XIII.—*A Contribution to the Anatomy of Sutroa.* By FRANK E. BEDDARD, M.A.,
 Prosector to the Zoological Society of London. (With a Plate.)

(Read 4th April 1892.)

Our knowledge of this remarkable genus of freshwater Oligochæta is at present entirely due to Dr GUSTAV EISEN. Within a year or two of discovering the type species, *Sutroa rostrata*,* Dr EISEN found a second species, evidently referable to the same genus, which has been named *Sutroa alpestris*.† Examples of both of these species have been most kindly forwarded to me by Dr EISEN; and I therefore take the opportunity of offering a few observations upon the structure of the genus, and upon its relations to other Oligochæta, as I am able, in a few matters, to supplement Dr EISEN's papers.

The account given by EISEN of *Sutroa alpestris* is evidently based upon a study of the living worm; it is therefore very full as regards the vascular system, but not quite so detailed where it concerns the generative organs, which are more conveniently studied by the section method. It is more especially to these organs that I desire to again draw attention.

It is, however, perfectly clear from EISEN's description that the genus is correctly referred to the family Lumbriculidæ. The contractile vascular cæca are alone sufficient to show this. So far as we know at present, no other family of Oligochæta possesses these peculiar appendages of the dorsal vessel. The reproductive organs also conform generally to the type met with in that family, although there are some differences in detail from the remaining genera of the family.

One rather important point in the external structure of the worm is not mentioned by EISEN: I refer to the *clitellum*. Several of the specimens kindly sent to me by my distinguished colleague were sexually mature, and in these the clitellum was fully developed. *I found it to extend over nine segments, beginning with the VIIth, and ending with the XVth.* In longitudinal sections it was not easy to fix with accuracy the commencement and ending of the clitellum; it did not either commence or end abruptly. As in all other aquatic Oligochæta, the clitellum consisted of a single layer of cells only. Those upon the clitellum differed from those upon other parts of the body by being more granular and by their greater depth.

The clitellar cells were perhaps twice the depth of the epidermic cells elsewhere; looking at a portion of the clitellum near to the middle, and comparing it with a fragment of epidermis from, say, the second segment of the body, it was quite impossible to confuse the characters of the epidermis of the two regions; but the ordinary epidermis

* On the Anatomy of *Sutroa rostrata*, a new Annelid of the family Lumbriculina, *Mem. Calif. Acad. Sci.*, vol. 2, No. 1.

† Anatomical Notes on *Sutroa alpestris*, a new Lumbriculide Oligochæte from Sierra Nevada, California, *Zoö.* vol. ii. No. 4.

passes so gradually into the clitellar epidermis that it is quite impossible to say where one leaves off and the other begins. In any case, the nine segments mentioned unquestionably belong to the clitellum.

The *male reproductive apparatus* is very peculiar in several points—notably in the “prostate glands.” EISEN’s figure (*Zoe*, vol. ii., Pl. xiv. fig. 1) gives the general appearance of the entire reproductive system as seen when the worm is viewed as a transparent object. I find, however, on checking that figure by longitudinal sections, that one or two points are not fully shown.

There are, as is there shown, two pairs of funnels by which the vasa deferentia communicate with the body cavity. They are represented by EISEN as all lying in one segment—the ninth. Dr EISEN reckons the prostomium as a segment; therefore, in accordance with the majority of naturalists, we may consider this segment to be the tenth. I find that the arrangement is not precisely as figured by EISEN. There are a pair of vasa deferentia funnels in the tenth segment, one on each side of the body of course. But the second pair, instead of lying in the same segment, are a segment further forward, *i.e.* in the ninth segment. This arrangement is more like that met with in other Lumbriculidæ, where one pair of funnels is in the segment which contains the atrial pores, and the other pair a segment in front of this. A very remarkable fact about these two pairs of funnels was the marked difference in size. The posterior pair were much larger than the anterior pair. Not only was this the case, but the tube arising from the posterior funnel was stouter than that arising from the anterior funnel. Concerning the opening of the vasa differentia into the atrium, EISEN remarks, “The exact place where the efferent ducts enter the atrium I have not been able to ascertain, but most probably this takes place in the extreme posterior part, possibly in somite XVIII.”

