

# TRANSACTIONS.

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I.—*Observations upon the Structure of a Genus of Oligochæta belonging to the Limicoline Section.* By FRANK E. BEDDARD, M.A., F.R.S.E., Prosector, and Davis Lecturer to the Zoological Society of London. (With a Plate.)

(Read 16th December 1889.)

Some time since I published in the *Transactions* of this Society a paper upon *Phreoryctes*; the present paper is the second of what I hope will be a series of memoirs upon the structure of the Oligochæta Limicolæ; this will be a parallel series to that upon the Oligochæta Terricolæ, which is being published by me in the *Quarterly Journal of Microscopical Science*.\* As I took pains in my paper upon *Phreoryctes* to point out, in accordance with views previously expressed by myself and by others, that it is impossible to draw a hard and fast line between those two groups of CLAPARÈDE, it may seem rather illogical to retain this classification—if only in the title of a paper; I do so simply as a matter of convenience, and without in the least desiring to revive these old divisions of the Oligochæta; indeed the genus *Moniligaster*, which is treated of in the present communication, is by most naturalists regarded as an earthworm; in many points it does undoubtedly agree with certain terricolous genera; but as its affinities, into the discussion of which I shall enter later, seem to me to be more with the Lumbriculidæ, I put it into the Limicoline series; it is useful to have a name corresponding to “earthworm” for those Oligochæta which are not earthworms, and are for the most part aquatic, and I therefore use that term.

The material upon which this paper is based I owe to the kindness of Mr H. E. BARWELL, who collected the specimens in Luzon; some were better, others not so well preserved.

## I. HISTORICAL.

The genus was first recorded by PERRIER [10] in a paper published in 1872; in this he gave a tolerably full description of the anatomy of *Moniligaster Deshayesi*; he

\* See vols. xxviii., xxix., xxx.

regarded this worm with a certain amount of doubt as forming the type of a group (Aclitellians), equivalent to each of the other groups Postclitellians, Anteclitellians, &c.; the distinguishing feature of this group was the complete absence of a clitellum.

The next paper upon the subject is by myself [1]; it contains some notes upon a species of *Moniligaster*, which I regarded, owing to the great discrepancies between my observations and those of PERRIER, as belonging to a new species termed *M. Barwelli*; the facts put forward in this paper and illustrated by a few figures, mainly concerned the anatomy of the reproductive organs. Subsequently Dr HORST [8] described a third species, *M. Houteni*, adding facts of importance to the descriptions of both PERRIER and myself, and supporting my interpretation of PERRIER's account of the reproductive apparatus. Dr HORST's paper was wider in its scope than my own, and dealt with the anatomy of the viscera in general as well as of the reproductive system. A short note [2] by myself emphasised the differences in the reproductive system between *Moniligaster* and all other earthworms, and its resemblance in this respect to some of the lower Oligochæta.

This was repeated with additions in a later paper [4], the genus being still retained among the earthworms, though regarded as forming a special group with strong affinities to some of the "Limicolæ."

Dr ROSA [14], in a paper upon the classification of the "Terricolæ," came to the conclusion that *Moniligaster* was distinctively an earthworm (ROSA regards the Terricolæ as a group not corresponding to a group Limicolæ, but to the various families—Tubificidæ, Lumbriculidæ, &c.—which were associated together to form the Limicolæ), and criticised some of my own statements.

I have already briefly [3] replied to this.

Professor BOURNE [6] in 1886, described, though very briefly, a large number of new species, of which one had a fully developed clitellum, thus showing the absence of that structure to be not distinctive of the genus.

The present paper, of which an abstract appears in the *Proceedings*, contains a somewhat extended recapitulation of the facts concerning the reproductive system, with a general account of the anatomy of the species *Moniligaster Barwelli*, which I have not yet attempted; and finally a discussion of the systematic position of the genus and its relations to other Oligochæta.

## II. ANATOMY OF *MONILIGASTER BARWELLI*.

### § 1. *External Characters.*

This is a very small species, not measuring much over one inch in length and  $\frac{1}{10}$  of an inch in diameter at the broadest part—the head end. The ventral surface posteriorly is rather flattened, while the dorsal surface is very convex. The colour of the spirit-

preserved specimens is a greenish-brown, and the body-wall is so thin that the nerve cord can be plainly distinguished through it.

None of the specimens showed any signs of a clitellum; I suggest later in relation to the affinities of the worm, that this may be due to the fact that that organ, as for instance in the Naidomorpha, is only developed for a very short period.

Among earthworms there is, as a general rule, a considerable inequality in length among the anterior segments of the body; it is only after the clitellum that the segments become equal in size; this is of course connected with the specialisation of the anterior segments in other respects. On the other hand, the rule among the Limicolæ—and to this rule I can at present recall no exceptions—is that the anterior segments, with the exception of the first, are equally sized, though perhaps having some advantage in size over the segments which follow the clitellum; I mention these facts—without desiring to give them undue importance—because *Moniligaster* is so far allied to the Limicolæ and differs from earthworms.

