2. On some Earthworms from British East Africa; and on the Spermatophores of *Polytoreutus* and *Stuhlmannia*. By FRANK E. BEDDARD, M.A., F.R.S.

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(Text-figures 83-88.)

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(1) On some Earthworms from Eastern Tropical Africa in the Collection of the British Museum.

Mr. F. Jeffrey Bell has been so good as to forward to me for identification a number of earthworms which were collected by Mr. L. S. Hinde, C.M.Z.S., at Titui, in elevated country some 3000 or 4000 feet in altitude. The specimens were sent to Prof. Lankester at the Museum, and are of two, possibly three, species. The larger individuals, of which there are three specimens with the head end perfect, belong to the genus *Polytoreutus*, a genus that is, so far as we know at present, peculiar to East and Central Africa; the small worms are referable to the genus *Benhamia*.

Of the larger specimens two at least belong to an undescribed species of *Polytoreutus*; while the third, upon which I shall offer some necessarily brief observations, seems to me not to belong to that species, but to some other which may or may not be new. I shall call the new *Polytoreutus*.

POLYTOBEUTUS HINDEI, n. sp.

The larger of the two specimens, the only one which is absolutely complete, is also fortunately fully mature, with the clitellum developed—so far as I can judge—to its full extent. It measures 130 mm. in length and is a fairly stout worm, having a diameter The external characteristics of this species enable it to of 5 mm. be distinguished from any other species; it seems to bear the closest likeness to Polytoreutus finni, to which species its internal anatomy also affines it; but there is no possibility, I believe, of confounding the two species. The present form is, as has been said, a fairly large and stout worm. Polytoreutus finni is strikingly characterized by its length and slenderness. Nevertheless the appearance of the area which surrounds the generative pores has a certain likeness in the two species, both of which differ in this respect from other species of *Polytoreutus*. As will be seen from the accompanying drawing (text-fig. 83, p. 337), the ventral area of the 1901.]

seventeenth and eighteenth segments is occupied by an exceedingly prominent sucker-like structure; this does not stray beyond the limits of the two segments mentioned. Its outline is that of a rounded square, and the walls which surround the central depression are well marked. In Polytoreutus finni each pore, both the male and the female, has a similar wall surrounding it. In the present species the two seem to have as it were fused together-a state of affairs which is not in the least due to a greater contraction of the worm, since the clitellar region was not at all contracted. The actual orifices within this area I could not detect, and did not wish to injure the specimen by an exploration. I imagine, however,

Text-fig. 83.



Clitellar region of Polytoreutus hindei. $\times 4$.

that the male pore is on segment xvii., a very general position, and that the pore of the spermathecal sac is either on xviii. or just on the verge of xix., *i. e.* that it is placed intersegmentally between segments xviii./xix., also a very general position. This sucker is exceedingly conspicuous, and can be readily seen to bulge ventrally on a lateral view of the worm. It is important to notice that it appears to be fully matured before the clitellum. For in the second specimen, which is only a little more than half the size of that which I have made the type of the new species, there is no trace of a clitellum, but the generative area is quite as well The clitellum of Polytoreutus hindei occupies segdeveloped. ments xiii.-xviii. and is developed all round the body.

Behind the clitellum the next four segments, i. e. xix.-xxii., show a ventral thickening such as occurs in Polytoreutus gregorianus and

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*P. kilindinensis*¹. The appearance is very characteristic of those species, and, apparently, of those only. The grooves between the several segments are perfectly distinct. The appearance of this "Pubertätspolster" is indistinct in the figure (text-fig. 83). 1 could not find a similar structure in *Polytoreutus finni*, between which and *P. kilindinensis* the present species seems to stand.

The settle have the usual arrangement which characterizes the genus, *i.e.* the two setle of the ventral couples stand apart, while those of the lateral couples are closely paired.

As is the case with some but not all of the species of this genus, the *prostomium* does not in the least impinge upon the buccal segment, but is sharply marked off from it by a transverse groove; the prostomium is in fact what Michaelsen has called "prolobisch." There are of course no *dorsal pores*. The *nephridiopores* are in front of the lateral couples of setæ.

Such are the principal external characters of the present species, which are, I think, sufficient of themselves to establish its distinctness. In internal characters the members of this genus mainly differ in the form of the spermathecal sacs and of the spermiducal glands. The other viscera are not so variable, unless, indeed, the form of the sperm-sacs in different species is really distinctive of them and not merely due to varying stages of development. I am disposed to think, from my observations upon the present species, that the sperm-sacs do offer characters of some use in discriminating the species of *Polytoreutus* from each other.

In describing Polytoreutus finni² I drew attention to the extraordinary slenderness of the sperm-sacs, which extend like white threads, hardly, if at all, thicker than the sperm-ducts, for some distance backwards. Michaelsen has by a query suggested that this appearance may be due to immaturity-and a reasonable And yet I am not altogether disposed to enough suggestion. agree with him, since in Polytoreutus hindei I find precisely the same state of affairs. The two sperm-sacs are slender threads which reach back to about the level of the commencement of the spermiducal glands and are swollen here and there like a ganglionated nerve-cord. Now the present specimen is fully mature, as was that of *Polytoreutus finni*, upon which I founded that species. The probabilities appear to me to be in favour of considering the condition of the sperm-sacs as characteristic of the species and not to be due to immaturity. However, the question cannot be settled definitely at present. The sperm-duct is very noticeable in the dissection on account of this thickness, which is fully that of the duct leading from the spermathecal sac to the egg-sac. It has a swollen sac at its beginning, as in the other species of the genus.

The two spermiducal glands are white thick tubes of some length; they have not the extraordinary thinness and length that characterizes those organs in *Polytoreutus finni*. Each gland was somewhat bent like an elbow, a feature often shown by these glands in

¹ See Beddard, P.Z.S. 1901, vol. i. text-fig. 50, p. 188, and text-fig. 51, p. 190.

² "A Contribution to our Knowledge of the Oligochæta of Tropical Eastern Africa," Quart. Journ. Micr. Sci. xxxvi. p. 241.

1901.]

Polytoreutus. The two glands open on to the exterior by a median bursa copulatrix of circular outline, which of course underlies the nerve-cord and the end of the spermathecal sac.

A more careful examination of the spermiducal glands shows that they can, like those of Polytoreutus gregorianus for example, be divided quite plainly into two regions. The "elbow," already mentioned, marks the boundary-line between these two regions. The proximal part of the gland, i.e. that which is nearest to the orifice into the bursa copulatrix, is perhaps one half of the length of the rest. It is oval in form and gradually tapers to a slender tube, which opens into the bursa copulatrix. At the very extremity of the latter, just before its orifice into the bursa, opens the spermduct, which is here as elsewhere covered with a thick layer of muscular fibres which dilate the duct to twice the diameter it would have were there no muscular coat, and, of course, thus accounts for its prominence in dissections. The distal part of the spermiducal gland has not the lateral diverticula that occur in Polytoreutus corruleus, according to Michaelsen's figures and descriptions 1; but it presents some hint of this in a series of irregularly disposed bulgings of the wall of the tube. The bursa copulatrix appears to have a circular contour; but when the upper part into which the spermiducal glands open is pushed aside it is seen to communicate with the exterior by a curved peduncle, so that on a lateral view it appears almost pear-shaped.

The spermathecal sac is like that of several species, including *P. kilindinensis* and *P. finni*, in that it has but two diverticula. The median part of the sac is very wide anteriorly and gradually shrinks in diameter until—where it traverses the bursa copulatrix it is of quite small diameter; from the anterior end two relatively huge lateral sacs are given off, one on each side. These reach back to nearly the point of external opening of the sac. From the underside of each of these, quite hidden until the diverticulum is lifted up, arises the tube communicating with the egg-sac and the oviduct, the arrangement of which parts is as in other species of the genus, there being also a representative of what Michaelsen has termed the "Samenkämmerchen" in *Polytoreutus caruleus*, &c.

This seminal chamber is a very extraordinary formation. In the specimen which I examined there was but one instead of the four figured in *Polytoreutus caruleus* by Michaelsen. The single chamber was choked by a mass of ripe spermatozoa (as I interpret the structure in accord with Michaelsen), the tails of which depended into the lumen of the oviduct, while their heads were apparently fixed in the epithelium of the chamber; this recalls the case of the spermathecal diverticula of many Megascolicidæ, where, as I first showed², the spermatozoa are confined to the diverticula and are there attached to certain glandular cells.

¹ "Beschreibung der von Herrn Dr. Franz Stuhlmann im Mündungsgebiet des Sambesi gesammelten Terricolen," JB. Hamb. wiss. Anst. vii. pl. i. fig. 10, p. 24.

² "On the Specific Characters, &c. of certain New Zealand Earthworms," P.Z. S. 1885, p. 830.

