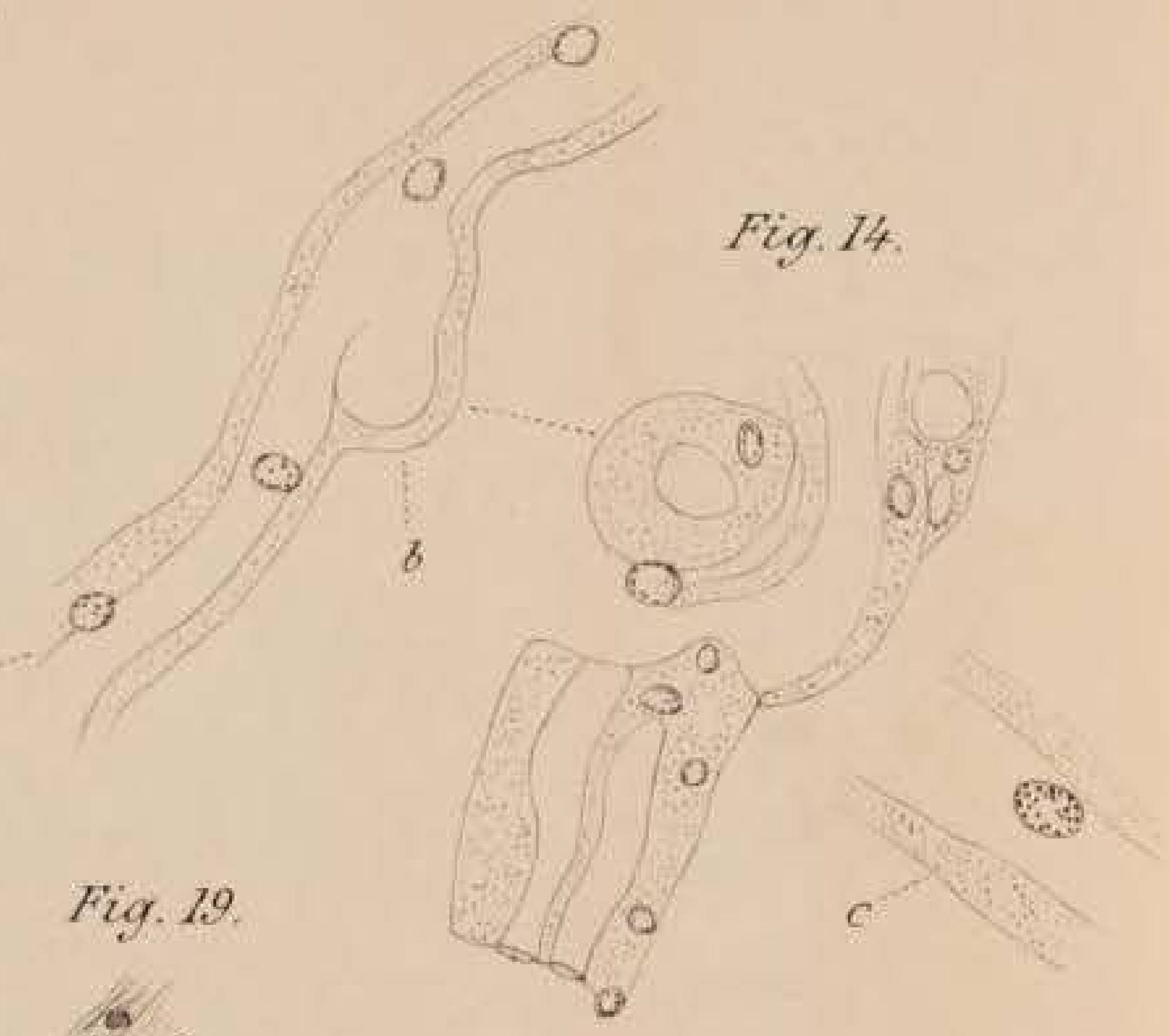
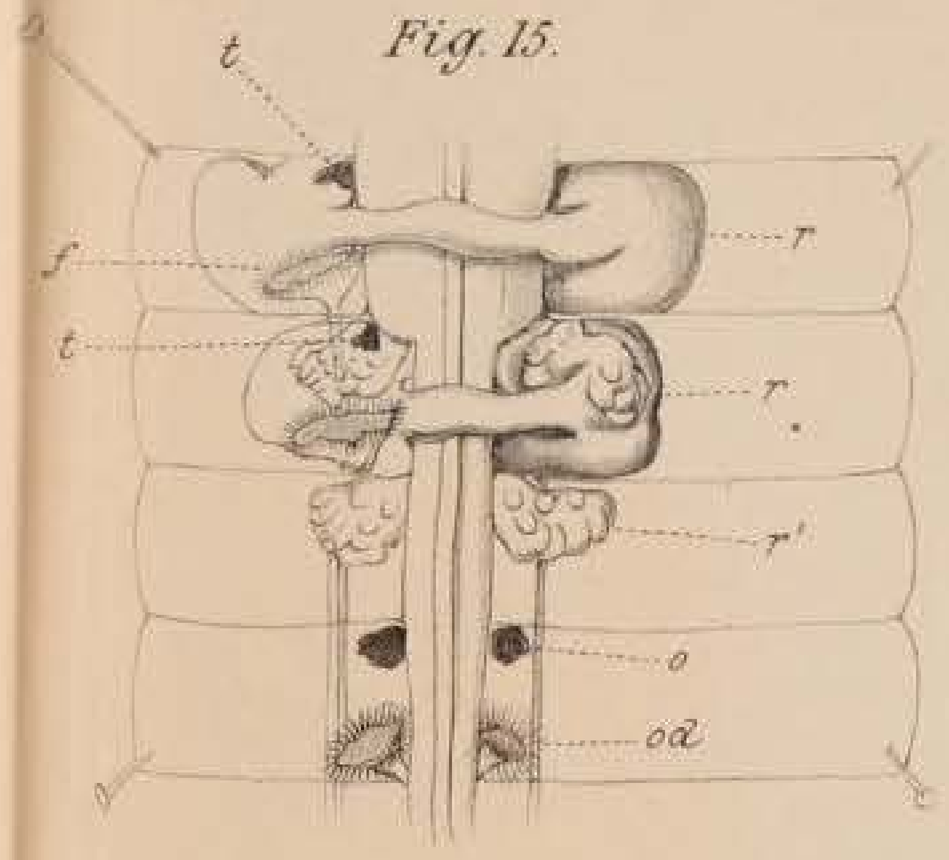


