On the Structure of Two New Genera of Earthworms belonging to the Eudrilidae, and some Remarks on Nemertodrilus.

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With Plates XVI—XX.

The worms which form the subject of the following paper were obtained in a living state from Kew Gardens, along with a number of others whose structure I propose to investigate later.

I had applied to Mr. Thiselton Dyer for leave to sift soil coming from tropical countries in the Wardian cases which are generally used for transmitting plants in pots. This Mr. Dyer very kindly permitted me to do, and in his absence Mr. Morris was so good as to put me in the way of carrying out my wishes. To both these gentlemen my thanks are tendered. In the earth surrounding a number of pots containing plants from Lagos, West Africa, I found about half a dozen worms, which proved on examination to belong to the family Eudrilidae.

Until quite recently one genus—Eudrilus itself—was the only known representative of the family; three years ago Dr. Rosa described from Scioa, Africa, another genus—Telegramus; and quite recently Dr. Michaelsen has received from Zanzibar and the mainland opposite, and from the mouth of the Zambesi River, a number of species, all belonging to this family, and referable to four new genera: the family is, therefore, in the present state of our knowledge, characteristically Ethiopian,
though the type genus *Eudrilus* has not yet been met with from the African continent.¹

The *Eudrilidae* which I obtained from Kew belong apparently to two distinct species, which are also generically distinct. Four specimens I refer to a new genus, for which I propose the name of *Hyperiodrilus*. The fifth specimen is a species of another genus—*Heliodrilus*, nov. gen. The sixth is a very minute worm, measuring barely an inch in length, and being sexually immature was indeterminable.

I.—*Hyperiodrilus africanus*, nov. gen., sp. nov.

The worms are of different sizes; the largest specimen measures (after preservation in spirit) about five inches; during life the length was rather greater. Their form is very slender, and their movements were active, though they did not show any power of jumping, such as is shown by *Perichæta*. While moving the buccal cavity is to a certain extent everted, and is made use of as a sucker for attaching the front end of the body; the eversion of the buccal cavity is not nearly so pronounced as in *Perichæta*.

The colour of this species is pinkish, and the posterior segments have a distinctly ringed appearance. There does not seem, however, to be much pigment in the skin; the colour is entirely due to the enclosed viscera, particularly, of course, to the blood-vessels—even the ringed appearance of the posterior segments is due to the same cause; the blood-vessels ramifying over the septa produce the appearance of bands of red pigment corresponding to the segments: the clitellum is yellowish.

§ External Characters.

An examination of the external characters at once shows that this worm is referable to the *Eudrilidae*, but that it cannot be included in any known genus of that family, with the possible exception of *Stuhlmannia*.

¹ Since the above was written Drs. Horst and Michaelsen have received from Africa specimens of *Eudrilus*.
The prostomium does not completely divide the peristomial segment; but it sends back (see fig. 6) a very narrow prolongation, which is embedded in the peristomial segment up to a point not very far distant from its posterior border. Such a narrow prolongation of the prostomium appears to be characteristic of the Eudrilidae; it is specially mentioned by Rosa (10) in the case of Teleudrilus, and is figured by Michaelsen (7, pl. iii, fig. 17) in Nemertodrilus.

The dorsal setae are in couples; of the ventral setae, the individual setae of each couple are some little way apart, as illustrated in figs. 9 and 12.

The clitellum is developed all round the body, and occupies four segments, Nos. 14, 15, 16, and 17, as in other Eudrilidae, where four segments is also the usual extent of the clitellum, though sometimes, as in Polytoreutus, exceeded. Only one specimen, however, had the clitellum developed upon the 14th segment, and here it was incomplete, extending only over the dorsal surface of that segment. In two other specimens the clitellum only occupied Segments 15, 16, 17.

Nephridiopores were obvious upon most of the segments of the body, particularly upon the clitellum, where the smooth swollen integument rendered them very easily visible. They lie almost in the intersegmental furrow in front of the dorsal setae. It may be noted that they occur, as shown in fig. 23 of Pl. XVIII, in the 14th and 17th segments, where the ducts of the generative organs open.

Dorsal pores could not be detected in any part of the body.

The apertures of the oviducts are upon the 14th segment near to its posterior border: each has the appearance of a minute hemispherical projection, which cannot be confounded with a nephridiopore; besides, as already mentioned, the 14th as well as the 15th segment has its nephridiopores.

The oviducal papillæ, as they may be more accurately spoken of, are situated behind the dorsal seta of the 14th segment on each side; in one case, as shown in fig. 23 of Pl. XVIII, they
were placed just in front of the nephridiopore of the segment behind; more usually, however, they are a little dorsal of the nephridiopore.

The aperture of the sperm-ducts is, as in Stuhlmannia and Teleudrilus, single and median; it lies at the end of the clitellum, between the 17th and 18th segments. It does not, however, present the appearance of an orifice, but of a prominent hemispherical papilla, as in the case of the ovi-
ducal pore; the papilla is in this case considerably larger.

In one specimen (that which had four clitellar segments) this papilla was connected by two grooves running obliquely forwards with a pair of conspicuous rounded papillae, placed near to the boundary line between the 17th and 16th segments; the two grooves diverged from each other at an angle of about 40°; each ran along a slight mound-like elevation, as shown in fig. 24 of Pl. XVIII, and more highly magnified in fig. 19 of the same plate. The two papillae are unsymmetrically dis-
posed, as also shown in the figure; the left-hand one is placed just behind the groove separating the 17th from the 16th segment; the right-hand one at about the middle of the 17th segment.

In a second specimen (Pl. XVIII, fig. 22) the median papilla was quite invisible, owing probably to the worm having died with the part in question retracted.

In the only other specimen belonging to this species, which was nearly mature, a prominent glandular swelling occupied the middle ventral line between Segments 17 and 18 (Pl. XVIII, fig. 20). A careful examination showed that the apparently single protuberance is not to be confounded with the median papilla described in the first of the three specimens; it really represents the two anterior papillae of the 17th segment closely fused; the groove issuing from each may be detected, and the median papilla itself is visible at the point where the two grooves nearly come into contact.

In Stuhlmannia variabilis (Michaelsen) the papillae connected with the male efferent apparatus show certain re-
similarances to those of the present species.
There is a median aperture (as in *Teleudrilus* and other *Eudrilidae*) of the “prostate glands” upon the 17th segment; this is spoken of as a slit-like orifice; but the apparent difference in this particular from *Hyperiodrilus africanus* may be a mere question of the state of contraction of the worm’s body. From the aperture upon the 17th segment a deep furrow runs forward to a process which bears the outlet of a peculiar gland; this process is median, but slightly inclined to the right side. This papilla, however, appears from Michaelsen’s description to lie upon the 13th segment, near to the ventral unpaired orifice of the spermatheca. As already mentioned, the lateral processes, though varying somewhat in their position upon the segment, are always on Segment 17.

On the 13th segment is a median aperture (see fig. 24) corresponding to the male generative orifice upon the 18th segment, though situated at about the middle of the segment, rather nearer to the anterior than to the posterior boundary. This aperture was not at all conspicuous upon any of the specimens examined, and might very easily be overlooked.

§ Integument.

The layers of the body-wall are as in other earthworms, except for the presence in the epidermis of certain peculiar organs, which appear to be met with in all *Eudrilidae* except *Nemertodrilus*; but this genus is in other respects (see p. 266) a very aberrant member of the family. These structures are described later.

The muscular layers of the body-wall show no noteworthy peculiarities as regards the structure and arrangement of the fibres. The longitudinal coat does not exhibit the bipinnate character which is frequently met with in earthworms, particularly in the *Lumbricidae*.

The muscular coats contain numerous irregular spaces filled with cœlomic corpuscles (see fig. 3); besides the ordinary corpuscles large multinucleate bodies are met with, which may be pathological formations. I believe that Kühenthal (13) was the first to specially call attention to the spaces.
in question. They are unusually abundant in both Hyperiodrilus and Heliodrilus—more so than I have observed in any other earthworm. In places each individual fibre was separated from its neighbours by quite large spaces filled with corpuscles.

§ Setae.

The arrangement of the setæ is somewhat peculiar; the more dorsally situated pair, which are in reality lateral, and not dorsal, are closely approximated; the ventral couple (fig. 12) are at some distance apart; the distance separating the 2nd from the 3rd seta¹ is twice that which separates the 1st from the 2nd. The arrangement of the setæ is such as to produce the impression that there are only three on each side of the body. It appears to me possible that Kinberg's genus Tritogenia has the setæ arranged in this way, having thus led Kinberg to make the statement that it possessed only six setæ per somite. Perrier, who has (9) re-examined this genus, has discovered that there are eight setæ in each segment; the position of the male generative pores of Tritogenia between the 16th and 17th segments (according to Kinberg) is another point of similarity between the two genera, which are very likely identical.

No other known genus of Eudrilidae has the setæ arranged in this way; there appears, however, to be a slight difference in Nemertodrilus griseus in the distance which separates the individual seta of each couple; this is a step in the direction of Hyperiodrilus.

§ Epidermal Sensory (?) Organs.

The epidermis of this worm is furnished with certain curious structures of doubtful nature, identical with those which I was the first to describe in Eudrilus.