The median part of the spermathecal sac is traversed by two longitudinal blood-vessels, of which one is the ventral blood-vessel and the other a special branch for this part of the body; the two give off branches laterally and have the relations of an artery and a vein.

The interior of the spermathecal sac was filled with a white mass friable, and when broken up of a "curdy" appearance. This when examined microscopically was seen to consist of a granular substance in which I could detect no structure and of multitudinous spermatophores (described below, p. 341).

The immature *Polytoreutus*, to which I have referred, is probably not an example of *P. hindei*. But I am unable to fix its specific identity further. I should have hardly thought it worth while to give any account of this worm were it not for the fact that a study of it enables me to point out that the female generative apparatus is not always developed before the male as I found to be the case in P. kilindinensis¹. In the present specimen the male pore was conspicuous and upon the middle of segment xvii. One of the ventral pair of set has disappeared-naturally the innermost one on either side. On the boundary-line between segments xviii, and xix, was the smaller aperture of the spermathecal sac. The ventral pair of setæ were not modified in the neighbourhood of this pore. Internally I could find no trace of the spermathecal sacs. On the other hand, the sperm-sacs were fairly developed and were divisible, as is often the case in this genus, into a thin proximal region and a stout distal region. They originated in segment xii., and the thin part of the sacs did not widen out until the fourteenth segment. At the distal end the two sacs were fused together as in P. gregorianus². The terminal apparatus of the male ducts was only represented by a bursa with muscular walls, and of a long and thin form, not a spherical pouch as in Polytoreutus generally. It suggested in fact the disconnected bursa of Stuhlmannia. If the shape was a transitory embryonic feature, it is of interest: but such a bursa may of course characterize the species.

(2) On the Spermatophores of Polytoreutus.

The spermatophores of this genus, the only genus of exotic earthworms save Alma³ known to possess these structures, were discovered by myself in P. magilensis 4 and later in P. violaceus 5.

In the present species they appear to have a very different general appearance from those of the former species mentioned, but they

¹ "A Contribution to our Knowledge of the Oligochasta of Tropical Eastern

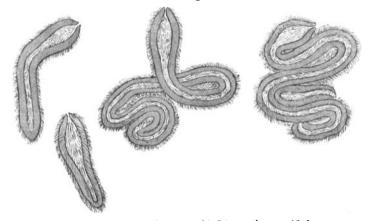
Africa," Quart. Journ. Micr. Sci. (n.s.) xxxvi. p. 240. ² P. Z. S. 1901, vol. i. p. 193. ³ See Beddard, "On the Clitellum and Spermatophores of an Annelid of the Genus *Alma*," P. Z. S. 1901, vol. i. p. 215.

4 "Two new Genera and some new Species of Earthworms," Quart. Journ. Micr. Sci. (n.s.) xxxiv. p. 250.

⁵ "A Contribution to our Knowledge of the Oligochæta of Tropical Eastern Africa," ib. xxxvi. p. 234.

resemble those of *P. violaceus*. The accompanying drawings (text-fig. 84) show their considerable variety of form, which is very striking when a portion of the contents of the spermathecal sac is teased out in glycerine. Claparède¹, as is well known, at first mistook the spermatophores of *Tubifex* for a parasitic organism which he termed *Pachydermon*, a mistake which was later rectified by himself and by Ray Lankester². Had Claparède made his discovery upon the present species, the mistake would have been equally natural. For these remarkable spermatophores, when of large size, are invariably twisted and coiled, precisely like

Text-fig. 84.



Spermatophores of Polytoreutus hindei, greatly magnified.

a bunch of parasitic Nematoids, which animals do occur in the tissues of earthworms. The vermiform appearance of the spermatophores is shown in the drawing (text-fig. 84). There are, however, many of the spermatophores which are much smaller, and 1 have selected a series to illustrate the main varieties which I have observed. The small spermatophores may subsequently grow, though I have noticed no signs of immaturity about them or evidence of any kind that they do grow while within the spermathecal sac.

The complicated coils into which some of the spermatophores have thrown themselves seem to me to indicate the strong possibility that they are motile. There is no doubt whatever that the

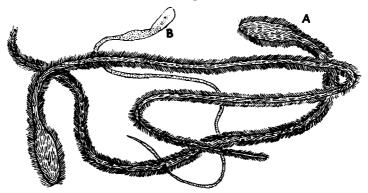
¹ "Études Anatomiques sur les Annélides, Turbellariés, Opalines et Grégarines observés dans les Hébrides," Mém. Soc. Phys. et Hist. Nat. Genève, xvi. 1861, p. 88.

² "On the Structure and Origin of the Spermatophores or Sperm-ropes of *Tubifex*," Quart. Journ. Micr. Sci. xi. p. 189. For a fuller account of the literature of the spermatophores in the Tubificidæ, see Vejdovsky's 'System u. Morph. d. Oligochæten,' Prag, 1884, p. 151.

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spermatophores of Tubifex and some of its allies are motile. Many observers have noted this fact. Thus one of the first, if not the first, to note the point, Jules d'Udekem¹, remarked that " ils font quelquefois plusieurs circonvolutions." Before him Budge² had described these structures in Tubifex or in Limnodrilus; and though stating that they bear "cilia" (which are of course the ends of the individual spermatozoa) did not comment upon their motility as a Gegenbaur in his 'Grundzüge' records the movement of whole. these spermatophores. Claparède 'observed that "ils agitent leurs cils longs à la manière des Dicyema, mais ne changent que peu de place. Leur pouvoir de locomotion paraît assez limité." On the other hand, in Psammoryctes umbellifer (or P. barbatus as it apparently should be properly called) Lankester 4 noted a movement of great rapidity which resulted in the description of "a figure of eight passing and repassing on the same track." The enormous quantity of the spermatophores within the spermathecal sac is very noteworthy and a difficult fact to understand. It must be borne in mind, however, that *Polytoreutus* produces a considerable quantity of eggs, while the Tubificidæ, in whose spermathecæ there is but room for a few spermatophores, have large-yolked and few eggs.





Spermatophores of *Polytorcutus magilensis*, greatly magnified. A, fully mature spermatophore; B, an empty case.

My original drawings of the spermatophores of *Polytoreutus* magilensis do not do entire justice to their remarkable form in that species, though the sketch given is quite an accurate representation of a spermatophore. I therefore exhibit some sketches (textfig. 85) which will enable the spermatophores of the two species

¹ "Histoire naturelle du Tubifex des Ruisseaux," Mém. cour. et Mém. des Sav. étrang. Acad. Belg. xxvi. p. 26.

²" Ueber die Geschlechtsorgane von Tubifex rivub. 100," Arch. f. Naturg. xvi. 1850, p. 7.

³ Loc. cit.

4 Loc. cit.

to be compared together. Up to the present these and P. violaceus are the only three species of the genus in which they have been 1 have re-examined P. gregorianus and P. finni in discovered. the hope of finding spermatophores, but quite in vain. The matter would be of obvious interest, since it is clear from the drawings exhibited that the two species with which I am concerned in the present communication can be amply discriminated by their spermatophores alone. In P. magilensis they are all of the same form and vary only in their length, which is in some cases (see text-fig. 85, p. 342) considerably in excess of the length which I originally figured. The spermatophore is extremely thin in proportion to its length, and is expanded invariably at one end into a spoon-shaped head. It dies away at the other end to a tine point. The body throughout is closely beset with a fine covering of spermatozoa, and I cannot but doubt that these spermatophores also are mobile during life. But they were not twisted into the tight coils so characteristic of those of P. hindei. The relative sizes and the differences in structure can be gathered from the sketches (text-figs. 84 & 85).

In originally describing these spermatophores 1 commented upon their likeness to immature spermatophores in *Tubifev*, and thought that they might be in a state of immaturity. However, the occurrence of abundant spermatophores of precisely the same form in a second individual of the same species which I record here seems to me to do away with that possibility. Furthermore, there were no intermediate stages which would suggest a development of the theoretically immature spermatophores of P. magilensis into fully formed ones like those of P. hindei and P. violaceus. All the spermatophores-a very large number and, as I have already stated, from two individuals-were at precisely the same stage, which must be therefore, I should imagine, their definitive stage. Among the fully-formed spermatophores were a number (textfig. 85, B) which had lost their contents, and were simply empty sacs, more or less hyaline in character, and preserving the exact form of the uninjured spermatophore. This material was not suggestive of the granular matter figured by Vejdovsky in the immature spermatophore of Tubifex, which he ascertained to proceed from the secretion of the cement-gland or at least from the atrium of that worm. It appears to me, in fact, that the spermatophores of *Polytoreutus magilensis* are really constructed on the same plan. those of the two other species of the genus in which they occur, but that the actual case of the spermatophore is much more slender and thus the spermatozoa project much further out. The result is an entirely different aspect, which is well shown in the drawings exhibited herewith. As to the spermatophores of Polytoreutus violaceus and P. hindei, their close likeness to those of the Tubificide other than Bothrioneuron is very striking, and applies to details of structure. Very often, though not in every case, the anterior end of the spermatophore, which is sometimes slightly swollen, was distinctly open, as shown in the 23*

drawings (text-fig. 84, p. 341). This peculiarity has been lately figured by Vejdovsky¹ in Tubifex blanchardi, a species of that genus discovered in Algeria. Among the exceedingly numerous spermatophores of P. hindei and P. violaceus, I did not discover any intermediate forms which were suggestive of immaturity. The shorter spermatophores I do not regard as immature, as they possess the same layers and are of equal thickness with the largest. I have been able to find no evidence at all of a conclusive nature as to the site of the formation of these spermatophores in the genus Polytoreutus, so remarkably like those of Tubifex, Limnodrilus, Psummoryctes, &c. Frequently the spermatophores could be observed imbedded among the tall columnar cells of the spermathecal sac, which has bowed right and left to make way for them. But in such cases there was no organic fusion between the cells and the spermatophores suggestive of their origin from these cells.