Fig. 14.



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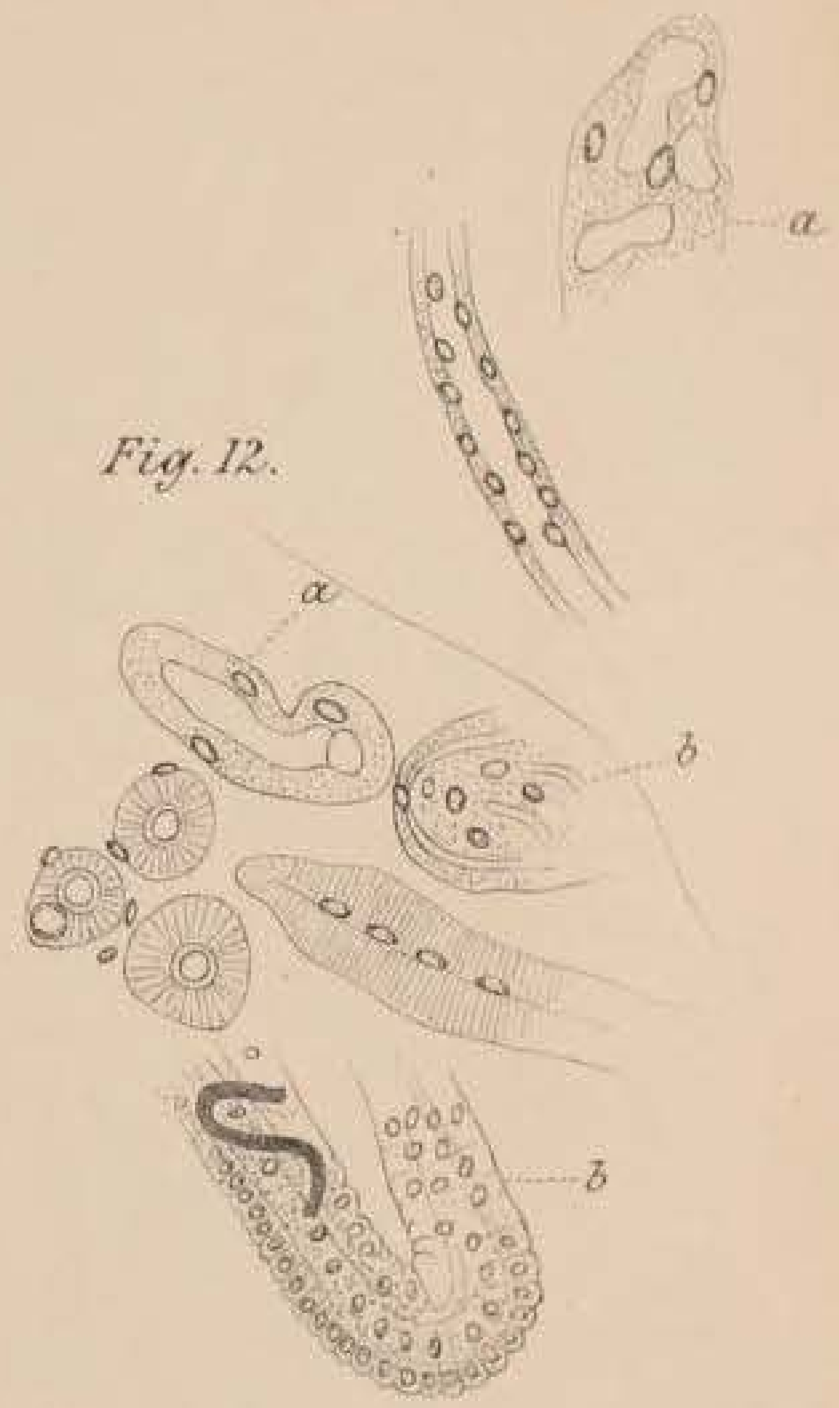