As Rosa has indicated the presence of these structures in Teleudrilus, and as I have found them in Heliodrilus, they may be regarded as characteristic of the Eudrilidae, and, as far as our present knowledge goes, confined to that

¹ The first seta is that nearest to the nerve-cord.
family as defined by myself. This, although a small point, is an additional argument in favour of retaining that family within the limits which I have proposed for it.

The structures in question are visible in the epidermis when the body-wall is examined as a flat preparation in glycerine; and they may be observed to be scattered irregularly over the segments, thus affording an example of another system of organs which have no perceptible relation to the metamerism of the body. In a preparation of this kind the sensory organs appear as longitudinal furrows, longer than broad, arranged after no system that I could discover, save that they were absent upon the intersegmental furrows. In transverse sections of the body-wall (cf. fig. 3) the sensory organs are seen to lie in the epidermis, but not to reach its surface; they generally cause the membrane which separates the epidermis from the underlying layer of transverse muscles to be bulged out towards the latter. Above each body is a row of short epidermic cells which divide it from the cuticle. The real form of the sensory bodies is better seen in longitudinal sections, for they lie for the most part parallel with the long axis of the body of the worm.

In such a section each sensory body is seen (see fig. 2) to consist of a central cylindrical core faintly stained by borax carmine, in which are embedded a variable number of large oval nuclei. Round the axis are a series of coats like those of an onion, which seem to be composed of an elastic membrane; in such sections, and in the transverse sections also, these coats appear as highly refracting fibres. In fragments of the skin mounted entire and viewed from above, the membranes present the appearance of a series of fine striae surrounding the axis of the body. Between the several membranous coats are darkly staining nuclei which are quite distinguishable from those which lie in the axis by their very much smaller size; the central nuclei are fully twice the size of the peripheral nuclei.

1 In a forthcoming résumé of the classification and distribution of Earthworms to be published in the 'Proceedings of the Royal Physical Society.'
These bodies have a striking resemblance to certain "end organs" which are found among the Vertebrata; they are particularly like the Pacinian bodies, having the same concentric lamellae surrounding a central sheath. It is this resemblance which makes me believe that the structures in question are of a nervous nature, for I must confess to having found no unmistakable evidence of nerve-fibres connected with them. It is, however, not easy to trace the ramifications of nerves in the skin of earthworms which have been preserved with alcohol.¹

§ Alimentary Canal.

In its main features the alimentary canal agrees with that of Heliodrilus, to be presently described.

The pharynx is large, and extends back to the 6th or 7th segment; there is no anteriorly situated gizzard, but a series of five or six, each occupying a single segment at the junction of oesophagus and intestine.

The oesophagus is lined with a thin chitinous cuticle as far back as the opening of the calciferous glands; beyond this point its walls are ciliated.

§ Calciferous Glands.

As in Eudrilus, and apparently other Eudrilidæ, the present genus is furnished with two kinds of calciferous glands.

(1) A pair of voluminous glands are attached to the oesophagus in Segment 13, the cavity of which they largely fill. The oesophagus itself is very narrow in this region, scarcely wider than the dorsal blood-vessel, which like it is completely hidden by the large glands. These glands appear of a reddish-purple colour in the spirit-preserved specimen, the colour being of course due to the abundant blood-spaces interspersed among the tissue of the glands. The glands have a trifid appearance as in Eudrilus, and a large blood-vessel passes over each.

In transverse sections these paired calciferous glands are

¹ Since the above was written Dr. Horst in a paper cited on p. 252, footnote, has suggested the sensory nature of the problematical structures.
seen to consist of numerous folds of epithelium with blood lacunae lying between the epithelial layers; the secretion of the glands has the form of small spherical particles.

(2) The present genus, like other Eudrilidae, possesses impaired ventral diverticula of the oesophagus.

The occurrence of these structures was first put on record by myself in Eudrilus sylvicola (1), where they are simple diverticula with the lining epithelium thrown into a few longitudinally running folds. Rosa (10) mentions the presence of three such glands in Segments 9, 10, 11, in Teleudrilus, but gives no special description of them.

To Michaelsen (7) our chief knowledge of these peculiar glands is due. He terms them "Chylustaschen," and compares them with certain glandular diverticula in the Enchytraeidae. The function of these structures is considered by Michaelsen to be not analogous to that of the calciferous glands; instead of secreting calcareous granules like the calciferous glands, or producing any other kind of secretion, it is supposed that they serve for the absorption of food—hence the term "Chylustaschen." It must be admitted that no calcareous spherules have been found in these pouches, although their structure recalls that of the calciferous glands; so far this is evidence, if not in favour of the suggestion of Michaelsen, at any rate of their performing a different function from that of the calciferous glands in the economy of the worms.

In Pygmaeodrilus the 9th segment contains a pair of lateral forwardly directed diverticula; it may be that the impaired glands of Eudrilus are formed by the fusion of a pair which get to be more and more approximated ventrally; on the other hand, the diverticula of Pygmaeodrilus rather suggest the calciferous glands of Urochæta, which really secrete calciferous particles.

No such structures are mentioned in Eudriloides or Nemertodrilus.

In Polytoreutus there are median impaired pouches as in Hyperiodrilus, three in number, besides the paired calciferous glands; the folds in the interior of the glands are so
complicated as to present the appearance of a bundle of longitudinally running vessels.

In Hypoderilus the ventral oesophageal pouches are in certain respects more remarkable. There are three of them in Segments 9, 10, and 11—one pouch to each segment.

The pouch appears to communicate with the oesophagus a little to the right of the ventral median line. The orifice is narrow, and the cells are at first identical with those which constitute the epithelial lining of the oesophagus; the cells are tall and columnar, and between their bases are spherical or pear-shaped darkly staining cells (fig. 31) like those of the oesophagus. Tracing the pouch back, the cells are seen to alter their character, and to become low and quadrangular in form, while the epithelium is so folded as to give the appearance of a series of tubes running approximately parallel to each other (fig. 25). At the point of origin of the pouch, as shown in fig. 31, the muscular wall of the oesophagus and the peritoneal covering becomes reflected over the gland in such a way as to leave a wide space between itself and the pouch; further back this space is obliterated by the coalescence of the muscular and peritoneal layers with the outer layer of the gland.

Further from the point of the opening of the gland into the intestine the appearance of parallel running tubes is increased, and they have become at the same time of smaller calibre. The cells which form the lining epithelium are broad and somewhat flat, though quadrangular in form; the nuclei are thus, owing to the large size of the individual cells, very far apart, and the cell outlines are not distinguishable. As the folding gets more and more complicated the "tubes" present more and more the appearance of having an intra-cellular lumen; this actually does take place at the extremity of the pouch. One of the last sections through a pouch is illustrated in fig. 26: it will be seen there that three comparatively wide tubules end in a complicated meshwork of fine capillary tubes; the section presents the strongest possible resemblance to a portion of a nephridial network such as I have figured in Acanthodrilus multiporus. Even the three large tubes
figured in that drawing appear to be excavated in the substance of cells, while there can be no possible question about the ramification of minute tubes.

One is tempted to regard every ductule excavated in the substance of cells as of nephridial nature, but the origin of the blood-capillaries in the leech by direct canalisation of cells, discovered by Lankester and confirmed by Lang, as well as unicellular glands with a central duct, shows that this conclusion cannot be always drawn.

The study of these oesophageal pouches in *Hyperiodrilus* is instructive as showing how folds may gradually acquire the character of a system of tubes, and how the subdivision of the tubes, without a corresponding decrease in size of the epithelium, may ultimately lead to an intra-cellular network. This series of facts shows also how irrational is the distinction, which some have attempted to draw, between nephridia with an intercellular duct and nephridia with an intra-cellular duct, e.g. between those of the Polychaeta and Oligochaeta.

The tubes are everywhere separated by an abundant plexus of blood-capillaries, which seems to form a continuous sinus.

In *Bucholzia* there is a dorsal diverticulum of the oesophagus, which Michaelsen has compared with the ventral pouches of *Eudrilus*; and in this Enchytræid the diverticulum is formed of a number of tubules with intra-cellular lumina.

§ Generative Organs.

1. Male Generative Organs.—I could only find a single pair of testes; as these were extremely small, it is possible that I may have overlooked the second pair. The pair found were in the 11th segment; each is attached to the vas deferens just where it issues from the septum separating this segment from the one in front. As will be seen later, after the other organs of the male reproductive system have been described, the peculiar arrangement of the vasa deferentia, which are bent upon themselves near to their cælomic opening, suggests that the missing pair of testes, if they are really present, will be found in the 12th segment.

The testes of *Hyperiodrilus* are not enclosed in a special
sac, as they are in Heliodrilus. The seminal cells must therefore trust to accident to find their way into the interior of the sperm-sacs.

There are two pairs of sperm-sacs (fig. 44) in Segments 11 and 12. Each depends from the anterior of the two septa which bound the segment by which it is contained. The sperm-sacs are not very large, and are perfectly independent of each other. The sperm-sacs are shaped something like a bean, the hilum being the point of attachment to the septum by means of a short pedicle. The interior of each sperm-sac is divided up by numerous trabeculae into a series of very small cavities, which contain decidedly more gregarines than developing spermatozoa.