It is interesting to note that an earthworm has now been shown to possess spermatophores which agree in all essentials, and even further, with the spermatophores of the Tubificidæ. On the other hand, Stole has shown in Bothrioneuron vejdovskyanum²-and I have been able to confirm his results in another species of that genus, B. iris³—that a Tubificid may possess spermatophores essentially like those of a Lumbricid. These two series of facts further break down---if any more destruction is necessary---the old division of the Oligochæta, devised by Claparède, into Limicolæ and Terricolæ. It is difficult, however, to understand why the form of the spermatophores should be so different in earthworms. It is true that many African forms-possibly including the species which is the subject of the present communication-are aquatic, unlike the majority of earthworms. But so are such genera as Alma and Criodrilus, which possess spermatophores of a different The difficulty would be got over were it certain that the form. spermatophores were invariably formed in the spermathecæ. But it appears on the whole that their elongated form and at least the central axis is a product of the spermiducal glands in *Tubifex*, and, according to Lankester, the bulk of the outer case is also a derivative of the epithelium of the atrium or of the cement-glands.

That they are moulded in the spermathecæ seems to be proved by Lankester's researches. There is, however, at present no evidence of a like formation for the sr_ matophores of Polytoreutus. They are, moreover, so totally different from the spermatophores of an allied genus of earthworms, Stuhlmannia, which I shall describe immediately and of which I shall indicate the probable origin, that the place of their formation seems hardly likely to be the same.

(3) On the Spermatophores of Stuhlmannia.

The site of the formation of the spermatophores in the Order

¹ "Note sur un Tubifex d'Algérie," Mém. Soc. Zool. France, 1891, p. 1. ² "Mongrafie Ceskych. Tubificidu," Abhandl. Böhm. Ges. vii.

³ "On an Aquatic Annelid of the Genus Bothrioneuron, &c.," P. Z. S. 1901, vol. i. p. 81.

Oligocheta has been much debated, and is, perhaps, not yet settled in all cases. It seems clear, however, that in such Lumbricids as Allolobophora constricta 1, Alma stuhlmanni 2, and, among the aquatic forms, the Tubificid Bothrioneuron 3, the spermatophores must be formed by the glandular tissue which envelops the exit of the sperm-duct on to the body-wall, since not one of these forms possesses either spermathecæ or tubercula pubertatis, which have been set down by various authors as the seat of their manufacture. Even in those genera of Oligochæta which do possess either spermathecæ or tubercula pubertatis, or both, there is not always substantial evidence in favour of assigning to one or other of these two structures the duties of the production of spermatophores. Thus the comparatively narrow lumen of the terminal enlargement of the male efferent apparatus in Tubifex' and its allies seems better suited to mould the elongated spermatophores of these Annelids than are the comparatively capacious spermathecæ. So too with the genus Polytoreutus, which possesses spermatophores, as I have just pointed out, of pretty nearly the same characters as those of the Tubificidæ: its extensive spermiducal glands with their narrow lumen is, at least on a priori grounds, admirably suited for the formation of the spermatophores, while the enormously capacious spermathecal sacs are distinctly not.

Nevertheless there are facts which seem to show that the permatophores of many Tubificidæ are-at any rate largelyproduced by the activity of the epithelium lining the spermathece. Lankester pointed out that in Tubifav rivulorum there was frequently to be observed a ridge round the "head" of the spermatophore, the form of which corresponded exactly with the contour of the distal end of the spermathecæ where it debouches on to the exterior; spermatophores were even found at this spot fitting into the short diverticula on either side of the end of the spermatheca, which is of course strong evidence of their having been moulded in situ. The same author mentioned in support of his opinion the fact that in Psammoryctes barbata, where the end of the spermatheca has no such crumplings, the spermatophores have not the peculiar head of those of Tubifex rivulorum-a fact which subsequent investigations upon Psammoryctes barbata have fully borne out⁵. At the same time, not all the spermatophores of T. rivulorum have this peculiarity of form; and it is remarkable that in the Algerian Tubifex blanchardi, whose spermathecæ are stated by Vejdovsky⁸

1 "Sull' Assenza dei Receptacula Seminis in alcuni Lumbricidi," Boll. Mus, Zool. Torino, iv. No. 71, Nov. 1889.

² P. Z. S. 1901, vol. i. p. 217. ³ "Monografic Ceskych. Tubificidu," Abhandl. Böhm. Gesells. vii. 1888; Beddard, P. Z. S. 1901, vol. i. p. 81.

" "On the Structure and Origin of the Spermatophores or Sperm-ropes of two Species of Tubifex," Quart. Journ. Micr. Sci. xi. p. 180. ⁵ Vejdovsky, "Ueber Psammoryctes umbellifer (Tubifex umbellifer E. R.

Lank.) und ihm verwändte Gattungen," Zeitschr. wiss. Zool. xxvii. p. 137; Stole, loc. cit. pl. iii. fig. 14.

" "Note sur un Tubifex d'Algérie," Méni. Soc. Zool. France, iv. p. 1.

to be like those of T. rivulorum (though he enters into no detail in the matter), spermatophores with sharply marked-off heads are not figured, the utmost being an oval swelling at that end of the spermatophore. The one positive fact, however, seems to be of more value than these negative discoveries. Prof. Lankester does not assert that the spermatophores are actually formed in the spermathece; he is of opinion that while the epithelium of those pouches " furnishes a secretion which occupies part of its cavity and in all probability also assists as a cementing material in the formation of the sperm-ropes," it is probable "that the bulk of the cementing material is introduced into them with the spermatozoa from the male organs of another worm." It is mainly the moulding and hardening which, according to Lankester, is accomplished in the spermatheca. On the other hand, Vejdovsky' leans towards the view that the axial core of the spermatophore is the result of the activity of the spermiducal glands in the Tubificidæ, while the transparent sheath is a product of the epithelium of the spermathece—a view mainly based upon the fact that immature spermatophores without the outer sheath are found in the spermatheca, and that a secretion enveloping and binding together the individual spermatozoa has been detected in the spermiducal glands. Vejdovsky would thus divide the labour of producing the spermatophores between the terminal portion of the male efferent apparatus and the spermathecæ; but would assign the most characteristic and important part of the spermatophore to the activity of the spermathecal epithelium.

I do not venture to dispute this view, as I have no new facts to urge either in its favour or against it; but I may point out that any actual secretion of the case of the spermatophore by the spermathecal epithelium has not been described. It is true that Nasse² has stated that during the epoch of sexual maturity the epithelium of the spermathecæ undergoes a change and partly breaks down into or secretes a fluid substance, which he compares in its nature to the spermatophore-case. On the other hand, the spermathece of many earthworms show the same features at the time of ripeness, and in them there is no question, apparently, that the spermatophores are not formed in the spermathecæ. Vejdovsky considers this as "höchst wahrscheinlich" '; but adds that the spermatophores of Limnodrilus hoffmeisteri and of L. claparedianus might settle the question, as their spermathece possess glandular cells which are coloured with a granular pigment. The spermatophore of the latter species has been since described by Stole; but it is not apparent from his figures that there is any pigment in the hyaline sheath of the structure. Neither does Vejdovsky again allude to the matter in his later account of the spermatophores of *Tubifex blanchardi*. In the meantime therefore the actual source of the materials employed in the manufacture of the spermatophores in those worms cannot be entirely traced.

¹ System u. Morph. d. Oligochæten, Prag, 1884, p. 153.

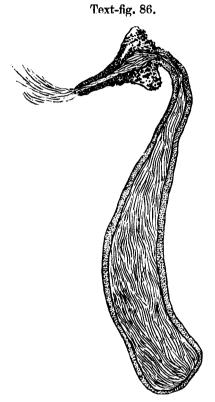
² Beiträge zur Anatomie der Tubificiden, Inaug.-Diss., Bonn, 1882.