The *prostomium* is extremely small, and projects above the mouth as a short hemispherical process; the first and second segments\* are both very narrow; they are of equal length to each other, and together are about equal to the third body segment. The setæ upon the first setigerous segment are much smaller than those upon the following segment; this fact, combined with the very indistinct line which divides the first from the second segment, led me to confound the two together, and thus to make an error of one segment in my former enumeration. Indeed, any one examining the worm only by the help of a hand lens would be almost certain to make this error, as with this slight magnifying power I found it impossible to distinguish the first and second segments. It is necessary to examine the worm with a tolerably high magnifying power to detect the setæ upon the narrow first setigerous segment; I have mounted two specimens in Canada balsam, and with a preparation of this kind it is possible to reckon the segments accurately.

The prostomium is not at all evident, as it is capable of an unusual (?) amount of retraction.

In one specimen, of which the anterior end was mounted in Canada balsam, I could not detect the prostomium at all; in another individual, mounted in a similar fashion, the prostomium looked like fig. 1; the connection between the prostomium and the first segment could not be detected, and it seemed to be surrounded by that segment. In longitudinal sections (fig. 7) the prostomium could be easily made out and distinguished from the first segment by its tall columnar epithelium; in that section it is seen to be greatly retracted; a very deep groove separates it from the peristomial segment.

The only *apertures* visible upon the outside of the body are the atrial pores in segment X (see fig. 1, ♂).

\* It is perhaps unnecessary to explain that the *first* segment throughout the following description is the peristomial segment, and that I reckon the first setigerous segment as the *second*.

§ 2. *Body-Wall.*

The chief fact to be noticed with regard to the body-wall is the much greater thickness of the anterior segments. Figs. 3 and 4 are drawn to scale, and show that in the front part of the body the total thickness of the body-wall is quite double that of the segments further back.

Attention has been called to this fact by PERRIER, who has suggested that this anterior region may function as a clitellum; as the clitellum in *Moniligastra* has been discovered by BOURNE [6], this is not perhaps very likely, and besides I do not find any difference in minute structure between the epidermic covering of the anterior and posterior segments; the former may perhaps be a little thicker, but that is the only difference. Furthermore, at the hinder end of the body, the thickness of the integument was almost if not quite as great as that of the anterior segments.

The characters of the epidermic cells do not differ from those of other Oligochæta. Large glandular cells with granular contents are separated from each other by fine "packing" cells.

A point of importance is that *the epidermis is vascular*; capillary loops penetrate between the epidermic cells, as is now known to be the case in many Oligochæta, especially among earthworms; in fact, since the vascularity of the integument in the Oligochæta was first pointed out by myself [5] in *Megascolex cæruleus*, many of the principal genera have been shown to share this peculiarity; even among the Limicolæ the penetration of blood capillaries into the epidermis is not unknown, but the thinness of the integumental layers among these smaller Oligochæta is no doubt responsible for the very slight degree in which the body-walls are supplied with hæmal vessels.

§ 3. *Alimentary Canal.*

The *mouth* leads into a *buccal cavity*, which is as usual defined posteriorly from the pharynx by the fact that the cerebral ganglia are placed in the interval between the two; as the cerebral ganglia lie between the third and fourth segments, the buccal cavity may be said to occupy the first three segments; it will be remembered, however, that the two first segments together are hardly equal in antero-posterior diameter to the third; hence the actual space occupied by the unimportant buccal cavity is not great.

The *pharynx* appears to occupy all the remaining space before the first thick mesentery, *i.e.*, two segments, Nos. IV, V. But as there is a considerable length of œsophagus also packed away in this space the pharynx must, I think, be considered to occupy only *one* segment, the IVth. In papers dealing with the anatomy of Oligochæta, the pharynx is often spoken of as occupying four or five segments; and this appearance is frequently presented by a dissection of the fore end of the body. But in many of these instances at least the pharynx itself really occupies a more limited space; its large size has caused the pushing back of that portion of the œsophagus which immediately follows it. There is nothing particular to say about the minute structure of the pharynx.

The *œsophagus* commences as a very narrow tube; this region is pressed up against the first thick mesentery, which separates segments V and VI. Its direction here is ventro dorsal; it must, however, in my opinion, be regarded as belonging to the Vth segment. In the VIth segment the *œsophagus* broadens out considerably, acquiring a calibre about twice as great as that which it possessed in segment V. The *œsophagus* here is quite as wide as the gizzard; this wide region of the *œsophagus* occupies seven segments—VI—XII. (inclusive). I could *not* find any evidence of the existence of *calciferous glands*. But as these structures appear to fluctuate very considerably in their size at different seasons of the year, it is possible that I have overlooked rudiments which might at stated times become large and important glands.

*Gizzard*.—Unless there is a very unusual degree of variation in the number and position of the gizzards, my earlier account [1, p. 94] is wrong. I then stated that *M. Barwelli* is distinguished from *M. Deshayesi* by the absence of a gizzard in the VIth segment, but agrees with that species in the presence of "four oval nacreous-looking dilatations of the *œsophagus* close to its junction with the intestine."