The vasa deferentia present close resemblances to those of Teleudrilus (Rosa, 10). The funnel opens into the sperm-sac, and therefore traverses the septum twice, since the sperm-sacs lie on the posterior aspect of the septa separating Segments 11, 12, and 10, 11 respectively. This is precisely what occurs in Teleudrilus, and I have recently pointed out that in a species of Moniligaster there must be something of the same kind, inasmuch as the funnel projects into the sperm-sac which is attached to the front wall of its segment. Generally when the sperm-sacs are attached in this way the funnel of the vas deferens is not in direct continuity with them, but projects freely into the interior of the segment a little way in front of the posterior septum of the segment.

The vasa deferentia open in the way that has been described by four rather small funnels completely concealed within the four sperm-sacs. On leaving the sperm-sac the vas deferens is at first a somewhat narrow tube, lined by numerous small quadrangular cells, which are of course ciliated; the peritoneal covering is slight, and there is no such conspicuous muscular coat as I have figured and described in Eudrilus. Almost immediately the vas deferens widens out exactly as in Teleudrilus, and is sharply bent upon itself, and again traverses the septum; directly it has passed through the septum it narrows. The wide U-shaped portion of the vas
deferens is lined by a tall columnar epithelium, and the cilia are very long. The narrow portion lying behind the septum is composed of an epithelial layer of low quadrangular cells comparatively few in number; the two vasa deferentia of each side pass down the body just covered by the peritoneum, and on a level with seta No. 3; they are accompanied by a blood-vessel which supplies them with capillary branches.

In the 17th segment is situated the terminal apparatus of the male reproductive organs, which consist of two large "prostate" glands or atria, opening on to the exterior by means of the protrusible penis.

Each atrium is furnished with a muscular duct which leads to the exterior.

The entire gland is sausage-shaped, and recalls the corresponding structure in Acanthodrilus; it has the same form as in that genus, and the same opaque white appearance. We do not find the nacreous appearance of these organs in Eudrilus; the reason for this difference is to be found in the absence from Hyperiodrilus of the thick muscular coats composed of longitudinal and circular fibres which are characteristic of Eudrilus. In Hyperiodrilus the muscular layer is indeed present, but it is reduced, as shown in fig. 38, to a very thin layer. This figure may be compared with that illustrating a transverse section through the atrium of Eudrilus (Beddard, 1, pl. xxx, figs. 8—10).

The interior of the distal part of the prostate is formed of a compact mass of cells loaded with darkly staining granules. I could not distinguish (see fig. 42) two layers of cells, such as appear to be met with in the prostates of all other earthworms in which those glands have the tubular form which they exhibit in the present genus; that this, however, is due to the obliteration of the distinction into two layers by the immense quantity of secretion present is shown by another specimen (fig. 38), in which the inner layer of columnar cells was quite plainly visible.

The vasa deferentia, which retain their distinctness up to the very point of opening, open into the glandular part of the
prostate nearer to the distal than to the proximal end. The
direct communication between the vasa deferentia and the
“prostate” appears to be the rule with Eudrilidæ; and this led
me to compare the so-called prostate in the terrestrial Oligo-
chæta to the atrium of the Limicolous forms. Quite recently
Benham (6) has expressed himself against this identification,
but admits that “a portion of the prostate in Perichæta,
Eudrilus, and other genera, in which the sperm-duct and
prostate form is probably the homologue of the ‘atrium’ of
Tubifex.’” In this case half of the glandular portion of the
terminal organ of the vasa deferentia in Eudrilus, Hype-
riodrilus, &c., will be the equivalent of the ‘atrium,’” while
the other half will be comparable to the “cementdrüse” of
Tubifex! This will hardly do, for there is no structural
distinction between the two halves; they form a continuous
whole. I need not recapitulate here the various intermediate
conditions which unite the Eudrilidæ with other genera; it
appears to me impossible to draw a line between the “prostate”
glands of Perichæta and those of Eudrilidæ; they are
obviously homologous structures. The name that is applied
to one must be applied to the other.

There are no penial setæ present.

2. Female Generative Organs.—These organs seem to
be most like those of Stuhlmannia variabilis, which have
been briefly described by Michaelsen as follows:—“The
orifice of the spermatheca situated in the middle ventral line
of Segment 13 leads into a wide atrium. From this is reached
an unpaired long sac-like crinkled spermatheca. From the
atrium arises on each side another spermatheca-like broad
canal. These two canals extend upwards and fuse together
above the gut, forming in this way a single short sac, which
communicates with the atrium by a ring-like canal surrounding
the gut. Two greatly coiled oviducts, each furnished with a
receptaculum ovarum, open laterally on Segment 14. On the
other side they communicate with the spermatheca. The two
ovaries lie anteriorly in Segment 13. (They are connected by
narrow canals with the oviducts?)”
On dissecting a specimen of *Hyperiodrilus*, the only part of the female reproductive system that could be at first detected (fig. 47) was a longish oval spermatheca lying upon the dorsal wall of the gut, in the 13th segment, and directed backwards. After carefully removing the calciferous glands, to which the spermatheca and neighbouring part of the reproductive organs are closely attached, the spermatheca was seen to divide into two thick-walled tubes; these (see fig. 1) are placed close to the septum which divides the 13th from the 12th segment, and which is conspicuous on account of its being the last of the specially thickened septa. The two tubes, as in *Stuhlmannia*, completely encircle the gut, and meet below in the small atrium which opens on to the exterior by the median pore already referred to as existing upon the 13th segment. Each of these two tubes is provided on the outer side (fig. 8) with a small prominence, which looks like a diverticulum of it, and which corresponds to the structure termed by Michaelsen "receptaculum ovorum" in *Stuhlmannia*; close to this arises on either side the oviduct, which passes straight to its opening on the 14th segment.

The atrium is not furnished with a second diverticulum corresponding to the "spermatheca" of *Stuhlmannia*. Fig. 47 represents the parts described as seen on the dissection of the worm. In fig. 8 is a more diagrammatic sketch of the same parts, in order to display their mutual relations, and their position with regard to the œsophagus and the dorsal blood-vessel.

An investigation by means of longitudinal and transverse sections shows that these structures, which are alone clearly visible on a dissection, and which form a continuous whole easily to be separated and mounted on a slide, do not represent the entire female reproductive system.

The ovaries are paired structures, lying as usual in the 13th segment; they are very compact bodies, not frayed out into numerous processes. Instead of lying freely in the cavity of the 13th segment, each ovary is enclosed in a special coelomic sac of a globular form; this sac also includes a
portion of the nephridium of the 13th segment (fig. 10); its walls are made up of muscular fibrils, and it has a coating as well as a lining of peritoneal cells. Each sac is situated near to the anterior wall of the 13th segment; traced backward by means of a continuous series of transverse sections, the sac abruptly diminishes in calibre, and forms a narrow tube which is continuous with the tube formed by the narrowing of the ovarian sac of the opposite side of the body. A section which illustrates these relations is illustrated in fig. 51.

The bursa copulatrix, which is spherical in transverse section, opens out to the exterior by the median pore of Segment 13. From the bursa copulatrix arises a single blind pouch, which may be regarded as the spermatheca. This has a lining of tall epithelial cells of a glandular appearance, and very thick muscular walls. The spermatheca directly it leaves the bursa becomes enveloped in a coelomic sac, as shown in fig. 11; this coelomic sac is not the connecting tube between the two ovarian sacs shown in fig. 51, but it is continuous with the sac involving the ovary of its own side; the spermatheca of each side runs up the side of the oesophagus for a short way, terminating blindly at about the middle of the dorso-ventral diameter. The sac in which the spermatheca is contained passes right round the oesophagus, and, fusing with its fellow of the opposite side of the body, is prolonged backwards as an unpaired median sac lying above the oesophagus; this structure is that which is illustrated in figs. 5, 11, and lettered sp'.

It must be noted, therefore, that what appears on dissection to be an unpaired spermatheca, lying above the oesophagus and connected with the bursa by a ring round the oesophagus, is really a coelomic sac containing the true spermatheca, and does not communicate directly with the exterior through the bursa copulatrix.

This coelomic space comes into close relations with the oviducal funnel which seems to open into the receptaculum ovarum (figs. 1, 5, 8, 11 r. o.), but does not involve the receptaculum or the oviduct.
The receptaculum, or egg-sac, as it may be more simply termed, is of considerable size, and is divided up into numerous compartments, which lodge the developing ova, by trabeculae; it is closely attached to the periesophageal coelomic sac, as shown in the figure (fig. 10), and in all probability opens into it, though I confess to not having been able to find the actual orifice of communication.

The oviduct is a short, straight tube, which passes directly from its opening into the egg-sac to the external aperture upon Segment 14. It is lined by a columnar ciliated epithelium, and it has strongly developed muscular walls.

The coelomic sac involving the ovaries, and continuous with the ring round the oesophagus, facilitates the passage of ova from the ovary to the receptaculum and to the oviduct; but the extension of the sac beyond the limits necessary for that purpose is a little difficult to understand.

I could not find any spermatozoa in the dorsal sac, nor, for the matter of that, in the spermatheca; and if impregnation takes place by the bursa copulatrix, there seems to me to be no way by which the spermatozoa could reach the interior of the sac. I could detect no orifice leading from the spermatheca to the sac which involves them, and such a connection seems hardly likely to occur.