The case is, I believe, different with the spermatophores of an earthworm which it is the object of the present paper to describe. The species upon which my observations were made is of the genus Stuhlmannia, an East-African Eudrilid whose general anatomy was detailed some years since by Michaelsen. I am in possession of a quantity of examples of that worm which are in an excellent state of preservation for microscopical work. This Annelid, like other Eudrilidæ, has no true spermathecæ like those of the majority of earthworms, unless, indeed, the actual external orifice of the pouches and the epithelium which passes from the epidermis of the bodywall for a short way into the interior be regarded as the equivalent of the spermathecæ; it has capacious sacs which are probably (in other forms of Eudrilidæ certainly) formed by the peritoneal epithelium, and whose cavities therefore are coelomic. They are lined throughout by an epithelium of tall columnar cells, whose characters I shall attend to in detail immediately. In the spermathecæ are frequently to be found masses of spermatozoa which are not compacted together by any cementing material apparent on staining, but which seem to be perfectly free and floating spermatozoa. This was the case with some examples which 1 studied. In two or three were these masses of spermatozoa compacted into spermatophores, which are always contained in the median sac¹.

The spermatophores of Stuhlmannia differ from those of any other Oligochæta whose spermatophores are known. Their characters are somewhat intermediate between the two types which these organs present in the Order. It will be recollected that in the Lumbricidæ, in Criodrilus, and in Alma the spermatophores are chitinous cases open at one end, but quite impervious elsewhere, of not very elongated form, which are found attached to the body-wall of individuals belonging to these genera in the vicinity of the generative pores. To this type belong also the spermatophores of one genus of Tubificida, Bothrioneuron, which has essentially similar spermatophores, and which, in accordance with their structural resemblance to those of the Lumbricidæ and the other genera mentioned, are attached to the body superficially. On the other hand, in the Tubificidæ (Tubifex, Limnodrilus, Psammoryctes, Clitellio), and in the genus Polytoreutus among the Eudrilidæ, the spermatophores are elongated structures, with often an aperture at one end, and always with the ends of the spermatozoa projecting through their chitinous (?) walls. These spermatozoa are capable of individual movement, which results in a movement as a whole of the spermatophore. They are invariably found in the spermathecæ. Of the first kind of spermatophores, it is certain now that they are formed by the epithelium surrounding the terminal male efferent apparatus. The second kind of spermatophores seem to be, in the case of the Tubificidæ at least, moulded in the spermathecæ, though the precise nature of their origin is

¹ See below (p. 351) for a description and figures of these sacs.

not completely ascertained; in *Polytoreutus* there are no facts which prove one or the other origin for these structures. The spermatophores of *Stuhlmannia* are very large; the largest which I measured was fully 3 mm. in length, and it must be noted that the diameter of the worm in which it occurred was only 2 mm. The spermatophore, therefore, has to lie longitudinally in the spermathecal sac.



Spermatophore of Stuhlmannia, greatly magnified.

The form of the spermatophore is illustrated in the drawing (text-fig. 86). It is not by any means unlike a cestoid worm, for which, indeed, for a moment I mistook it. The strongly pronounced "head" and the bag-like body widening irregularly is very like the immature stage of those parasitic worms. The shape is not, however, suggestive of that of any other spermatophore with which I am acquainted, either at first hand or by descriptions. It has the length of the longest spermatophores of *Polytoreutus*, but the wideness and bulk generally of the spermatophores in the Lumbricidæ. The head end is in several respects reminiscent of the corresponding region of the spermatophore of Tubifex rivu*lorum.* There is a terminal beak, which is followed by a thick collar, after which the-at this part narrow-spermatophore gradually widens out into the bag-like posterior region. The spermatophores are so bulky that there is only room for two in the large spermathecal sac; at least I have not seen more than two, though the sac might accommodate perhaps three with some little difficulty. In every case the mouth of the spermathecal sac was plugged with one spermatophore, while another lay further up the sac and not in contact with the first spermatophore. Lankester, as I have already mentioned, found in Tubifex rivulorum that the head of the spermatophore was moulded by the terminal part of the spermatheca; he proved this not merely by the correspondence in form, but by the actual occurrence of a spermatophore with the projections of the head fitting into the lateral depressions of the spermatheca. I find precisely the same thing in these spermatophores of Stuhlmannia. The wing-like processes of the head fit into concavities and on to convexities on the walls of the spermathecal sac with great accuracy, while the beak-like anterior termination of the spermatophore corresponds to the narrow terminal duct of the sperm-receptacle. There can be, therefore, in my opinion, but little doubt that this part of the spermatophore at least is moulded by the form of the spermathecal sac. The rest of the spermatophore also shows evidence of being moulded by the spermathecal sac. The sac is narrower at first and then widens out. In the same way the spermatophore is narrower at first and afterwards becomes broader. Its diameter is throughout not far short of the sac in which it lies.

The only alternative locality for the formation of the spermatophore in *Stuhlmannia* is the spermiducal gland, or possibly the unpaired muscular sac which opens on to the exterior in relation to the spermiducal glands. But the lumen of neither of these organs has anything like the requisite breadth for the inclusion of the fully formed spermatophore, which cannot therefore. so far as I can see, be possibly moulded in its entirety anywhere save in the spermathecal sac. This, however, is not tantamount to saying that the spermatophore is altogether formed in the spermathecal sac. But before discussing the actual place of its origin, the rest of its structure must be dealt with. The walls of the spermatophore are much thicker at the collar region than elsewhere; in front of the collar the thin and narrow beak has thin walls, and is widely open at the end. This, it must be remembered, is the end which is turned towards, and indeed is not far from, the external orifice of the spermathecal sac. In examining closely with a high power the end of the spermatophore, I observed a stream of spermatozoa which had evidently issued from the open mouth. Why this apparent waste takes place I do not know, but that it must under normal circumstances take place is clear from the width of the mouth, which is not narrow enough to keep the active spermatozoa safe inside. In having this open end the spermatophore of Stuhlmannia agrees with the spermatophores of all(?) other Oligochæta. The walls of the spermatophore behind the thickenings at the neck are thin; their constitution suggests that they are not hardened in the specimens which I have examined. The walls are of a granular appearance, being compacted entirely of smaller and larger, more or less obvious, granules, some of which are more, and others hardly at all, stained by borax-carmine. The spermatozoa within the spermatophore closely fill the case, and for the far greater part, if not entirely, lie with their long axes parallel to the long axis of the sac. At the head-end, but after the beaklike process in which the spermatophore terminates in front, there are a quantity of greenish-black granules imbedded in the walls of the spermathecal sac. I have always seen these pigmented granules in the spermatophores, and with equal constancy at the head part and nowhere else. The point is of some little importance, as will be seen presently. Although the interior of the spermathecal sac is densely packed with spermatozoa, they do not protrude anywhere through its walls. In this characteristic the spermatophore of Stuhlmannia is more like those of the Lumbricide than those of the Tubificidæ, or its near ally *Polytoreutus*. Its soft and collapsible looking walls are, however, different from the hard chitinous cases of the spermatophores of Lumbricus, Criodrilus, Alma, and Bothrioneuron. It may, however, on looking back at its various characters, be regarded as intermediate in form and structure between the two types of spermatophores which I have briefly detailed above.

The question now arises,- Is the wall of the spermatophore formed out of materials provided by the spermathecal sac or does this material, as it does at least to some extent in Tubifex and its allies, reach the interior of the spermathecal from some other source, such as the spermiducal glands? It seems to me that the evidence, as I read it, points to a double origin for the material of the walls of the spermatophores. I have already briefly called attention to the granular and apparently soft walls of the sperma-An examination with high powers of the microscope tophore. shows that among the irregular granules of which the wall is mainly composed behind the neck are bodies which seem to be of the nature of nuclei. I cannot in fact distinguish them from the nuclei of the elongated and irregularly shaped cells of the lining membrane of the spermathecal sac. The size, general shape, and reaction to the staining reagent were identical in both cases, while the cells of the inside of the spermathecal sac were evidently undergoing some breaking up. I may remark at this point, that some observations of Dr. Michaelsen support this interpretation of the characters of the wall of the spermatophore.