As will be seen from the accompanying figure (fig. 2) one vas deferens *does* join the atrium at the extreme posterior end, running alongside it up to that point; but the other enters the atrium just at the point where it (the atrium) becomes invested by the prostates. This latter vas deferens is the stouter one, which is connected with the posterior funnel. The atrium itself is a long narrow tube, ciliated throughout the whole extent. It communicates with the exterior by a muscular penis which has been described by EISEN; I have nothing to add to his description of this copulatory apparatus, except to say that I did not observe the glands at the external orifice. When the atrium leaves the penis it is coiled upon itself once or twice; it is lined by a columnar epithelium, and is invested by muscular walls, the fibres of which run for the most part in a longitudinal direction; from the eleventh segment onwards the atrium is loosely covered by a thin membrane which lies at some distance from it, and later on comes to be outside the prostates and the sperm-sacs. This membrane looks like the peritoneal investment of the atrium which has got detached. That region of the atrium which is surrounded by the prostates is not ciliated; the prostates are globular masses, of which there were five in the individual which I examined. Eisen figures seven; no doubt there is some variation in individuals. Besides, the membrane, which has already been

spoken of as loosely surrounding the commencement of the atrium, allows plenty of room for the subsequent development of additional prostates. The prostates, as EISEN says, are composed of masses of pear-shaped cells; the ducts of which (a prolongation of each cell forms its duct) open into the lumen of the atrium.

The efferent apparatus of this worm is evidently very interesting; it is constituted upon the plan of the Lumbriculidæ; but there are differences from the typical Lumbriculidæ. The chief difference is in the structure of the atria. In all the Lumbriculidæ hitherto known the atria are globular sacs with a specially thickened peritoneal layer—occasionally termed “prostate.” The same kind of prostate occurs in a genus of Tubificidæ recently described by myself under the name of *Branchiura*,* and also in the genus *Moniligaster*.† In both these genera the large pear-shaped cells which clothe the atrium externally do not communicate with the lumen of the atrium; the prolongations of the cells do not perforate the muscular layer which separates them from the epithelial lining of the atrium. Nor do they, according to VEJDovsky's figures, in *Rhynchelmis*.‡ On the other hand, in the Tubificidæ the “Cement-drüsen” are masses of cells which look at first sight very much like the glandular investing cells of the Lumbriculidæ, but are really outgrowths of the epithelium of the atrium. This has been proved developmentally.

The origin of the prostates of *Sutroa* has yet to be studied; but in the meantime they suggest those of the Tubificidæ more than those of other Lumbriculidæ.

The next question is, What is the nature of the membranous sac surrounding the atria and the prostates? It should be mentioned as a preliminary that this sac also surrounds the sperm-sacs. I think that in all probability this delicate membranous sac is the proper wall of the sperm-sac. The other organs only happen to lie within it, just as the testes lie within the sperm-sacs among earthworms.

A year ago I communicated to this Society a paper upon a remarkable new genus of Oligochæta, which I named *Phreodrilus*; in this worm the atria and the vasa deferentia were surrounded by a membranous sac§ which appeared to be merely the peritoneal layer of the atrium and the vas deferens separated from the subjacent layer. The sac thus formed contained spermatozoa; I compared this arrangement to something of the same kind described by EISEN in *Eclipidrilus*. It may be that here too we have a sperm-sac surrounding the atrium and the vas deferens; but while in *Phreodrilus* the sac in question is nothing more nor less than the peritoneum stripped off from the atrium, in *Sutroa* a layer of peritoneum remains behind.

The study of the development can alone tell us whether there is in *Sutroa* an actual splitting of the peritoneum, or whether there is a formation of a separate sac comparable to the sperm-sac of other Oligochæta.

* On the Anatomy of a new Branchiate Oligochæte (*Branchiura Sowerbii*), *Quart. Journ. Micr. Sci.*, vol. xxxiii.

† On some Earthworms from the Philippine Islands, *Ann. and Mag. Nat. Hist.*, Feb. 1886.

‡ Anatomische Studien an *Rhynchelmis limosella*, *Zeitschr. f. wiss. Zool.*, bd. xxvii.

§ Anatomical Description of two new Genera of Aquatic Oligochæta, *Trans. Roy. Soc. Edin.*, vol. xxxvi. part ii. No. 2.