In nearly all the Eudrilidae the ovary is contained in a special coelomic sac, which communicates indirectly with the exterior. The principal exception is Nemertodrilus; but here the reduction in size of the cavity of the 13th segment seems to guide the ova to the aperture on to the exterior of the body, and there is thus no need of the formation of a special tube (see p. 266).

The remarkable genitalia of Polytoreutus are perhaps rendered more intelligible by the facts which I have been able to make out in Hyperiodrilus. I have little doubt that the median sac, communicating on the one hand with the "spermatheca," and on the other with the oviduct, will prove to be a coelomic space perhaps surrounding the true spermatheca. It seems to be possible that the female organs of
Teleudrilus will bear re-investigating from this point of view. The two tubes which are described by Rosa (10) as diverticula of the spermatheca have a certain likeness to the narrow cœlomic sac of Hyperiodrilus, which puts into communication the ovarian sacs and the space surrounding the spermatheca; and they approach each other in the middle line, which suggests the possibility of their being really fused.

The mature ova have the characters illustrated in fig. 49. The most remarkable feature is a thick, darkly staining membrane, which completely surrounds the ovum; this membrane is traversed by numerous pores.

I have described something of the same kind in Eudrilus (2), where, however, it forms a cap at one end only of the ovum. After examining Hyperiodrilus it seemed possible that I was mistaken in considering that the membrane in question was limited to half of the ovum in Eudrilus. I cannot, however, find that I have made any mistake in this matter in my description of Eudrilus.¹ This being so, it does not seem very likely that the cap of darkly staining cubical bodies which cover one pole of the ovum in Eudrilus are comparable to a radiately striated egg-membrane; such a membrane would surely be produced round the whole of the periphery of the ovum at once. There are, therefore, still reasons for adhering to the opinion which I expressed in the paper dealing with the structure of that ovum, viz. that the columnar layer is in reality a product of the follicular cells, being formed by the metamorphosis of a certain number of them. This opinion is considered by Vejdovsky (12) to be probably true.

The resemblance between this structure in Eudrilus and the complete membrane which surrounds the ovum of Hyperiodrilus is close; but I do not feel sure that they actually correspond; a membrane surrounding one half of the ovum seems to be exceedingly anomalous. The ova within

¹ My description has been confirmed in a paper by Dr. Horst which I received after the present memoir was sent to Professor Lankester, "Sur quelques Lombriciens exotiques appartenant au genre Eudrilus," Mém. Soc. Zool. de France, t. iii, p. 223 (cf. fig. 11 of plate).
the compartment of the egg-sac are associated with a few germinal cells, which are generally closely attached to the ovum, and frequently show signs of degeneration. The masses of immature germinal cells and ova, in all stages of development, which I have figured and described in Eudrilus (2) are not to be found in the present genus.

II.—*Heliodrilus lagosensis*, nov. gen., n. sp.¹

Among a number of earthworms which arrived in a Wardian case at Kew Gardens from Lagos, West Africa, was a single specimen which I refer to a new genus, belonging, like *Hyperiodrilus*, to the family Eudrilidæ.

§ External Characters.

It is of about the same size and colour as *Hyperiodrilus*, but the external characters of the specimen when killed and preserved are quite unlike those of the former species.

The prostomium is of the same form as that of *Hyperiodrilus*.

The setæ have precisely the same arrangement as in *Hyperiodrilus*—that is to say, the ventral couple are at some little distance from each other, while the lateral couple are very closely approximated.

The clitellum was not very distinctly marked, but appeared to comprise four segments, 14—17.

Dorsal pores could not be detected.

The nephridiopores are placed in front of the lateral setæ.

The oviducal pores, as in all Eudrilidæ, are lateral in position; they are upon the 14th segment, and are quite conspicuous, owing to their being surrounded by a slightly raised margin.

The male generative pore is unpaired and median in position; it lies upon the border-line between Segments 17 and 18: the pore is situated upon the summit of a prominent elevation.

¹ The generic name might be confused with *Helodrilus* if there were any chance of that problematical form ever being properly identified.
The spermathecal orifice was not visible upon the exterior; by means of transverse sections it was found to be upon Segment 11.

The most characteristic external mark of this species is afforded by a series of sucker-like structures. There are six of these, one to each of Segments 10—15. The last three are accurately median and ventral in position, and are situated on about the middle of their segment. The two in front are placed considerably to the left of the middle line, as shown in fig. 21; the first is nearer to the middle line.

§ Integument.

The epidermis of Heliodrilus agrees in every particular with that of Hyperiodrilus, as does also the structure of the clitellum. The limits of this modified region of the body-wall could not be ascertained with certainty by an inspection of the worm; transverse sections show that it extends over Segments 14—17.

The peculiar sensory organs which are so characteristic of the Eudrilidae occur in Heliodrilus; their structure calls for no remark, as they resemble in every particular those of Hyperiodrilus, which have been already described on p. 236.

The muscular layers of the integument are also identical in every respect with those of Hyperiodrilus.

§ Alimentary Tract.

The buccal cavity occupies the first three segments.

The pharynx extends back to the 6th segment.

The oesophagus is very narrow, and passes back without any change as far as the 10th segment; here it becomes narrower, and the lining epithelium is thrown into a series of regular longitudinal rugae; at the mesentery before the 11th segment, as in the case of the subsequent segments, it becomes a trifle wider, recurring to its former dimensions, which are between one third and one fourth of the diameter of the body of the worm in this region. The first of the two ventral oesophageal pouches lies in this segment, and is directed forwards, having anteriorly no connection with the wall of the oesophagus;
further back it is suspended by two closely approximated and very delicate mesenteries, which later become continuous with a bridge of tissue, along which blood-capillaries pass from the periesophageal blood-sinus to the vessels of the pouch. This bridge forms the walls of the aperture of communication between the oesophagus and the pouch. The minute structure of the pouch is as in Hyperiodrilus, but there is no splitting of the muscular layer of the oesophagus at the origin of the pouch, such as I have figured and described in that earthworm.

The second pouch, which lies in the 12th segment, has a precisely similar origin from the oesophagus, and is identical in all respects with the first.

In the next segment is a third oesophageal pouch, which is very much smaller than either of the other two; its interior is not so subdivided by the development of folds, and the aperture into the oesophagus is distinctly larger; it has the characters rather of a folded-off portion of the oesophageal tube than of a diverticulum.

After this the tube remains narrower for some distance, with the epithelium longitudinally folded; it is here, as throughout its whole extent up to this point, lined by a thin chitinous layer; there is, however, no gizzard upon the oesophagus, and no special thickening of its muscular coat which could be compared to a gizzard.

In the 14th segment the oesophagus becomes wider, and receives the ducts of the calciferous glands; these ducts have exactly the same structure as the oesophagus, and are not of a very greatly inferior calibre. Their epithelium is distinctly ciliated; each duct opens by a wide aperture on to the side of the oesophagus. After the opening of the ducts of the calciferous glands the epithelium of the oesophagus alters its character and becomes ciliated. The diameter of the tube is at the same time larger, and the plexus of blood-vessels more richly developed. Commencing with the 18th segment the alimentary canal is provided with six gizzards, one to the 18th and to each of the five following segments, connected by sections of thin-walled intestine.
§ Body-cavity.

As is usual in earthworms, the first few segments are not separated from each internally by regular septa; irregular fasciculi of muscles attach the buccal cavity and the pharynx to the parietes. The 5th segment is separated from the 6th by the first regular intersegmental septum; this and the 7th which follow are specially thickened, and consist of several layers of muscular fibres. These septa (fig. 48) fit into each other like a series of cups; they arise from points which correspond accurately with the intersegmental furrows.

The cælom in this worm is further broken up into the compartments which lodge the testes and extremities of the vasa deferentia, and into those which lodge the ovaries and the spermatheca; finally a special sac encloses the supra-intestinal blood-vessel. All these cælomic chambers are specially described under the different organs which they enclose.

As in other Oligochaeta (cf. Kükenthal 13), the cælomic corpuscles are of two kinds.

§ Vascular System.

The supra-intestinal vessel exists in Heliodrilus, and is connected with the hearts, as Perrier was the first to point out in some other genera.

In Heliodrilus this vessel is small, and lies in a special cælomic space above the gut. A transverse section through the supra-intestinal vessel and this perihæmal sac is illustrated in fig. 46. The sac has exceedingly thin walls, which are connected with the walls of the blood-vessels by irregularly disposed trabeculae; the interspaces are largely filled with corpuscles which have the characters shown in the figure; these cells are quite similar to those which occur in the walls of the intestine. The inclusion of the supra-intestinal vessel in a sac recalls the similar perihæmal space which I have described in Deinodrilus (4) as surrounding the dorsal blood-vessel.

The large “hearts” of Segments 11—13 communicate with the supra-intestinal as well as with the dorsal vessel. The
supra-intestinal vessel does not, as it does in Eudrilus, become double above each of the ventral oesophageal pouches.

§ Generative Organs.

(1) Female Organs.—As in most of the genera belonging to the family Eudrilidae, there is a complicated system of coelomic spaces developed in connection with the ovaries and the other organs belonging to the reproductive system.