Dr. Michaelsen¹ noticed constantly in the spermathecal sac of

¹ "Beschreibung der von Herrn Dr. Fr. Stuhlmann auf Sansibar und dem gegenüberliegenden Festlande gesammelten Terricolen," JB. Hamb. wiss. Anst. ix. p. 27.

this worm a peculiar compact body, "whose structure I was unfortunately unable, on account of the unfavourable preservation of the material, to understand. The whole interior of this body appeared to be formed of a structureless granular mass. An outer layer encloses this mass. This outer layer seemed to me to possess a cellular structure"¹. Michaelsen then suggested the possibility that this body was an embryo- a by no means unnatural suggestion in view of its size and appearance in a badly preserved specimen. I emphasize, however, the remark that the outer layer appeared to be of a cellular nature; as this opinion was no doubt founded upon the observation of the deeply staining bodies, which, I think, must be the nuclei of the cells lining the spermatheca. I am far from asserting, however, that the outer case of the spermatophore is a layer of living cells. This may be so; but in the meantime I should regard it rather as produced by the broken down débris of the cells of the spermatheca, including liberated nuclei, all of which will possibly lese their characters as the spermatophore gets riper. The facts, however, so far do not permit, as I think, of a decisive statement of opinion. So far, then, the case of the spermatophore appears to be a product of the spermathecal sac where it is found. At the head-end of the spermatophore the case is filled with the dark granules already mentioned, which are particularly thickly clustered along the narrow beak. The cells of the spermathecal sac contain no granules of this character. They are like those of the chloragogen cells; but in this particular worm I noticed no chloragogen cells which might serve to explain the origin of the granules. The only place where there were cells filled with such granules were the innermost layer of cells of the spermiducal gland.

The evidence seems to me therefore to be strongly in favour of the view that the wall of the spermatophore in the head-region is derived from materials existing in the spermiducal glands. The final plug of granular matter must therefore be added after the spermatozoa have been injected into the spermathecal sac from the male orifice. There is a remarkable analogy here with the (or a) supposed use of the prostatic fluids in mammals. It has been held that it serves as a plug to retain the sperm in the female organs, and it may apparently harden into a definite plug useful for that purpose. The use of spermatophores of the type described here may be largely to prevent the sperm from wandering and from finding its way out of the receptacle intended for its storage. But it must be remembered that we are at present in absolute ignorance of the way in which fertilization is effected in these Annelids.

(4) On the Ovaries, Oviducts, and Sperm-ducts of Stuhlmannia.

Although the main features in the structure of this Eudrilid genus have been amply elucidated by the careful observations of

' The italics are mine,

Michaelsen ', which 1 am able to confirm, there remain one or two points, in addition to the structure of the spermatophores, which he has not treated of so exhaustively. It is to these that I desire to call attention in the present communication.

I have pointed out myself that there is often in the species S. variabilis², to which my present observations appear to apply, a curious asymmetry of the reproductive organs resulting in the entire disappearance of one of the two receptacula ovorum. The same asymmetry in examples which I have examined by microscopical sections has involved the ovary, there being in at least one specimen but a single ovary which corresponds to the receptaculum ovorum, both being those of the left side. The ovary itself I have succeeded in finding.

Michaelsen's description does not exactly apply to these gonads in the worms which I have examined. His account of the matter, translated, is as follows :---" From the bottom of the sacs [which enwrap the intestine] stretch out small lobulated cellmasses into the lumen of the tubes. These cell-masses stain in picrocarmine with more intensity than the epithelium cells of the walls [of the tube], and can only be regarded as ovaries. This interpretation is supported, apart from their appearance, by their position. The wide atrium extends beyond the level of its external opening forwards, and the point of origin of the two sacs lies anteriorly in the thirteenth segment; thus the cell-masses contained in it lie in the position where the ovaries are normally found among earthworms." There is no suggestion that Michaelsen's second species of Stuhlmannia, viz. S. gracilis, differs from the type species in this point.

Now I find that the single ovary-I found but one, as already stated-is contained in a special forward diverticulum of the terminal atrium of the female spermathecal system, which is in connexion with the two sacs which surround the gut, but is quite distinct from them as a special outgrowth of the complex system of sacs which constitutes in this worm the spermathecal sac. This small forward diverticulum nearly, but not quite, touches the septum dividing the two segments xii./xiii. At the very end the walls of the sac are slightly imperfect so that the tissue of the base of the ovary is there free ; it is not, however, in contact with the septum. The appearances suggest that the ovary has been, so to speak, forcibly torn away from the septal wall by the growth of the sac which has surrounded it. It is important to notice the distinctness of the ovarian sac from the rest of the spermathecal apparatus, since in *Eudrilus* and in other forms a longish duct intervenes between the sac which contains the ovary and the external orifice of the spermathecal sac. The ovarian

¹ "Beschreibung der von Herrn Dr. Fr. Stuhlmann auf Sansibar und dem gegenüberliegenden Festlande gesammelten Terricolen," J.B. Hamb. wiss. Anst. ix.; and "Die Regenwürmer Öst-Afrikas," in Deutsch-Ost-Afrika, iv. p. 23.

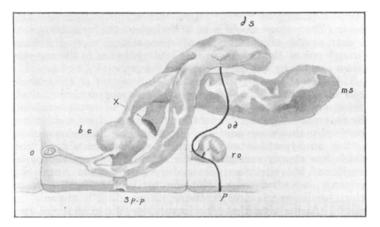
² A Monograph of the Oligochæta, Oxford, 1895. It must remain for the present uncertain whether this species is really *S. variabilis*,

tissue was not much in amount, and I detected no ripe ova therein; but there were cells far on the way to become ova. This gonad, in fact, as always, contrasts with the testes, where the germinal cells are loosened and float into the sperm-sacs before undergoing much development. I direct attention to the diagrammatic sketch (text-fig. S7, p. 354) of the complicated female reproductive system of this Annelid, which has not been figured. It will be noted that the cells from the ovary of the thirteenth segment have to travel an exceedingly devious course to reach the receptaculum ovorum, where, according to current views, they complete their development. The passage would have to be through the terminal atrium to one of the circuncesophageal spermathecal sacs, and then through one of the two ducts only leading thence to the receptaculum ovorum by way of the oviducal funnel.

The alternative view is to suppose the transport of the ovarian cells at a period before the spermathecal sacs are established. But it is not easy to suppose that in such an immature condition the reproductive products would be sufficiently ripe; and if they were, why should so much be left behind? I am disposed to resume an hypothesis which I advanced some years ago¹, and which was stoutly combated by Dr. Horst², but is accepted by Dr. Eisen³, viz., that the contents of the receptaculum ovorum are an ovary, a second ovary belonging to the fourteenth segment which has become evolved in the septal sac which is the receptaculum. At the time that Dr. Horst wrote, the existence of two pairs of ovaries and ducts in the embryo Octocheetus' was not known, nor the double oviducts of Lumbriculus. These and a few other examples show that there is no a priori objection to two pairs of ovaries in an Oligochæte. It is permissible to attempt to show a prima facie case for the enquiry; but I hope to bring forward actual facts in support of the contention. Two ovaries might exist without the presence of two pairs of oviducts; but it is not necessary to weaken the position by allowing only a single oviduct which alone exists in Eudrilus. Stuhlmannia seems to me to have the requisite two pairs of oviducts. The receptaculum ovorum has no communication with the body-cavity or with the outside world except through the oviducal funnel; this is much plicated, and enters nearly every one, if not all, of the chambers into which the receptaculum is divided. Immediately after the funnel narrows into the oviduct it divides into two branches, neither of which is appreciably thicker than the other. I can find no "Eitrichterblase," as Michaelsen terms it. As is shown in the accompanying figure (text-fig. 87, p. 354), one branch runs to the body-wall and opens upon the exterior in the xivth segment in the usual way that the oviducts of earthworms open. The other branch has a rather longer course, and, passing fairly straight,

- ¹ P. Z. S. 1887, p. 376.
- ² Mém. Soc. Zool, France, 1890.
- ^a Proc. Calif. Acad. Sci. ii. No. 2, 1900.
- ⁴ Beddard, Quart, Journ. Micr. Sci. xxxiii.

without windings, opens into the spermathecal sac above the alimentary canal, just at the point where the two sacs surrounding the gut coalesce. The mode of its opening is, however, important for description. The duct, I may say in the first place, has a minute structure which is very similar to that of the part of the oviduct which runs from the funnel to the exterior. It is ciliated



Text-fig. 87.

Semidiagrammatic representation of the female generative system of Stuhlmannia. $\times 6$.

he, bursa copulatrix; ds, dorsal prolongation of spermathecal sac; ms, median region of the same; o, ovary; od, oviduct; p, oviducal pore; sp.p, spermathecal pore; ×, cut end of spermathecal sac.

for a short way below, but higher up appears to lose its cilia. It is lined, however, with cubical cells, and has a thickish muscular wall. The sac into which it opens is of a very different nature: the cells which line it are tall and glandular-looking; it is thus easy to demarcate the orifice of the tube where it opens into the sac. At this point the lower epithelium of the duct is spread out for a short distance round its actual orifice in a fashion quite reminiscent of the funnel of some of the lower Oligochæta; more than this, the cells were ciliated in this region.