Apart from this matter, the efferent ducts of this worm have an interest. The reduction of the anterior pair of funnels and vasa deferentia suggest a commencing disappearance of these; were they absent, the structure of the reproductive organs would be that of the Tubificidæ; and more especially of my genus *Branchiura*. In that worm it will be remembered that the atrium is divisible into two regions—apart from the terminal copulatory apparatus. The distal section of the atrium is invested by the prostate; at the junction of this with the proximal half opens the vas deferens; this is precisely what we should find in *Sutroa*; if, that is to say, the anterior pair of vasa deferentia were to disappear. If, on the other hand, the posterior pair of vasa deferentia were to vanish—of which, however, there is no indication—we should get a state of affairs much as is found in the more typical Tubificidæ.

I have suggested that the anterior pair of vas deferens funnels are on the road to disappearance; the tube itself is very much thinner than the vas deferens connected with the posterior funnel; the funnel also is in the same way much reduced. The comparatively large funnels which open into segment X, though spread along the septum, are a good deal folded. On the other hand, the funnels which depend into segment IX are perhaps one quarter the size of the following pair, and are not folded. Moreover, these anterior funnels are so far purposeless that there are no testes corresponding to them. I searched most carefully for the missing testes of segment IX, but to no purpose. I can therefore at the very least say that the testes if present are very inconspicuous; indeed, I think that there is very little doubt as to their total absence.

The testes are fixed by EISEN as occurring in somite X—*i.e.* in somite XI, according to the more usual enumeration of the segments in *Sutroa rostrata*; in *S. alpestris* they are figured (*loc. cit.* Pl. xiv. fig. 1, tes.) as lying in the same segment as that which contains the penis, *i.e.* the Xth; they are spoken of as being “large, and deeply and repeatedly lobed.”

I found, on the other hand, that the testes are not lobed in a distinct manner; they are solid, almost square-shaped organs. But close to them are a pair of peculiar bodies, which are also found in the preceding segment. In the figure referred to as illustrating the reproductive system of the worm the correspondence is clearly shown: I think, therefore, that Dr EISEN has overlooked the testes, and has confounded with them the peculiar structures already referred to as existing in the Xth as well as in the XIth segment. These structures are called “albumen glands,” and the duct leading to the exterior is figured. I am myself of opinion that these bodies (fig. 6) cannot be regarded as of a glandular nature; I could find no trace of a duct, and the tissue of which they are composed is not suggestive of the glandular tissues met with elsewhere in these Annelids.

They spring from the septa, and are, as EISEN has pointed out, of a racemose form; their walls are delicate and muscular; the contents are loosely packed cells, which are like the cœlomic corpuscles. They are not at all like gland cells. I should be disposed to compare them with the “septal sacs” so often met with in the Perichætidæ and in *Acanthodrilus*.

The probability that these sacs are coelomic spaces, and not glandular structures at all, is rendered very great by the fact that on one side of the body a single diverticulum of the spermatheca lay within the sac.*

The ovaries are figured by EISEN as occurring in the XXXIInd segment. The true ovaries, however, lie in a more normal position; I found them in segment XI, corresponding exactly in position to the testes. They appear to be attached not only to the septum of that segment, but also to the cells of the vas deferens funnel. It is true that these supposed ovaries contained no ripe ova, so that I cannot be absolutely certain about the identification. Ripe ova occurred in two of the posterior segments enclosed within the sperm-sacs. The ova, as in all the aquatic genera, are very large, and are filled with spherical yolk corpuscles.

The oviducts open on to the intersegmental groove XI-XII. In sections through the organ a deep cleft is seen to separate the oviduct anteriorly into two halves. In this has collected a quantity of débris, evidently on its way to the exterior.

The single median spermatheca is, as will be gathered from an inspection of EISEN's figure (*loc. cit.*, Pl. xiv. fig. 7), very remarkable in shape. It consists of a large median pouch, from which arise a number of narrow tubular diverticula. Of the homologies of the organ, EISEN writes as follows:—"Considering this central spermatheca in *Sutroa* in connection with the two spermathecæ in *Rhynchelmis*, two theories are admissible. One is, that in *Sutroa* one of the spermathecæ has failed to develop, and that the remaining one has become central by being moved towards the central ganglion, which latter it considerably displaces. The other theory is, that in *Sutroa* the two spermathecæ are represented by, or homologous with, the pairs of branched spermathecal sacs opening into the spermathecal atrium. The latter, then, is only an unfolding of the body-wall deep enough to cause the spermathecæ to become merely appendices to the central spermathecal sac or atrium. I believe this latter theory to be the correct one." It seems to me that there is no need for the existence of a "spermathecal atrium." What has happened is, that there has been a fusion between the originally paired sacs, resulting in a single median sac; in *Cryptodrilus unicus* we have another example of a similar fusion of the spermathecæ in the middle line. The spermatheca (see fig. 5) is divided into two parts; distally it is a large, comparatively thin walled sac; the proximal part is a duct, with more muscular walls, opening on to the exterior. At the junction of the two are given off the diverticula. The existence of diverticula in an aquatic genus is a remarkable fact, particularly in the Lumbriculidæ. They agree, moreover, with the diverticula of earthworms in being of a different structure from the main pouch. The epithelium is lower and more darkly staining; the muscular walls are thicker. Furthermore, the diverticula contain nearly all the sperm. This, again, is a point in which they resemble the diverticula of earthworms. EISEN mentions that he found in one instance "an interior porus in the free end of the spermatheca similar to the one described by