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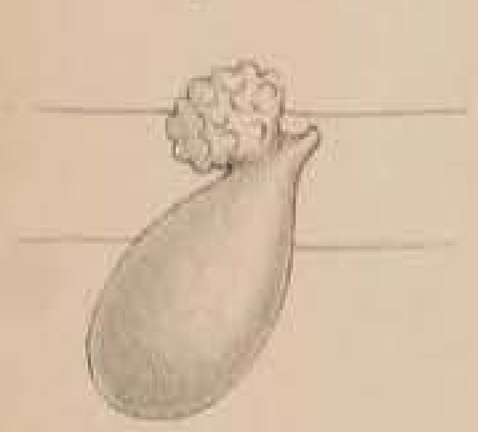

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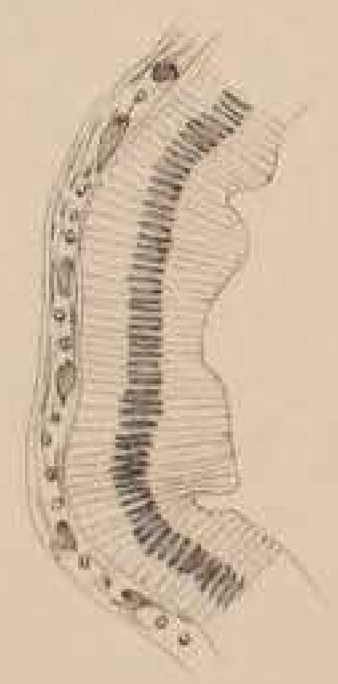