As to the ciliation as a criterion of the oviducal nature of the duct, it is apparently not necessary to insist upon it. Eisen distinctly states that the oviduct, the undoubted oviduct of *Eudrilus*, is not ciliated; and Horst did not find cilia everywhere. Now it must be borne in mind that the sacs of the spermathecal apparatus belong to the xiiith segment. Their enormous development causes a growth backwards; but nevertheless the orifice of the mouth of the tube must be placed in the xiiith segment. I cannot in fact explain the structure of this part of the egg-conducting apparatus except on the view that we must look upon the tubes illustrated in the figure as two oviducts with two funnels, each of which funnels will then correspond to one of the two ovaries. The tube which opens into the sac is clearly continuous at the other end with the oviduct which leads to the exterior. It is as clearly not a diverticulum of the spermathecal sac, so different is the histological structure of the two. The only view that I can take of it is to put it down as a second oviduct which unites with the other, as the two sperm-ducts unite on their, way to the exterior; the inappropriate position of the two funnels, which seems to militate against such a view, may be fairly explained by the growth of the enormous spermathecal-sac system.

1 would further point out that the funnels of the oviducts which open into the receptaculum ovorum look backward; they are absolutely turned round, and the tube leading to the exterior starts from the front of the funnel and not from behind it, as is normal in Oligochæta. The same is the case with the presumed funnel of segment xiii., corresponding to the only funnel of The fact that the second (presumed) funnel of segment xiv. segment xiii, looks forward may be perhaps put down to the disappearance of the ovaries and of the receptacula seminis of that side of the body, a fact which has already been referred to. It has retained or reverted to what is presumably the ancestral condition. On the opposite side of the body to that which I have just described, there is no receptaculum ovorum and apparently no ovary; but of this latter fact I cannot be so certain as I am about the former, of which, indeed, there is not the slightest doubt. It became a matter of interest therefore to ascertain what were the conditions of the oviduct. At its orifice into the spermathecal sac above there was no difference whatever. The tube, expanding into what I consider to be a funnel anteriorly, left the sac as a tube in which I did not detect cilia until it arrived at the level of the missing receptaculum. At this point-where I could not find the least vestige of a receptaculum-the tube passed without any change of calibre into the ciliated region, which I traced, not absolutely, but very nearly, to the exterior. The two tubes made one continuous tube with the same low columnar epithelium and thick muscular walls, and without any more vestige of a second funnel than there was of a receptaculum. Both of the two structures have absolutely vanished. We have thus on the left side of the body a single tube of quite different histological structure to, but leading from, the coelomic pouch, which constitutes the spermatheca of this worm, to the exterior.

This arrangement of the oviduct is not, however, peculiar to Stuhlmannia. In Lybiodrilus the oviduct divides before the tube ends in its funnels. One branch opens by the usual funnel into the receptaculum, the other into the spermathecal sac. Neither funnel is large, and I could not see any ciliation in either. I find that my account of Hyperiodrilus and Heliodrilus¹ is not quite accurate as regards the relations of the oviducal funnels.

¹ "On the Structure of two new Genera of Earthworms, &c.," Quart. Journ. Micr. Sci. xxxii. p. 235.

1901.]

In both genera the oviduct gives off a branch before it ends in the funnel lying inside the receptaculum ovorum which opens into the spermathecal sac system near to the position occupied by the ovary of its side. The two funnels are, as in Lybiodrilus, not very different in size, a feature in which they both contrast with Stuhlmannia, where the funnel opening into the receptaculum is enormous and explores every nook and corner of that sac. In Alvania¹ I find, on a reconsideration of my preparations, an identical arrangement. I may mention, with regard to this latter genus, that the cæcum of the oviduct, which I described as being visible in sections, is not an abnormality, as I thought at first, after ascertaining its presence, that it might be. For it also exists in Hyperiodrilus and Heliodrilus-a further reason, I must admit, for uniting these three genera, as has been done by Michaelsen. The same condition appears to exist in other Eudrilidæ, as I judge from certain figures. Thus I am disposed to believe that the tube lettered "os," in Rosa's figure 2 of the female organs of Paradrilus rosa, is the oviducal tube opening into the coelomic sac of the spermathecal system. Possibly also the tube lettered "sq" by Michaelsen³, in his sketch of the genitalia of Unyoria papillata, is of the same nature. In his original description of Stuhlmannia, Michaelsen notes the opening of the oviducts into the spermathecal sac. He does not, however, state explicitly that there are two funnels, only referring to the fact that the oviduct is provided laterally with a receptaculum. In his later and more detailed account of the species, Michaelsen speaks of a funnel situated in the "ovarialblase." The latter paper deals in an appendix with the comparative anatomy of the "Teleudrilinen." a group afterwards abandoned by the author, which contained only those forms with unpaired generative orifices. In that review of the anatomical characters the author mentions in an isolated sentence that "Bei Platydrilus kommuniziert die Samentasche durch je einen Kanal mit den beidern Eileitern." In other cases he speaks of the "Eitrichterblase," by which term the somewhat swollen muscular coat at the junction of the two branches of the oviducts and the tubes themselves are described. The term tends rather to imply a distinct structure, and does not appear to me on this account to be quite appropriate.

I hope that the diagram (text-fig. 87, p. 354) given with this description may render the relations of the oviduct to the coelomic spermathecal clear in Stuhlmannia and some of its allies.

It will be obvious from the foregoing that, whatever view be taken of the homologies of the parts concerned, many, if not all, of the more complex forms of Eudrilidæ undoubtedly possess two oviducal funnels.

¹ "Two new Genera and some new Species of Earthworms" Quart. Journ. Mier. Sei. xxxiv. p. 271.

² "Die exotischen Terricolen des k.-k. naturhistorischen Hofmuseums," Ann. k.-k. nat. Hofm. 1891, pl. xiv, fig. 13. ³ "Die Regenwürmer Ost-Afrikas," in Deutsch-Ost-Afrika, iv. pl. ii. fig. 24.

In many earthworms, for example in *Sparganophilus*¹, the oviducal funnel opens partly into the xiiith segment, but the greater part opens into the egg-sac behind. It might be held that the Eudrilidæ present us with a simple exaggeration of this state of affairs. The separation between the two parts of the oviducal funnel is more emphasized, and at last results in its complete division into two funnels.

On the other hand, as Dr. Benham has pointed out, the actual change which seems to be more possible is that the funnel entirely loses its orifice into the xiiith segment, and comes to open entirely into the egg-sac; this at least is what occurs in Eudrilus. It must be borne in mind that in that genus, which is in some respects the most specialized of the Eudrilide, the spermathecal system is constructed on lines rather different from those upon which the spermathecal system of other genera of the family are built. Now it has been shown that a large part at least of the complicated series of sacs which constitute the spermathecal system originate from the septa of which they are outgrowths, like the egg-sacs or the sperm-sac. It seems therefore at least a possible view that the lateral sacs of Stuhlmannia which encircle the gut are to be compared to the egg-sacs of the xivth segment; that, in fact, they are an anterior pair of egg-sacs belonging to the xiiith segment. To these the second pair of funnels belong. In Eudrilus, where there are no such lateral sacs, there are no oviducal funnels in the xiiith segment. Just as in Stuhlmannia, where on one side of the body the egg-sacs of the xivth segment are wanting, there is a corresponding absence of the funnels of that segment.

Before leaving this matter I would direct attention again to the remarkable asymmetry—which I found so frequently that I am disposed to regard it as normal—of the female reproductive apparatus in this species. I may compare with this an apparently similar, and also apparently quite normal, atrophy of one oviduct and the absence of its external orifice in *Typhoeus nicholsoni*, a species recently described by myself², and the asymmetry of the pores in *Polytoreutus gregorianus*. Asymmetry, of at all a constant character, is so rare in Annelids, that it is legitimate to emphasize these two cases.

The sperm-ducts of the genus *Stuhlmannia* show a peculiarity which has not been apparently mentioned. It was first pointed out by Rosa³ in the case of the genus *Teleudrilus* that the funnels of the sperm-ducts, instead of opening in the normal way opposite to the testes in the xth and xith segments, bent round and opened into the xith and xiith segments. I found subsequently the same arrangement in *Hyperiodrilus*. I had thought, however, that this peculiarity was confined to the Eudriline division of the Eudri-

¹ Benham, "A new English Genus of Aquatic Oligochæta, &c.," Quart. Journ. Micr. Sci. XXXIV. p. 155.

² P. Z. S. 1901, vol. i. p. 195.

³ "Lombrichi delle Scios," Ann. Mue. Oiv. Genova (2), vi. p. 574. PROC. ZOOL. SOC.—1901, VOL. I. NO. XXIV. 24 lidæ. In any case I have ascertained that in several genera of the Pareudriline division the arrangement of the funnels with reference to the testes is carried out on the normal Oligochætous plan. However, in *Stuhlmannia*, with which I deal here, the funnels bend round and open into a funnel which faces the hinder end of the body precisely as they do in *Teleudrilus* and *Hyperiodrilus*. Moreover, a slight swelling of the sperm-duct just after it escapes from the funnel suggests a rudiment of the large chamber into which the sperm-duct of such genera as *Eudrilus*, *Teleudrilus*, and *Hyperiodrilus* expands in the same region. This fact brings closer together the two divisions of the Eudrilidæ. It may be also pointed out that in being thus turned round the sperm-duct funnels correspond more accurately with the oviducal funnels than they do in some worms.