* Compare the enclosure of the spermatheca of *Hyperiodrilus* and *Heliodrilus* within a coelomic sac (*Quart. Journ. Micr. Sci.*, vol. xxxii. p. 235).

VEJDovsky in the receptacula seminis of *Rhynchelmis limosella*. The object of such an opening is not at present understood." In the fully mature worm the reason for the existence of this pore is evident; *there is in fact a direct communication with the lumen of the gut*, quite obvious in sections (see fig. 5). The aperture of communication was very wide, and I could observe the spermatozoa in the gut itself, some bundles being partly in the spermatheca and partly in the intestine. Those who are acquainted with the anatomy of this group of worms will recollect that this fact is by no means new. Dr MICHAELSEN was the first to show that in certain Enchytræidæ the spermatheca has a similar connection with the intestine. He also was able to put the existence of this communication beyond a doubt by observing spermatozoa within the lumen of the gut; the method of staining used made the matter perfectly clear. I have myself had the opportunity of confirming Dr MICHAELSEN's observations upon the Enchytræids. More recently still, something of the same kind has been noted in the Eudrilidæ; of *Paradrilus Rosæ* Dr ROSA† speaks as follows:—"Die beiden terminalen Schläuche der Samentasche setzen sich frei fort, bilden einen unregelmässigen Ring um den Magendarm und kommen mit letzterem ungefähr im 19. Segment in Verbindung. Es ist sehr merkwürdig, dass diese Schläuche wirklich mit dem Lumen des Magendarmes communiciren, doch ist daran nicht länger zu zweifeln. Michaelsen sagte darüber: 'Wahrscheinlich schliessen sie sich (jene Schläuche) oberhalb des Darmes zusammen; bei dem untersuchten Exemplare erscheinen die beiden Enden zerfasert, wie durch einen Missgriff auseinandergerissen.' Bei dem mir vorliegenden Exemplare hatten die beiden Enden der Schläuche ganz dasselbe von Michaelsen beschriebene Aussehen. In Verbindung mit ihnen waren noch einzelne Stücke des leider sehr schlecht erhaltenen Magendarmes, und man hatte den Eindruck als ob jene Röhren wirklich mit dem Lumen communicirten. Diesen Sachverhalt theilte ich meinem Freunde Dr Michaelsen brieflich mit, worauf ich folgende bemerkenswerthe Antwort erhielt (10 Februar 1891): 'Ich habe neuerdings noch zwei interessante *Paradrilus*—Arten untersuchen können. An den einen habe ich, angeregt durch Ihre briefliche Mittheilung, die Einmündung der Samentasche in den Darm mit Sicherheit nachweisen können.' Ein solches Verhältniss ist übrigens nicht ganz neu. Michaelsen selbst hatte schon 1886 eine Communicirung zwischen Samentaschen und Darm bei mehreren Enchytræiden entdeckt. Bemerken will ich noch, dass Michaelsen bei dieser Gelegenheit erwähnte, dass eine Communicirung zwischen Verdauungs—und Geschlechtsapparat (und zwar zwischen Darm und Eileiter) schon von Ijima bei einigen Trematoden (*Polystomum*, *Diplozoon*, *Octobothrium*) beschrieben wurde. Da Zeller seitdem diese Angaben Ijima's für unrichtig erklärte, ist es hier nicht überflüssig zu erwähnen, dass dieselben von Anderen Seiten wieder bestätigt worden sind, so von Wright und Macallum für *Sphyrnura* und in neuester Zeit von Goto (in Tokio) für *Axine*, *Microcotyle*, *Octobothrium* und *Diplozoon*."