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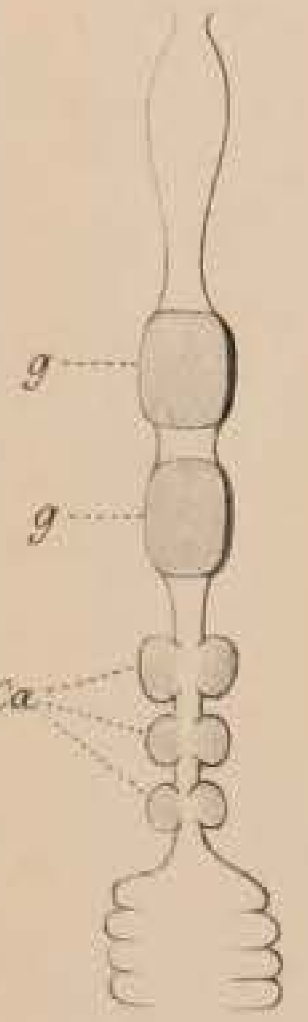
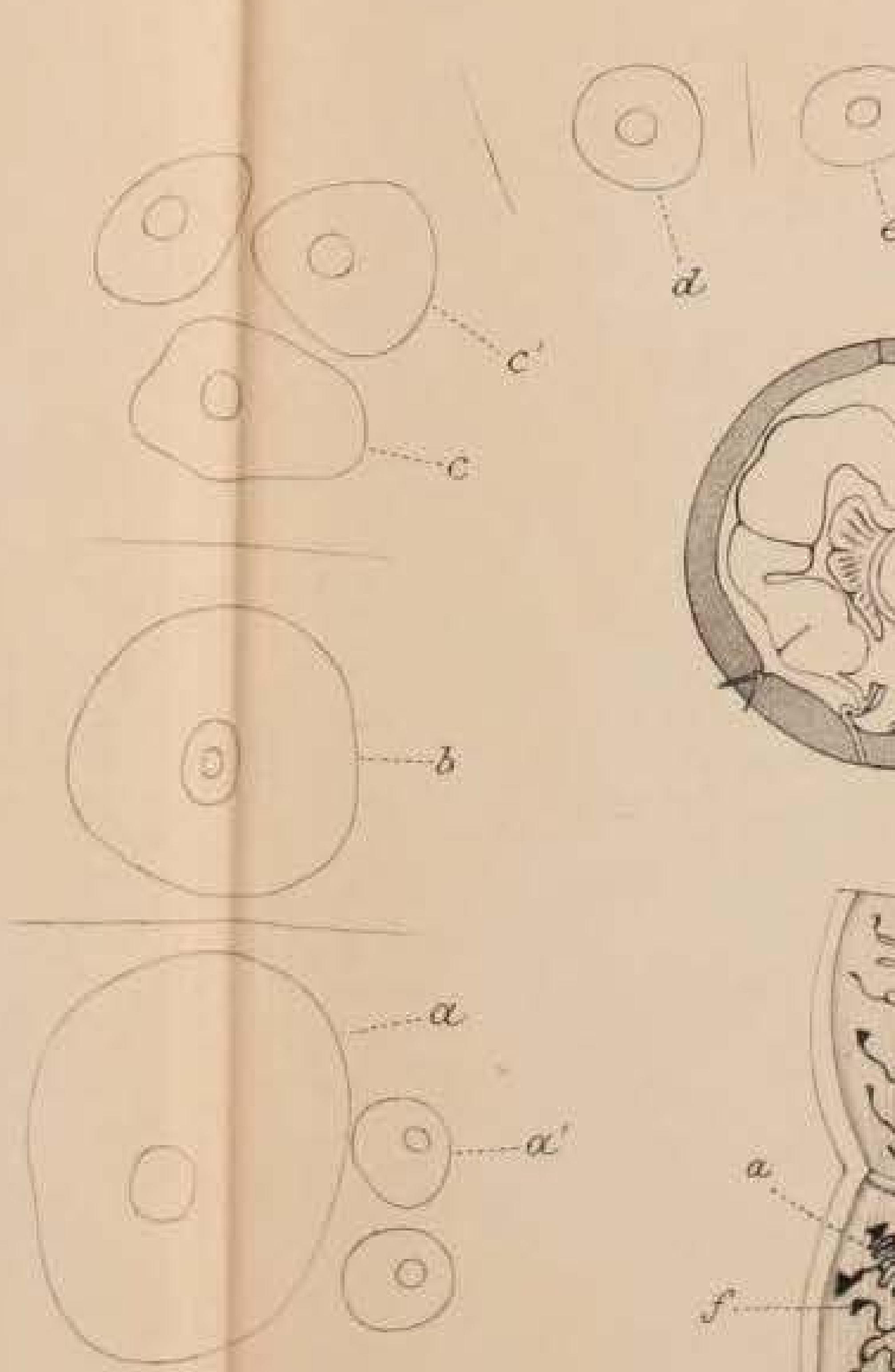


Fig. 21.

Fig. 20.