(5) Contributions to our Knowledge of the Genus Gordiodrilus.

This genus was founded ten years ago by myself¹, and five species of it were described, to which a sixth from East Africa was subsequently added². Since that period the genus has not received attention at the hands of any naturalist, though the genus as such has been universally accepted. In the present communication I have some further facts to add to what is known about Gordiodrilus, and the material upon which these observations were made necessitates the creation of one new species. This material was collected in the neighbourhood of Lagos on the west coast of Africa by the late Mr. Alvan Millson. I have examined three examples of Gordiodrilus, which seem to be referable to two distinct species. A fourth worm, though, so far as could be judged, clearly a member of the same genus, was not sufficiently mature to be placed with certainty in its proper species. Indeed none of the species appeared to be quite fully mature. The nearest approach to complete sexual maturity was shown by the one individual which I consider to represent a new species, for which I propose the name of

GORDIODRILUS PAPILLATUS, n. sp.

Of this distinctly new form of Gordiodrilus (text-fig. 88, p. 359) I have had, as already stated, but a single example, nearly if not fully mature. It is a long slender worm like all the members of the genus, and its marked tenuity is more suggestive of Gordiodrilus tenuis than of any other species. It has, moreover, as will be seen in the sequel, other points of likeness to that, the most anomalous species of the genus. The transparency of the body-walls is apparent even in the spirit-preserved individual, and the sperm-sacs show through the delicate body-wall quite plainly. This is also a feature of G. tenuis.

¹ "On a new Genus of Oligochæta comprising five new Species belonging to the Family Ocnerodrilidæ," Ann. Mag. Nat. Hist. (6) x. p. 74.

² F. E. Beddard, "A Contribution to our Knowledge of the Oligocheta of tropical Eastern Africa," Quart. Journ. Micr. Soi. (n. s.) xxxvi. p. 252.

The length of the single specimen was 63 mm. and the diameter varied from 1.50 mm. to 2.75 mm. The latter, the greatest diameter, was taken across the swollen areas on the generative segments, to which reference will be made immediately.

Text-fig. 88.



Ventral aspect of clitellar and neighbouring segments of Gordiodrilus $papillatus. \times 6$.

The prostomium was a little difficult to study accurately. It appears, however, to be like that of other species of the genus and to be what Michaelsen ¹ has termed "zygolobisch," *i. e.* the

¹ "Oligochæta" in 'Das Tierreich,' 1900.

prostomium is not cut off from the peristomial segment by any furrow.

The setce present on the whole the characters of those of Gordiodrilus tenuis in that there is a difference in size between the ventral and the lateral pairs. The ventral pairs are much more marked than the lateral, especially in a few segments just anterior to those which bear the male generative orifices. In this situation they appear to the naked eye as strongish hooks. Five segments or so showed these particularly strong setæ. But an examination of the very last segments of the body showed a similar difference in size, only that here the difference was not so pronounced. The condition of the set of the present species is in some respects intermediate between that which characterizes Gordiodrilus tenuis and G. robustus. In the latter species the ventral setæ of a few segments in front of the male genital pores are markedly larger than the rest. In G. tenuis, on the other hand, the whole series of ventral setæ are much larger than the lateral, and their increased size can, as has been pointed out, be readily felt when the worm is handled. As in some other species of Gordiodrilus, the ventral setse of the generative segments are partly absent.

The *clitellum* is a little difficult to map on a naked-eye inspection of the worm. Segments xviii.-xxii. appeared to be those occupied by this modified region of the integument.¹

The genital region of this species shows several characters which enable the species to be differentiated from all its allies. As will be seen by the accompanying figure (text-fig. 88, p. 359), the segments which carry the male pores are somewhat swollen when compared with those that immediately precede and succeed. On these two segments, which are the xviiith and the xixth, a somewhat figureof-8-shaped tumid area extends from end to end on each side; this is traversed by a longitudinal groove; the whole area of each side measures 3.25 mm. and the groove about 1.8 mm. The swollen structure would seem to be capable of performing the function of a sucker. But in addition to it there are four pairs of genital papillar, the presence of which has suggested the name of the species, and which serve at once to differentiate Gordiodrilus papillatus from any of the other species of the genus which have been hitherto described. These papillæ are arranged in pairs following each other. The first pair are in front of the anterior end of the figure of 8. The last pair occupy a corresponding position behind this figure of 8, and in the middle are the two remaining pairs, closer together than either of them is to the first or to the last pair of papillæ. The groove which traverses the swollen sucker-like structure widens at both the anterior and at the posterior end, and at these points open the spermiducal glands. After an interval of four segments there are three segments, each

 1 I am indebted for the sketch from which the above drawing was made to Miss Fedarb.

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of which bears a median squarish papilla, which are shown in the figure already referred to. The segments which bear these are xxiv., xxv., xxvi. When the worm is viewed laterally these papilla are seen to project markedly. Otherwise they are not very conspicuous by reason of colour or texture.

As in other species of Gordiodrilus, there is a single calciferous gland in segment ix. There are two pairs of hearts in segments x., xi. The gizzard appears to be entirely absent, as is generally the case in the species of the genus. The septa dividing segments v_x . are thickened, the last septum not to so great an extent as are those which precede it.

Male Organs of Generation.—This species of Gordiodrilus, like the majority of its congeners, has two pairs of *testes*, which occupy the usual segments and the usual position in those segments. They are attached, that is to say, to the anterior septum of segments x., xi. There is nothing noteworthy about the structure of these gonads.

The sperm-sacs are rather unusual in number and position. In most of the species of this genus sperm-sacs are present, and it may be that the differences recorded in the number of pairs and the segments which they occupy will prove to be distinctive as marks of specific difference. In Gordiodrilus papillatus there were three pairs of sperm-sacs lying in segments ix., x., xi. These sacs showed the racemose character so often exhibited by these In addition to the three sperm-sacs, which had thin but sacs. perfectly recognizable walls, a mass of loose sperm fills up the ventral part of segments x., xi., which lodge the funnels of the sperm-ducts. It does not appear that these masses of sperm had any walls of their own, so that they cannot be regarded as spermreservoirs; they are merely, as has been stated, masses of sperm for which presumably no room could be found in the sperm-sacs, as the latter were completely filled with the usual masses of developing spermatozoa.

The sperm-ducts commence by large funnels in segments x., xi. They lie, as is always the case, opposite to the corresponding testes. They are much folded, and have not the simple cup-shaped character that sometimes distinguishes the funnels of the lower earthworms. From each funnel arises a sperm-duct, and the two ducts of each side are perfectly independent for the greater part of their course. They lie above the muscular layers of the bodywall. A segment or two in front of their opening into the terminal muscular bulbus, to be described immediately, the two ducts of each side unite, so that there is but a single orifice into the muscular bulbus.

The glands and other structures associated with the external orifice of the sperm-ducts help by their structure to bridge over the not very wide gap that separates the two African genera Gordiodrilus and Nannodrilus¹. The latter genus, originally described

¹ "On two new Genera comprising three new Species of Earthworms," P. Z. S. 1894, p. 388.

by myself, is distinguished from Gordiodrilus by the fact that the sperm-ducts open by a single orifice on each side of the body into a terminal muscular sac; into this also opens one of the two or three pairs of spermiducal glands. In the first described species of Nannodrilus the spermiducal glands are but two pairs, of which the posterior opens into the muscular bulbus on the xviiith segment. In Dr. Michaelsen's subsequently described species N. staudei there is in addition a third pair of spermiducal glands which open behind the muscular bulbus; so N. africanus can be derived from that species by a suppression of the last pair of spermiducal glands. In Gordiodrilus, on the other hand, the sperm-ducts open directly on to the exterior, and not through any terminal muscular bulbus; that at least is the structure of those species which have been investigated up to the present The new form described in the present communication is. time. however, different. There are as usual two pairs of spermiducal glands which open, the one pair behind the other, on to segments xix. and xx. On to segment xix./xx., just at the boundary-line and between the two pairs of spermiducal glands, open the sperm-These ducts, instead of simply burrowing their way ducts. through the integument, open first of all into a largish spherical muscular bulbus like that of Nannodrilus, which is not provided with an appended spermiducal gland. This species is thus intermediate between Nannodrilus staudei and the genus Gordiodrilus as hitherto defined. The middle pair of spermiducal glands may be supposed to have disappeared. *Pygmceodrilus* is a still further reduction of the same structural plan. There is but one pair of spermiducal glands, and the end of the vas deferens is involved in a muscular sheath, which may be looked upon-as Michaelsen has suggested-as the last remnant of such a muscular terminal sac as is possessed by Nannodrilus or Gordiodrilus papillatus. Coming now to the details of structure of these various glands, the spermiducal glands themselves are long and extend through four or five segments in front of their point of opening. It does not seem to be important in which direction the glands lie, but in the present species they are coiled and lie in front of the pores. The glands themselves are, as in other species of the genus, lined with a single glandular layer of cells. The terminal part which perforates the body-wall is short and of less calibre than the glandular part. It is lined by smaller and non-glandular cells ; the muscular layer enveloping it is thin. At the actual orifice one of the two ventral setæ has disappeared; one, however, is clearly present, so that in this matter Gordiodrilus papillatus seems to differ from at any rate some of the other species of the genus, in which the ventral pair of setæ, and not merely one of the two setæ, has disappeared.