The ovaries are paired, and in Segment 13. Each ovary is enclosed in a sac which it almost completely fills; a narrow tube running dorsal to the nerve-cord connects the ovarian sacs of the two sides of the body; there is further a communication between the ovarian sac and the egg-sac of its own side, as in Teleudrilus and Hyperiodrilus; this communication is effected by a coelomic tube which is at first very narrow; as it approaches the egg-sacs it becomes wider, and finally forms a somewhat oval sac enclosing the funnel of the oviduct and communicating with the egg-sacs, into which the oviducal funnel also opens. So far as I can make out from a complete series of transverse sections the arrangement is, so far, very like that which has been figured and described by Rosa in Teleudrilus (10); but Heliodrilus apparently differs from Teleudrilus, and certainly agrees with Hyperiodrilus in the communication between the right and left ovarian sacs. I found it quite easy to trace the course of the tube which connects the ovarian sac with the considerable space surrounding the funnel of the oviduct; but any doubt as to the reality of this connection is removed in the present instance by the occurrence of ova floating freely in the wide space round the funnel; for the most part these ova were to be observed singly, each surrounded by a follicular layer of flattened cells, of which the nuclei alone were conspicuous: in a few cases the ova were also surrounded or partially surrounded by groups of germinal cells, as a rule comparatively few in number. The ova in the ovary, as well as those which I found in the sinus surrounding the funnel of the oviduct, had a well-developed vitelline membrane, but showed no traces of the
remarkable striated membrane which I shall refer to directly in describing the ova within the egg-sacs.

The oviduct has been incidentally referred to in the foregoing description; it opens into the egg-sac and into the celomic space continuous with the perigonadal sac; it is a short tube, and passes straight to its opening upon the 14th segment; it is not twisted upon itself, as is the oviduct of Eudrilus. The oviduct has fairly thick muscular walls, the fibres of which are for the most part arranged in a series of rings round the tube, and a lining of columnar ciliated cells. The calibre of the oviduct diminishes gradually from the funnel to the external aperture.

The egg-sacs are also situated in the 14th segment: the septum dividing this segment from the one in front is entirely or largely absent; but the position of the egg-sacs within the 14th segment suggests that they lie near to where the anterior wall of that segment should be. The interior of the egg-sacs is divided up by trabeculae anastomosing with each other into a series of very small compartments, only just broad enough to contain a single ripe ovum; the compartments, as in other earthworms, are lined with small peritoneal cells (see fig. 29).

The mature ova do not present any noteworthy differences from those of Hyperiodrilus.

Spermatheca.—As in Hyperiodrilus, there is only a single spermatheca present, which lies on the right side of the body—the opposite side, therefore, to that which the spermatheca occupies in Hyperiodrilus. The spermatheca in Heliodrilus is a large conspicuous organ, which can be seen, on a dissection of the worm, to reach on to the dorsal side of the gut; it contrasts, therefore, with the very small spermatheca of Hyperiodrilus. As in the latter worm, the apparent bulk of the spermatheca is increased by a prolongation of the perigonadal sinus which partially surrounds it; but the arrangement of this sinus in Heliodrilus is very curious, and quite unlike that of Hyperiodrilus. But before describing the sinus I will direct attention to the characters of the spermatheca itself, which differs in certain points from the
spermatheca of any other Eudrilid, or in fact any other earthworm at present known.

It is a large oval sac lined by columnar cells; a portion of one of the walls is represented highly magnified in fig. 37: below the layer of columnar cells are some smaller cells, the contours of which are not very clear, though their nuclei are; outside these are a few muscular fibres, which make up a layer of no great thickness. The interior of the spermatheca contains a granular substance which appears to be formed by the columnar cells. The calibre of the spermatheca (fig. 41) gradually diminishes towards the apex and towards the ventral side of the body; here the cells lose their glandular character, and become at the same time considerably shorter, so that the muscular coat appears to acquire an additional thickness. The narrow duct of the spermatheca does not open upon the 13th segment as in Hyperiodrilus, but bends under the nerve-cord and runs forwards, always lying beneath the nerve-cord, as far as the 11th segment; throughout the whole of its course beneath the nerve-cord it is a narrow tube with thick muscular walls, and a lining of short columnar cells, which, it is perhaps unnecessary to remark, show no traces anywhere of cilia. The diameter of the spermathecal tube in these segments is about equal to that of the nerve-cord. In the 11th segment the spermathecal tube perforates the body-wall, and opens on to the exterior by an inconspicuous orifice which is situated on the median ventral line. The ventral sucker-like organ of this segment is pushed to one side, as shown in fig. 21, and does not therefore interfere with the accurately median position of the spermathecal pore.

The number of segments occupied by the spermatheca is thus considerably in excess of that which is found in any other earthworm.

If the spermatheca is developed in the Eudrilidae as in the Lumbricidae by an inpushing of the epidermis, the point of opening will fix the morphological position of the organ; hence Heliodrilus serves in this respect to connect the Eudrilidae with other earthworms, for the spermatheca opens in front of
the ovarian segment, and yet the main part of the organ lies in that segment.

The apex of the spermatheca cannot be seen on a dissection of the worm, for the reason that it lies embedded in a coelomic sac. Figs. 32—34 represent a series of sections showing the relations of the spermatheca to this sac. The sections are part of a series running from behind forwards; towards the posterior end of Segment 14 the end of the spermatheca is seen to lie between two coelomic spaces, which are really continuous, and envelop the apex of the spermatheca as seen a few sections later; in this section the extremity of the spermatheca is seen in transverse section to lie in the middle of the coelomic sac, which is incomplete dorsally: this is, however, merely due to an accidental cut; the sac is really closed. Round the spermatheca is a mass of tissue which is seen in a later section to be the wall of a second sac lying within the first. The spermatheca is pushed against the wall of this, driving it before it for a little way, but it hardly enters the second sac: fig. 34 is therefore a little exaggerated in this particular; the cavity of the spermatheca does not appear to be continuous with that of the second sac, although I should have preferred longitudinal sections to decide the point; in any case the character of the lining cells is absolutely different. This second sac which lies within the first is also closed; it has the same general structure, consisting of two layers of peritoneum, between which are a few fibres of what appears to be muscular tissue; but the lining peritoneum, as shown in fig. 33, is very much thicker, and the cells are larger and rounded.

In both sacs masses of corpuscles lie here and there within the lumen.

The outer coelomic sac gradually narrows ventrally, and ultimately becomes an extremely narrow tube, which is attached to the spermatheca by the mesentery; it finally becomes continuous with the perigonadal sinus. The general disposition of the female reproductive organs and of these coelomic sacs connected with them is shown in a semi-diagrammatic form in fig. 41. In
reconstructing this figure from the transverse sections I have put in the intersegmental septa between Segments 12, 13, and 13, 14, which I have not actually observed; I imagine that they will be found to be partially absent, as in Hyperiodrilus. The position of the coelomic sacs is also not quite as in nature; they have been slightly altered to permit of everything being seen in one figure: but these alterations do not affect the mutual connection of the various parts; these are, I trust, accurately displayed in the figure, and also in fig. 36, which represents the apex of the spermatheca (sp.). Comparing the arrangement of these parts in Heliodrilus with that of Hyperiodrilus we find an increase in size of the spermatheca, and a decrease in size of the coelomic sac involving the spermatheca. The latter, instead of forming a complete ring round the oesophagus completely enclosing the spermatheca on one side, is only developed on one side of the body, and surrounds only the extremity of the spermatheca. The second sac, lying within the dorsal dilated part of the sac which surrounds the extremity of the spermatheca, is peculiar to Heliodrilus, and is an extraordinary structure, concerning the meaning or function of which I can offer no suggestion. The enormous development of the lining cells of the circumoesophageal sacs of Hyperiodrilus into the similitude of a glandular epithelium is not found in Heliodrilus. It is possible, however, that it is a periodical occurrence which does not happen to have taken place at the time when the only specimen of Heliodrilus that I possess was killed. The reduction of the coelomic sac surrounding the spermatheca not only in size, but also in the extent to which it involves the spermatheca, culminates in Eudrilus, where, as far as I can see, there is no vestige of any perispermathecal sac left. I should like to make this point quite certain, but in any case it is evident that if such a sac does exist, there must be merely traces of it. The question is whether Eudrilus represents the last term in this series of modifications, or whether Hyperiodrilus does; from what we know of the anatomy of the Oligochaeta it seems more reasonable to suppose that the development of these
The coelomic spaces is secondary. Accordingly, as regards the Eudrilidae, Eudrilus represents perhaps the most archaic form. This is also, it may be remarked, in accordance with the fact of its geographical distribution. It occurs in South America, the West Indies, St. Helena, New Caledonia, and New Zealand, being therefore one of the most widely spread of earthworms. It seems, therefore, permissible to argue from Eudrilus to the other Eudrilidae; and this I have attempted to do in the case of the ovarian oviducts and atria (see p. 268). It would be interesting to ascertain how far the spermathecal coelomic spaces are represented in Teleudrilus; the connection between the perigonial sinus and the egg-sac is developed in that genus as in Heliodrilus and Hyperiordrilus, but not Eudrilus.

2. Male Generative Organs.—The testes are, as usual, paired structures which lie in the 10th and 11th segments.

Each testis has a number of processes of unequal sizes, as is so very generally the case with earthworms. The testes, however, do not conform to the general rule in their position; they lie near to the posterior septum of their segment, as in Acanthodrilus annectens (4), alone among earthworms at present known.