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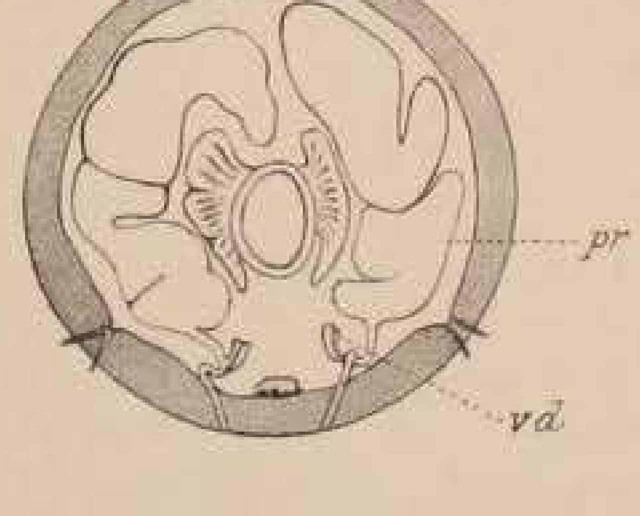


Fig. 16.

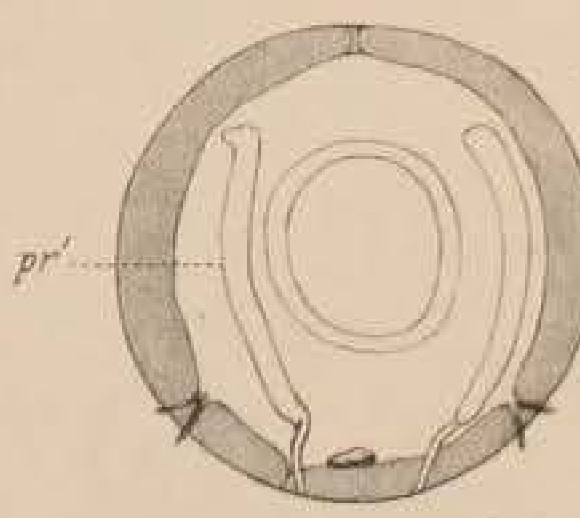
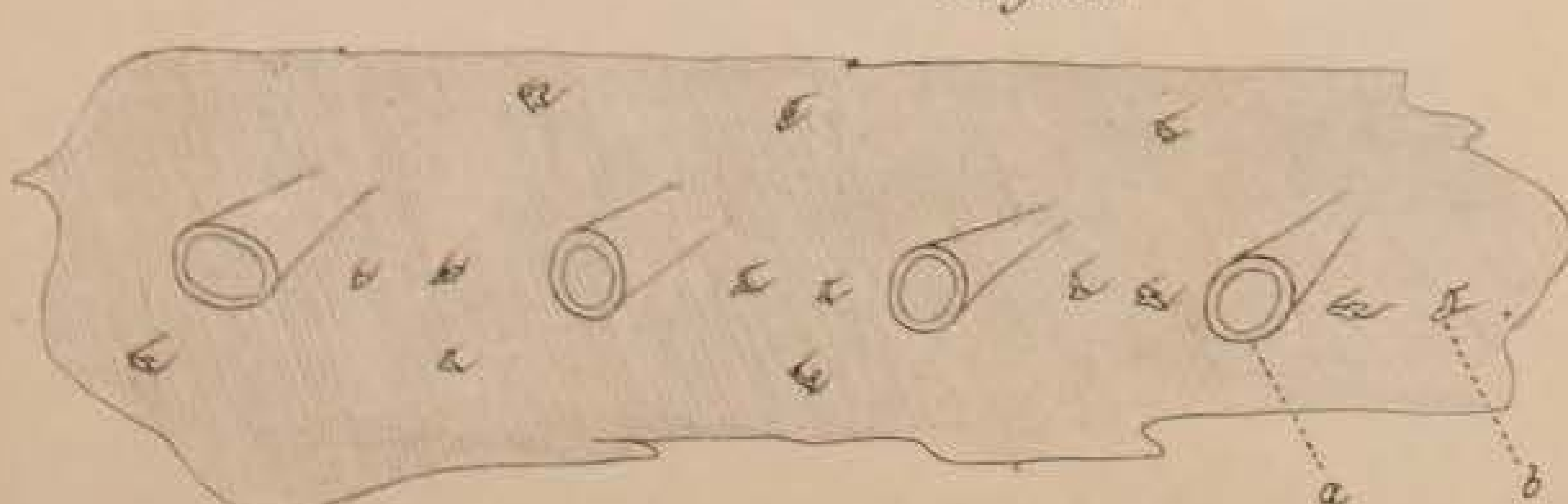


Fig. 17.