It must be, however, remembered that the so-called "spermathecae" of the Eudrilidæ are not the homologues of the spermathecae of other Oligochaeta; they are,

† "Die Exotischen Terricolen des k. k. naturh. Hofm.," *Ann. k. k. naturh. Hofm.*, 1891, p. 391.

as I myself was the first to point out,* and as ROSA also showed subsequently in time of publication, though independently, coelomic pouches. It has been suggested that this opening of the spermathecae into the gut serves to get rid of the superfluous spermatozoa.

It is rather remarkable that those who are on the look-out for vertebrate affinities among the lower animals have not fixed upon these pouches as gill-slits; they would make much more respectable gill-slits than many structures which have been pressed into the service.

The *Nephridia*, as EISEN has pointed out, have a peculiar brown body in the course of the tube just behind the funnel. This appears (fig. 7) to be made up of a mass of round cells, the borders of which are indefinable. Their nuclei are, however, quite obvious, as is shown in my figure. The cells are filled with round spherules of different sizes, which are very closely pressed together. These spherules look exactly like yolk granules. I could not find any lumen running continuously through this mass; at one end a few fine canaliculi were visible, but they seemed to be soon lost. Among the Naidomorpha, in the genus *Ilyodrilus*, and in some other forms this glandular tract following the funnel is met with. In those worms, as Dr STOLC first pointed out, the swelling is permeated by a network of tubes. I think it very possible that the same state of affairs exists in *Sutroa*; but I have at present no certain evidence upon the point. The spongy mass of cells intervening between the funnel and the tube may act as a filter keeping out the grosser particles from choking the lumen of the nephridium. The first pair of nephridia lie in segment VII. There are then a number of segments without any nephridia; they recommence in the XIIIth segment.

EXPLANATION OF PLATE.

- Fig. 1. Semi-diagrammatic longitudinal section through the efferent apparatus of the male organs of *Sutroa alpestris*. *At.*, atrium; *Pr.*, prostate; *v.d.f.*, funnel of vas deferens; *T.*, testis; *Ov.*, ovary; *s.*, muscular sac surrounding the atrium and prostates, and also enclosing the developing sperm; *p.*, penis; beyond the end of the prostates are a series of sacs, one to each segment, filled with developing sperm and ova; *Vd.*, vasa deferentia.
- Fig. 2. Longitudinal section through the atrium and sperm-sacs. *At.*, distal part of the atrium, enclosed within a delicate sac (*S*); *At'*, proximal part of the atrium, surrounded by the prostates (*pr.*), and also lying within a continuation forwards of the same sac; at the upper end of the figure the peri-atrial sac is seen to contain developing sperm; further forwards still (not shown in the figure) the sac contains only developing sperm and ova; *v.d.*, posterior of the two vasa deferentia, which opens into the atrium at the junction of the prostatic with the non-prostatic portion; *v.d'*, anterior vas deferens, opening into the atrium at its extreme end.
- Fig. 3. A more highly magnified section through the epithelium of the prostatic portion of the atrium. *Ep.*, epithelium of the atrium; *pr.*, a few cells of the prostate; *d.*, ducts of the prostates; *m.*, muscular
- Fig. 4. Cross section through the distal part of the atrium. *Ep.*, lining epithelium (ciliated); *m.*, muscular coating; *p.*, peritoneal covering.

* On the Structure of an Earthworm allied to *Nemertodrilus*, &c., *Quart. Journ. Micr. Sci.*, vol. xxxii. p. 539.

- Fig. 5. Longitudinal section through the spermatheca. *Sp.*, spermatheca opening at *a* into the lumen of the œsophagus (*œs.*); *div.*, diverticula of the spermatheca, filled with spermatozoa; these are also shown in the main pouch and in the lumen of the gut; *O.*, orifice of the spermatheca, leading into the distal muscular part of the organ.
- Fig. 6. One of the branched coelomic sacs attached to the septum of segment X. *c.*, cells within the sac; *Sp.*, septum.
- Fig. 7. Funnel and proximal part of a nephridium. *f.*, funnel; *gl.*, glandular mass immediately following the funnel; *n.*, nephridial tube.
- Fig. 8. Region of atrium illustrated in fig. 3, cut longitudinally to show muscular layer (*m.*) perforated by ducts of prostate (*pr.*); the ducts (being prolongations of the individual cells) appear as dots, among which are occasional nuclei.