Furthermore, each testis, instead of lying freely in the coelom, is surrounded by a small sac, which is only large enough to contain the testis (see fig. 15); this sac is attached to the lateral parietes some way above the nerve-cord by a thin mesentery (fig. 15, mes.), and directly to the septum which divides its segment from the one following. This sac has for its size tolerably thick muscular walls, and of course a lining as well as a coating of peritoneal cells.

The vasa deferentia have the same curious arrangement that Rosa was the first to describe (10) in Teleudrilus, and which I have already mentioned as occurring in Hyperiodrilus; each vas deferens perforates septa 10, 11, or 11, 12, and then, passing back, again perforates them to reach the interior of one of the sperm-sacs which depend from the posterior surface of these septa.
But in Heliodrilus there are some differences of detail. The expanded portion of the vas deferens, which lies in front of septa 10, 11, and 11, 12, is proportionately much larger, while the narrow neck by which it is connected with its funnel is much longer than in Hyperodrilus.

Furthermore, the expanded portion lies in the coelomic space which contains the testis, or rather it is closely invested by a narrow space (figs. 11, 16, and 18, coelom), which is perfectly continuous with that enclosing the testis. Sections show that there is no real demarcation between these spaces, which form on each side a pair of sacs—one larger enclosing the vas deferens, and one smaller containing the testis. It should be mentioned that the vas deferens itself on the posterior side of each of the septa lies quite freely in the coelom.

The dilated region of the vas deferens is quite similar in structure to the rest of the tube; it is lined by a layer of low columnar ciliated cells, and is invested by a sheath containing a few muscular fibres. The interior, as in Eudrilus, was filled with loosely lying spermatozoa, not compacted together in any way.

The proportions of this dilated sac to the oesophagus are shown in fig. 11, which is copied from a drawing made by the help of the camera lucida. The details of structure and the proportions of the investing sac are more clearly shown in fig. 35.

Atria.—I term the structures in question “atria” rather than “prostates” for the reason that I have given elsewhere (4), and recapitulated briefly on p. 248 of the present paper. They form a pair of long tubes, which were disposed as follows in my specimen. On the right side of the body the atrium, which opens, as already stated, on to the 17th segment, passed straight back as far as the 24th segment; it was then sharply bent back upon itself, and again reached the 17th segment, where it ended blindly. On the left side the atrium was entirely contained within the 17th, 18th, and 19th segments, being much folded (fig. 18).

A dissection of the worm did not show any differentiation of
the atrium into a glandular and an efferent section, such as is found in *Hyperiodrilus* and in other earthworms. There is no such sharp demarcation between the highly glandular more distal part of the atrium and the duct which perforates the body-wall, and is lined with simple columnar epithelium.

The glandular part of the atrium has the typical structure, although the demarcation between the two layers of cells was obscured by the great abundance of secretion; the inner layer could be only detected by the presence of a regular row of nuclei. Towards the external aperture the character of the lining epithelium gradually alters: this alteration affects, in the first place, the thickness of layers; they become gradually thinner, until not far from the external orifice there is but a single layer of cells. The cells in this layer (fig. 39) are of two kinds—large swollen glandular cells with a scanty amount of protoplasm lie embedded in a mass of narrow columnar cells; when the tube enters the body-wall on its way to the exterior the glandular cells disappear, and there are only columnar cells present of a non-glandular character.

The vasa deferentia, as in *Hyperiodrilus* and *Eudrilus*, open into the glandular portion of the atrium, which is, I should remark, not divided into two chambers bound up in a common sheath, as it is in *Eudrilus*. The two vasa deferentia retain their distinctness, and open into the atrium (fig. 42) at some little distance from each other.

The glandular part of the atrium has a very thin muscular sheath; this becomes thicker towards the external orifice, where it is plainly divisible into two layers—an outer layer of circular fibres, and an inner layer of longitudinally running fibres. The layers, however, are even here very thin, and do not consist of more than two rows of fibres. The two atria traverse the body-wall independently of each other, and unite at the bottom of a tubular depression which communicates directly with the exterior. The structure of the parts is such that it does not appear to be capable of eversion as a penis. There are no penial setæ present. The body-wall is considerably thickened in the region of the atria for some distance on
either side of the ventral line; the thickening ceases at the first seta.

A curious fact in relation to the atria is the connection of the nephridia with these organs. In the other segments of the body the nephridia open in front of the lateral setæ; but in the 17th segment the duct of the nephridium traverses the ventral body-wall in an oblique direction, and joins the atrial duct just before its opening into the external depression already spoken of (fig. 40). As this occurred on both sides of the body it does not seem likely to be an abnormal condition characterising the individual only.

§ Summary of more important facts in the structure of Heliodrilus and Hyperiodrilus.

(1) The epidermis is furnished as in other Eudrilidæ, and in that family alone, with peculiar organs possibly of a sensory nature; these consist of a central nucleated core surrounded by many nucleated sheaths; the organs have a certain resemblance to Pacinian bodies of Vertebrates, and are scattered irregularly over the surface of all the segments save the first.

(2) The alimentary canal has a single pair of large lobed calciferous glands in the 13th or 14th segment; in each of Segments 10, 11, 12, is a median diverticulum of the oesophagus, of which the epithelium is much folded, so that it presents the appearance of a series of parallel tubes; peripherally the cells themselves are excavated, and form a ramifying system of ductules; the pouch of Segment 10 is smaller, and the foldings are much simpler and do not anastomose. There is no anterior gizzard, but six gizzards, one to each segment, at the junction of the oesophagus with the intestine.

(3) The supra-intestinal blood-vessel in the oesophageal region is enclosed in a special coelomic compartment, which is almost filled by deeply staining nucleated corpuscles.

(4) The male genital pore is single and median upon Segment 17. The "atria" are glandular and very long; in Heliodrilus the vasa deferentia open into them in both genera. In neither are there any penial setæ, but in Hype-
riodrilus there is a penis, which is a hollow process of the body-wall. In both genera the vasa deferentia open in the 11th and 12th segments into the interior of the sperm-sacs; each vas deferens perforates the septum, from which the sperm-sac depends, twice.

(5) The ovaries are enclosed in special coelomic sacs which communicate with the egg-sac, and are prolonged dorsally so as to entirely (Hyperiodrilus) or partially (Heliodrilus) enclose the single spermatheca which opens on the middle line of the 13th (Hyperiodrilus) or 11th (Heliodrilus) segment; in the latter case the spermatheca itself lies in the 13th segment, and has a long duct. In Hyperiodrilus the perigonadal sacs form a ring round the oesophagus, and are connected with a dorsal unpaired sac.

III.—Some Notes upon Nemertodrilus griseus, Mich.

The principal points in the anatomy of this Eudrilid have been already made out by Michaelsen; there are, however, a few facts of minor importance which I have been able to note down from the examination of specimens which Dr. Michaelsen was so good as to place at my disposal. With regard to the female reproductive organs, I can only confirm the accurate description given by Michaelsen; but the structure of these parts suggests certain reflections concerning the homologies of the various organs which constitute the female reproductive system in the Eudrilidae. As Michaelsen has stated, the cavity of Segment 13 is greatly reduced, so that the ovaries are enclosed in a narrow chamber; the receptaculum ovorum communicates with this segment, and is also connected with a large pouch extending on each side of the body through several segments.

Michaelsen suggests that these large pouches may be possibly the equivalents of the receptacula and the distal part of the spermatheca. The proximal part of the spermatheca on this supposition is represented by a pair of orifices, of which more later, opening into the exterior of the body from the reduced cavity of the 13th segment. Dr. Michaelsen decides, however,
that most probably the sacs in question are simply extensions of the egg-sacs, inasmuch as there is no definite break between them and the egg-sacs; the trabeculae which divide up the interior of the egg-sac into a series of more or less isolated compartments, as in other earthworms, get gradually less and less until the cavity becomes perfectly smooth.

The paired orifices upon the 13th segment are considered by Michaelsen to represent the rudiments of spermathecae which open into this segment in other Eudrilidae.

These orifices are fringed with numerous frayed-out cellular processes, which would appear to be of the nature of proliferations of the peritoneum.

The effect of these must be analogous to the twigs of a lobster-trap; they would prevent egress from the interior of the segment, but would permit the penis to be thrust in. It seems most likely that these orifices are used in copulation; the sperm can then readily find its way into the interior of the egg-sacs; and as a matter of fact I can fully confirm Michaelsen’s statement that bundles of spermatozoa are found in the interior of these sacs.

The large sacs which extend from the 14th to the 17th segment seem to me to be in all probability equivalent to the coelomic sacs which I have just described in *Hyperiodyrilus* as encircling the oesophagus and fusing above it to form a large unpaired sac. I consider that Michaelsen is quite right in deciding that they do not represent a portion of the two spermathecae cut off from the duct leading to the exterior; but, on the other hand, I regard my own identification of these openings as a little more probable than that of Michaelsen.