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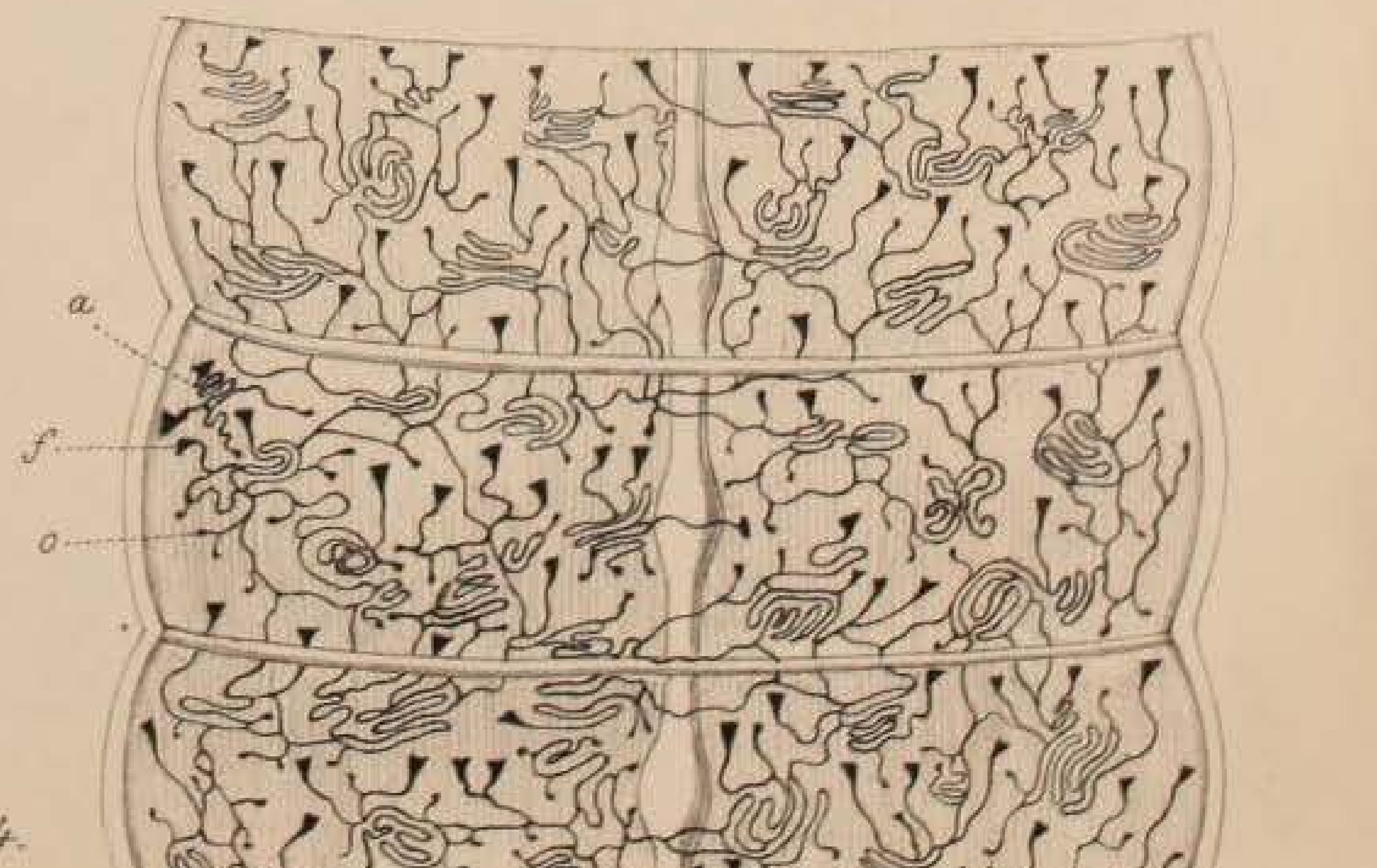

Fig. 24.

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