Female Organs of Generation .- The ovaries and oviduots furnish

' "Neue und wenig bekannte afrikanische Terricolen," JB. Hamb. wiss. Anst. xiv.

no material for comment. They are quite normal in position and structure.

The spermathecæ are rather peculiar. There are two pairs, which lie in segments viii., ix. Each consists of an oval sac with a simple lining of cells and a very thin muscular wall; this communicates with the exterior by an extremely long slender duct, which is much longer than the pouch itself, and is so thin as to hardly exceed the dimensions of the sperm-duct. There is no trace of a diverticulum. On the left-hand side of segment viii. there were, in the single example of the species which I have had for investigation, two spermathecæ, each with its separate long duct. The two pouches appeared to communicate. It is clear that the spermathecæ of the present species closely resemble those of G, tenuis in the length of their ducts.

It is plain that the species described in the present communication not only, as already pointed out, bridges over the not very wide gap which has hitherto separated the two genera Gordiodrilus and Nannodrilus, but that it also connects the somewhat extreme Gordiodrilus tenuis with the more "normal" species of the genus. The peculiarities of G. tenuis would seem almost to necessitate its inclusion in a separate genus. The existence of only a single pair of testes and of sperm-ducts and the backward position of the male orifices, together with the curious form of the spermatheca, are three points which might be regarded as collectively entitling to generic separation. Gordiodrilus papillatus, however, while agreeing with G. tenuis in the form of the spermathecæ, in the large size of the ventral sets, and approaching it in the position of the male genital orifices, has the normal pair of testes in each of segments x. and xi. The clitellum, too, is like that of other species, and is not so prolonged as is the clitellum of G. tenuis. The setæ, moreover, do not show throughout the body such a marked discrepancy of size as is exhibited by the species G. tenuis.

I shall conclude with a brief definition of

GORDIODRILUS PAPILLATUS, n. sp.

Length 63 mm. Setæ of ventral pairs larger. Male pores on xix., xx., and xix./xx. Gizzard absent. Four pairs of genital papillæ on xix., xx., and three median papillæ on xxiv., xxv., xxvi. Testes two pairs. Sperm-ducts open into a muscular bursa. Spermathecæ, two pairs without diverticula and with enormously long and slender duct.

Hab. Lagos.

GORDIODRILUS ROBUSTUS.

G. robustus, F. E. Beddard, Ann. Nat. Hist. (6) x. p. 82; id. Mon. Olig. 1895, p. 508.

G. robustus, Michaelsen, Oligochæta, Das Tierreich, Lief. x. 1900, p. 374.

Two examples of this species allow of certain additions to the

earlier account of this species, and of a few corrections in matters of detail. The larger of two examples examined measured 72 mm. by a greatest diameter of 2 mm. The worm is thus quite as slender as *Gordiorlrilus elegans*, and the more robust form of the original specimens is perhaps merely a matter of greater contraction.

The openings of the two pairs of spermiducal glands is, as correctly stated in the original description of this worm, upon segments¹ xvii. and xviii. As to internal characters, it has been noted that this is the only species of Gordiodrilus which possesses a gizzard. The structure of this part of the alimentary canal shows some further peculiarities which have not yet been referred to. The gizzard in segment viii. has quite stout muscular walls, but the lining of cuticle is not strongly developed as is the case with earthworms where the gizzard is a prominent structure. Moreover, the gizzard by no means occupies the whole of the viiith segment; the last one-fourth or thereabouts is occupied by a portion of cosophagus, which differs from other parts of that tube in that the muscular layer is rather thick, about as thick as the epithelium lining it. There is thus evidence that the gizzard of this species is in a state of degeneration. In segment vii, there is a similar thickening of the muscular walls of the cesophagus, the layers being again about as thick as is the epithelium beneath them. Here, therefore, is another, and a rudimentary, gizzard to be taken account of. The species seems to be descended from some form in which there were two gizzards in vii. and viii., and while one of them has nearly disappeared the other is commencing to undergo reduction. These facts further emphasize the bond of union between the genus Gordiodrilus and its ally Nannodrilus, though in a different way from the likenesses shown between Gordiodrilus papillatus and Nannodrilus. The genus Nannodrilus has two gizzards, which lie in the two consecutive segments vii. and viii. The facts, however, must apparently be interpreted on the assumption that from Nannodrilus arose two separate lines of descent, one represented by Gordiodrilus robustus, from which again G. dominicensis can be derived as well as perhaps G. ditheca. The second line gave rise to G. pupillatus in the first place, from which may have arisen G. tenuis on the one hand and G. elegans on the other. The relations of G. zanzibaricus² are not so plain as the others appear to me at present to be.

¹ It is necessary to emphasize this fact since some error has crept into my original paper upon this genus in respect to the positions of the spermiducal gland-pores. I find on re-examination of my preparations that in *G. elegans* the pores are correctly stated (upon pp. 84 and 90) to be upon segments xviii. xix., and incorrectly stated (upon p. 95) to be upon segments xviii. On the other hand, in *G. dominicensis* the same pores are, as in *G. robustus*, upon xvii, xviii, as correctly stated on the table on p. 95 of my memoir; they are incorrectly stated upon pp. 91 & 94 to be upon xviii, xix.

² As a small matter it may be well to note that "Gordiodrilus matthewsi," spoken of on p. 453 of the Mon. Olig., is not, as Michaelsen has suggested, a lapsus pennæ for G. robustus but for G. zanzibaricus.

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In the original account of G. robustus the position of the first nephridium was not fixed. The first pair seem to be in segment v. The segments in front of this are so filled up by the pharynx and associated glands that there would appear to be hardly room for a pair of nephridia. The median calciferous gland of this species was single, not paired as seems to be sometimes the case in the species.

The spermathecæ have an extraordinarily long duct, the length of which in relation to the pouch is inadequately represented in the figure illustrating it in the original memoir. It is no thicker than the sperm-duct and runs a straight course to its orifice.

3. Some Notes upon the Anatomy and Systematic Position of the Ciconiine Genus Anastomus. By FRANK E. BEDDARD, M.A., F.R.S., Prosector and Vice-Secretary of the Society.

[Received April 3, 1901.]

(Text-figures 89-91.)

Two out of the three examples of Anastomus oscitans acquired by the Society on Jan. 4th having died, I am able to contribute to our knowledge of the structure of the Order Herodiones by an account of certain points in the anatomy of this genus. So far as I am aware, Anastomus is one of the few genera of Storks which has not been dissected; and, as the genera of this order show some differences of structure, it is important to ascertain how Anastomus stands in relation to its allies. The chief sources of information as to the structure of the viscera and musculature of the Ciconiidæ are those stated below¹.

These various memoirs and books contain information upon nearly all the genera of Storks; the only prominent genus which has not been treated of is that which forms the subject of the present communication. There has not been, so far as I am aware, any doubt as to the truly Stork-like characteristics of *Anastomus*.

GADOW, "Aves" in Bronn's 'Klassen und Ordnungen des Thier-Reichs.'

¹ GARBON, "On the Carotid Arteries of Birds," P. Z. S. 1873, p. 457; id., "On certain Muscles of the Thigh of Birds, &c.," *ibid.* 1873, p. 628; id., "On the Form of the Trachea in certain Species of Storks and Spoonbills," *ibid.* 1875, p. 297; id., "Note on an Anatomical Peculiarity in certain Storks," *ibid.* 1877, p. 711; id., "On the Trachea of Tantalus loculator, &c.," *ibid.* 1878, p. 625.

WELDON, "On the Anatomy of *Phanicopterus* and its Allies," P. Z. S. 1883, p. 638.

FÜRBRINGER, Untersuchungen über Morphologie und Systematik der Vögel, Amsterdam, 1888, passim.

BEDDARD, "A Contribution to the Anatomy of Scopus umbretta," P. Z. S. 1884, p. 543; id., "On certain Points in the Visceral Anatomy of Balæniceps rex," ibid. 1888, p. 284; id., "Notes on ... the Syrinx in certain Storks," ibid. 1886, p. 321; id., "A Note upon *Dissura episcopus*, with Remarks upon the Classification of the Herodiones," ibid. 1896, p. 231; id., The Structure and Olassification of Birds, London, 1898.