The relationship of the egg-sacs to the coelomic sacs in this genus and in *Hyperiodyrilus* is something like that of the sperm-sacs in *Dichogaster* and other worms to certain sacs connected with the testes and the funnels of the vasa deferentia. It is, perhaps, worth remarking that the connection of these sacs above the intestine is curiously paralleled by the connection of the ovarian sacs in *Hyperiodyrilus*. Next, with regard to
the paired orifices upon Segment 13, Michaelsen considers these to be the remains of the spermathecae which open on to this segment in Eudriloides, Teleudrilus, and other Eudrilids. This identification cannot be regarded at present as being anything more than possible. The spermathecae of Lumbricus are developed as involutions of the epiblast, and if the course of development of the spermathecae in the Eudrilidae is the same, it is not likely that they could ever come to be represented by pores.

Considering the matter necessarily in the absence of any knowledge of the development of the parts in question, it seems possible to regard these pores as the rudimentary equivalents of oviducts.

In describing the structure of Eudrilus I have pointed out that there are apparently two pairs of oviducts present in that worm. One pair, represented in all other earthworms, open on to the 14th segment; the other pair are short tubes connected with the sac involving the ovary in Segment 13; they open in common with the spermatheca and the other oviducts on to the 14th segment.

These peculiarly modified organs in Nemertodrilus are quite intelligible on the hypothesis that they have been derived from the corresponding organs of Eudrilus.

I pointed out that there was some evidence in favour of regarding the oviducts of Segment 13 as being in course of degeneration; they are very short, with feebly developed walls, and the lining epithelium is not ciliated. This reduction is carried further in Nemertodrilus; the oviducts are reduced to the condition of the oviducts in the Enchytraeidae, where there is little more than a pair of orifices. At the same time the cælomic cavity of the segment is greatly reduced; this renders it easy for the ova to reach the exterior through the oviducts of the 14th segment, which are apparently as well developed as in Eudrilus.

In Teleudrilus there is no trace (?) of the oviduct of Segment 13, and, except for the continuity of ovarian sac with the receptaculum, the female reproductive organs of this genus
are not far removed from those of the more typical Oligochaeta.

It is perhaps possible to regard the pores in Nemertodrilus as the earlier condition. Observations upon the abdominal pores and oviducts of certain Ganoids and Teleosteans seemed at one time to indicate that the pores were the primitive structures, and that a groove in the peritoneum, converted later into a tube, connected these pores with their respective gonad. But if Jungersen 1 is right in looking upon the oviducts of Teleostei as being after all Müllerian ducts, this view must fall to the ground. Sedgwick 2 brings forward many facts towards proving that in Peripatus the genital ducts are coelomic sacs communicating with the exterior by pores. The ovary in Nemertodrilus, closely invested by the coelom which opens on to the exterior by a pore, is comparable to the gonad and its duct in Peripatus; it is possible, as I have already suggested, that in Eudrilus the oviduct is only a portion of the coelom connected with a pore; but I am more disposed to hold that Nemertodrilus is in these points a degenerate form of Eudrilus; the reduction of the coelom of Segment 13, and the disappearance of the spermathecae bears out this view.

In any case two pairs of oviducts seem to imply two pairs of ovaries, which are reduced to one by the disappearance of the anterior oviducts. And we thus arrive at the normal condition of the female reproductive organs in earthworms.

In Teleudrilus the complete disappearance of one pair of oviducts is correlated with the disappearance of the second pair of ovaries.

In short, the new facts discovered by Dr. Michaelsen lend support to the conclusions which I formulated in the paper referred to above, apart altogether from the question as to the

primitive or non-primitive condition of the reproductive system in Eudrilus.

The atria present the appearance of the corresponding organs in Acanthodrilus or Pontodrilus—that is to say, they form two somewhat bent tubes of an opaque white colour; they differ, however, in the fact that it is impossible to distinguish a muscular and a glandular portion: in the two genera mentioned, and in many other forms in which the atria are tubular, the organ communicates with the exterior by a narrow duct; this duct is lined with an epithelium which is not in the least glandular, and is surrounded by a tolerably thick muscular coat. In Nemertodrilus no such duct is present; the organ is identical in structure throughout with the glandular part in Acanthodrilus: its epithelium is of two kinds; the innermost layer is formed by a single row of unusually short columnar cells; beneath these are the usual layers of pyriform gland-cells, each with a long slender prolongation which reaches, or nearly reaches, the lumen of the gland.

As Perrier (8) first remarked, the atrium of Eudrilus is remarkable on account of its nacreous appearance and perfectly straight course. The nacreous appearance is due to an enormously thick muscular coat, which I figured in transverse section in a paper dealing with the structure of Eudrilus sylvicola (1).

In Nemertodrilus, as I have already implied by comparing the appearance of the organs to that presented by the atria of Acanthodrilus and Pontodrilus, the nacreous appearance is entirely wanting. Sections of the atrium, however, show that the muscular coat itself is not absent, but is greatly reduced as compared with Eudrilus and, according to Rosa's observations, Teleudrilus. The whole organ, in fact, is a little more degenerate than that of Eudrilus. Considering the absence of the duct, which is so universal a feature of the atrium among earthworms, I should be disposed to regard the atrium of Nemertodrilus as having been derived from that of Eudrilus by reduction,
and not vice versa. There is at any rate nothing in the facts which is opposed to this view, though the converse might be asserted with some probability.

As Dr. Michaelsen has pointed out, the two vasa deferentia of each side retain their distinctness, but are accurately superimposed, thus giving rise to the impression that but one tube is present.

A curious peculiarity in the vasa deferentia of Eudrilus, which appears to be confined to that genus and to other Eudrilidae, was first pointed out by myself. In those genera each vas deferens has, like the atrium into which it opens, a well-developed muscular tunic; each vas deferens, moreover, in those very aberrant earthworms commences with a very wide dilatation immediately connected with the funnels.

In both these points Nemertodrilus differs from its two allies—the vas deferens has neither the oval or spherical dilatation nor the muscular coat; it conforms, in fact, in every particular to the usual type met with among earthworms.

Michaelsen mentions that the two vasa deferentia of each side, maintaining their distinctness to the very last, become lost in the body-wall just in front of the atria.

This is undoubtedly the impression which a dissection of the Annelid produces, but it is not perfectly accurate. The point is one of some little importance as touching the affinities of Nemertodrilus to Eudrilus.

In the latter genus I showed that the vasa deferentia opened into the atrium at about the middle of its length. In Teleu-drilus Rosa has stated that the vasa deferentia also open into the atrium.

In Nemertodrilus a series of longitudinal sections shows that the two vasa deferentia cross the atrium close to its external aperture; they then traverse the muscular coat exactly as in Eudrilus, and each may be recognised still preserving its independence as a ciliated tube lying between the epithelial lining and the muscular coat. They finally open into the interior of the atrium.

Michaelsen has pointed out two characters in which Nemertodrilus...
Nemertodrilus differs from the Eudrilidae: the first is the position of the nephridiopores, which are situated in front of the ventral instead of the lateral setae; the second character is the absence of any glandular diverticula to the alimentary tract.

To these I can add a third character—the absence of those integumental bodies which occur in all other Eudrilidae that have been sufficiently well examined.

The structure of Nemertodrilus shows that it is decidedly an aberrant member of the family Eudrilidae. But the alterations in structure from the typical Eudrilidae do not definitely point in the direction of the Cryptodrilidae, with which family, as I distinguish it, Rosa unites the Eudrilidae.

The only reasons for referring this genus to the Eudrilidae are (1) the absence of spermathecae lying in front of the testes, (2) the completely separate vasa deferentia opening into the interior of the atrium, (3) the large coelomic sacs connected with the egg-sacs, (4) the muscular oviduct.

The absence of any specialisation into the atrium, of dilatation upon the vasa deferentia, of integumental organs, are perhaps indications of degeneration. The fact that the ovary is not, as is the rule among the Eudrilidae, enclosed in a special compartment of the coelom, might be used as an argument for the primitive position of Nemertodrilus among the Eudrilidae were it not for the reduction of the cavity of the thirteenth segment. The reduction of this segment renders the development of any such sacs unnecessary, though of course it does not necessarily follow that they were originally present and have been lost. On the other hand, the pores upon Segment 13, whether Michaelsen's explanation of them or mine be correct, seem to be in all probability rudimentary structures of some kind.

London; September 9th, 1890.
STRUCTURE OF TWO NEW GENERA OF EARTHWORMS. 273

LIST OF MEMOIRS REFERRED TO.

1. Beddard, F. E.—“Contributions to the Anatomy of Earthworms.”


12. Vojnovsky, F.—‘Entwicklungsgeschichtliche Untersuchungen,’ Heft i.

EXPLANATION OF PLATES XVI—XX,

Illustrating Mr. Frank E. Beddard's memoir "On the Structure of Two New Genera of Earthworms belonging to the Eudrilidæ, and some Remarks on Nemertodrilus."

PLATE XVI.

Hyperiodrilus africanus.

Fig. 1.—Female reproductive apparatus, seen after opening body-wall from above and removing one of the calciferous glands. ca. Calciferous gland. sp'. Large ccelomic pouch, connected with a perioesophageal ring. r. o. Receptaculum oovorum. ad. Oviduct. as. Òsophagus. d. v. Dorsal vessel. s. Intersegmental septum.

Fig. 2.—Integumental sense (?) organs in longitudinal section.

Fig. 3.—The same in situ. Transverse section. This drawing also shows the lymph-spaces between the fibres of the circular muscular coat.

Fig. 4.—Diagram of structure of the same.

Fig. 5.—Diagrammatic lateral view of the different parts of the female reproductive apparatus. The segments are numbered. sp. Spermatheca. ov. Ovary. Other letters as in Fig. 1. The walls of the ccelomic spaces are here and there cut away so as to display the contained viscera.

Fig. 6.—Anterior segments from above, to show form of prostomium.

Fig. 7.—A portion of integument, highly magnified, to show relationship of nephridiopore (sp.) to seta (s.) of dorsal pair.

Fig. 8.—Female reproductive apparatus removed from body, but with its relations to other organs indicated. β. Bursa. Other letters as in Figs. 1 and 5.

Fig. 9.—Transverse section to show arrangement of setæ.

Fig. 10.—Transverse section through a portion of perigonadial sac and the neighbouring body-wall. n. Nephridium. Other lettering as in Fig. 8.

Fig. 11.—Diagrammatic view of female reproductive organs. The perioesophageal sinuses and the unpaired dorsal sac in which they meet are pushed back; the Òsophagus is cut away, but the nerve-cord is left. On the left side the anterior wall of perigonadial sinus and perioesophageal sinus is removed in order to display enclosed viscera. The segments are numbered. Lettering as in Figs. 1, 5, and 8.

Fig. 12.—A few segments pressed out to show arrangement of setæ (s.) and position of nephridiopores (n.) by lateral setæ.
PLATE XVII.

Hyperodrilus africanus and Heliodrilus lagosensis.

Fig. 13.—Diagrammatic transverse section of Hyperodrilus in neighbourhood of the female reproductive organs, to be compared with Fig. 14, representing a corresponding section through Heliodrilus.

Fig. 15.—Heliodrilus. The sac, containing testis and its attachment to the body-wall. mes. Mesentery. lm. Longitudinal muscle-fibres.

Fig. 16.—Heliodrilus. Dissection of celomic space, containing testis and first part of vas deferens. The wall of the sperm-sac is partly removed to show funnel.

Fig. 17.—Transverse section through alimentary canal (int.) and the dilated part of the vas deferens (v. d.) of Heliodrilus.

Fig. 18.—Dissection to show male reproductive system of Heliodrilus. ves. sem. Sperm-sacs. atr. Atrium uncoiled; on the opposite side it is left coiled up.

PLATE XVIII.

Hyperodrilus africanus and Heliodrilus lagosensis.

Fig. 19.—Hyperodrilus. Magnified view of the ventral surface of a portion of Segment 17 to show the papillae (pap.) connected by grooves with the penis. The left papilla is on the boundary line between Segments 16 and 17; the right hand one in the latter segment. s. Setae.

Fig. 20.—17th and neighbouring segments of another individual.

Fig. 21.—Heliodrilus. Ventral aspect of anterior segments to show position of male pore (♂), spermathecal pore (♀), and papillae (pap.).

Fig. 22.—Hyperodrilus. A third individual, 17th and neighbouring segments. In this specimen the papillae are symmetrical and upon the 17th segment.

Fig. 23.—Hyperodrilus. Lateral view of genital segments, showing oviducal pores (♀), nephridiopores (♂), and male pore (♂).

Fig. 24.—Hyperodrilus. Ventral view of 17th and neighbouring segments of same individual as that represented in Fig. 19. p. Penis, slightly protruding from male pore. ♀ Spermathecal pore. pap. Papillae.

Figs. 25 and 26.—Hyperodrilus. Sections through ventral oesophageal pouch at two points; for explanation see text.

Fig. 27.—Hyperodrilus. Vasa deferentia, with their peritoneal coat.

Fig. 28.—Hyperodrilus. Dilated portion of vas deferens.

Fig. 29.—Heliodrilus. A portion of a section through the receptaculum

**Fig. 30.—Hyperodrilus.** Transverse section through unpaired œsophageal pouch, to show blood-spaces (*black*) and lumina between folds of epithelium.

**Fig. 31.—Hyperodrilus.** Origin of unpaired œsophageal pouch (*ca.*).  
*d.* Glandular (?) cells found among the ordinary epithelial cells.  
*p.* Peritoneum.

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**PLATE XIX.**

**Heliodrilus lagosensis.**

**Figs. 32—34.—** A series of sections to show the investment of the apex of the spermatheca by coelomic spaces.

**Fig. 32.** The apex of the spermatheca (*sperm.*) lies between two outgrowths of the coelomic sac (*cael.*).

**Fig. 33.** The apex of spermatheca (*sp.*) is now enclosed within the coelomic sac, and the commencement of a second coelomic space within the first is just visible.

**Fig. 34.** This section lies beyond the apex of spermatheca, which just reaches the interior of the sac (*cael''), lying within that (*caelom*) which is continuous with the perigonadal sac.

**Fig. 35.—** Diagrammatic representation of the extremity of the spermatheca (*sp.*) enclosed within a sac, which is itself enclosed within an extension of the perigonadal sac; the narrow canal leading from the latter to the ovary is seen. Portions of the walls of the different sacs are removed to show their contents.

**Fig. 36.—** Section through dilated portion of vas deferens with surrounding coelomic sac.  
*vd.* Ciliated epithelium of vas deferens.  
*p.* Peritoneum covering coelomic sacs; in its interior are seen clumps of cells.

**Fig. 37.—** Section showing structure of spermatheca.  
*ep.* Epithelium.  
*gr.* Granular matter thrown off from cells into the interior of the spermatheca.  
*m.* Muscular coat with blood-vessels, shown black.

**Fig. 38.—** Section showing structure of distal part of atrium.  
*musc.* Muscular coat.  
*n.* Nuclei of innermost epithelial layer.

**Fig. 39.—** Section showing structure of atrium, near to its external orifice.  
Large glandular cells (*gl.*) are seen, separated by interstitial cells.  
*musc.* Muscular coat.

**Fig. 40.—** Section through common orifice of atrium and nephridium.

**Fig. 41.—** Diagram of female reproductive system.  
*sperm.* Spermatheca.  
*sp. o.* Its external orifice.  
*ov.* Ovarian sac, represented as being cut open on
the left side to show the contained ovary. \( sp. \ sac. \) Coelomic sac involving a second sac, in which lies apex of spermatheca; the walls are represented as partly cut away. This part is shown more highly magnified in Fig. 35. \( r. \ o. \) Receptaculum ovarum, represented as being cut open on left side to show funnel of oviduct (\( od. \)). The nerve-cord is removed for the greater part to show the underlying narrow duct of the spermatheca.

Fig. 42.—Section through atrium at the point where the two vasa deferentia open.

Fig. 43.—Section through a portion of one of the ventral cesophageal pouches. \( bl. \) Blood-vessels, coloured black. \( sh. \) Peritoneal covering. \( n. \) Intra-cellular part of lumen.

PLATE XX.

**Hyperiodrilus africanus**, *Heliodrilus* lagosensis, *Nemertodrilus griseus*, *Teleudrilus ragazzii*, and *Eudrilus*.

Fig. 44.—**Hyperiodrilus**. Diagram of male reproductive organs. \( s. \ c. \) Sperm-sac. \( v. \ d. \) Vas deferens. Atria and testes also shown.

Fig. 45.—**Hyperiodrilus**. Longitudinal section through duct, leading from egg-sac. \( c. \) Outer. \( c'. \) Inner peritoneum.

Fig. 46.—**Hyperiodrilus**. Supra-intestinal vessel, enclosed within a peritoneal space, which is divided by trabeculae. In the interstices lie clumps of cells. The peritoneal sac is connected to the dorsal vessel (\( d. \ vess. \)) by a mesentery.

Fig. 47.—**Hyperiodrilus**. Dissection of the anterior end of the worm. \( sp'. \) Anterior. \( sp. \) Posterior of thickened intersegmental septa. \( as. \ sac. \) Cesophageal pouches. \( ca. \) Calciferous glands. \( sp. \) Coelomic sac, connected with periosophageal ring, seen anteriorly. \( v. \ d. \) Vas deferens. \( at. \) Atria. \( g. \) First of posteriorly-situated gizzards. The segments are numbered from the 6th to the 17th.

Fig. 48.—**Heliodrilus**. A few of anterior segments to show overlapping and interconnection of thickened intersegmental septa.

Fig. 49.—**Hyperiodrilus**. Ripe (\( b. \)) and nearly ripe (\( a. \)) ovum. \( z. \ r. \) Zona radiata. \( v. \) Vitelline membrane.

Fig. 50. **Hyperiodrilus**. Germinal cells from ovary.

Fig. 51.—**Hyperiodrilus**. Section through ovarian sacs, to show their interconnection. \( v. \ b. \) Ventral blood-vessel.

Fig. 52.—**Heliodrilus**. Gizzards and commencement of intestine.

Fig. 53.—**Eudrilus**. Diagram of female reproductive system. \( ov. \) Ovary, surrounded by a sac continuous with a duct (\( od. \)). \( ov'. \) Second ovary, sur-
rounded by a sac (receptaculum ovorum) continuous with oviduct (ov.). sp.
Spermatheca. ♀. Female pore.

FIG. 54.—Nemertodrilus. A similar diagram. Lettering as above. od. is simply a pore.

FIG. 55.—Teloudrilus. A similar diagram. Letters as above.