Longitudinal sections (of two individuals) show plainly that *there are only three gizzards*, placed in consecutive segments, and each occupying a segment near to the junction between the *œsophagus* and the intestine. In confirmation of this, a specimen (unfortunately the last which I possess), dissected in order to compare it with the longitudinal section, showed plainly three gizzards situated close together and in consecutive segments. I feel therefore pretty sure that I must in my earlier account have mistaken for an additional gizzard a swelling of the *œsophagus*. The probability of this is increased by BOURNE'S [6, p. 672] observation, that in *M. ruber* "in segments X, XI, and XII, there were soft-walled swellings of the intestine looking like gizzard, only not muscular." The segments occupied by the gizzards appear to be XIV, XV, and XVI. This statement is made on the strength of the dissected individual, and one of the two that were cut into longitudinal sections; the second specimen which I prepared in a series of sections did not show very plainly the exact position of the gizzards.

To the naked eye the gizzards present a longitudinally striated appearance, as is commonly the case with this organ. The striation appears to be chiefly due to the longitudinal direction of the blood-vessels upon the surface of the gizzard; each gizzard, on account of its peculiarly compressed shape and this longitudinal striation, has a most extraordinary resemblance to an onion. This is illustrated in fig. 5 of the Plate.

Fig. 10 illustrates a diagrammatic longitudinal section through the fifteen anterior segments, to show the number of segments occupied by the successive regions of the gut. It is not meant to illustrate the proportionate lengths of these different regions; for example, the pharynx appears much longer than in the figure, while the *œsophagus* is much shorter. This is brought about by the increased space available in segments IV and V, due to the course of the septum separating segments V and VI; this same structural peculiarity reduces the space occupied by the *œsophagus*.

### § 5. *Nephridia.*

The *nephridia* do not commence until the Vth segment; after this there are a pair to each segment of the body, not excepting those which contains the reproductive organs; there is therefore in the position of the first pair of nephridia no striking resemblance to the Limicolæ, such as is shown by *Photodrilus* and *Pontodrilus*; on the other hand, it is perhaps usual among earthworms for the nephridia to commence before the Vth segment, so that *Moniligaster* is in a position somewhat different from that of most genera of earthworms, and pointing towards the aquatic Oligochæta.

The *nephridia* appear to resemble those of *Moniligaster Houteni* in being furnished with a sac-like diverticulum; this again is a decidedly Terricolous character, so many genera of earthworms (*e.g.*, *Acanthodrilus*, *Microchæta*) being provided with such a diverticulum; there does not seem to be any Limicolous type in which the nephridia have a diverticulum.

The external aperture is apparently in front of the more dorsal pair of setæ, but I have not perfectly satisfied myself about this. The internal funnels are quite obvious in longitudinal sections; they are placed on either side of the nerve cord, and lie in the segment anterior to that which contains the nephridium itself.

There is no modification of the anterior nephridia, that I could observe, except that they are perhaps rather larger than those which follow; the funnel occupies the usual position.

### § 6. *Reproductive Organs.*

*Testes.*—These organs have not as yet been described in the genus *Moniligaster*; I have succeeded in finding them in *M. Barwelli*. Fig. 9 of the Plate illustrates the sperm sac and vas deferens; just below the vas deferens funnel on either side is a mass of tissue, which I have for some time believed to represent the testis, without being able to be certain upon the point. Longitudinal sections, through another individual somewhat better preserved, have shown that the body in question is unquestionably the testis. A portion of a section through the genital segments of this individual is represented in fig. 8. In that figure the testis (*t*) is seen to be attached by a somewhat narrow base and to be frayed out at its free extremity into several processes; its shape is quite that of the testes in many Oligochæta (*e.g.*, *Pachydrilus*, *Acanthodrilus*), and the minute structure renders it impossible to doubt that this is really the male gonad.

A comparison of the two figures cited will show an apparent difference in position of the testis and vas deferens, although the two structures themselves have a similar relation, being in actual contact. I may remark, in the first place, that this close connection between the testes and the funnels is very unusual; it occurs in *Acanthodrilus annectens*, where I have figured [4, pl. xii. fig. 13] the testes attached very close indeed to the funnel of the vas deferens which belongs to them; but I am not acquainted with any other species among earthworms in which the same thing occurs.

To return to the apparent difference in position of the testes and vasa deferentia : it looks almost as if in fig. 8 the testes and vasa deferentia funnels were attached to the posterior wall of segment IX ; on the other hand, in fig. 9, the position seems to be different ; the testes seem to be attached to the anterior wall of segment X, and the vas deferens funnel to be attached to the same septum, without perforating it so as to lie in segment IX. Fig. 8 is from a series of sections taken through Xth and neighbouring somites, and it seems to agree with another series taken from the whole of the anterior part of the body, which, however, were not in a very good state of preservation.

I do not see how it is possible to reconcile these two sketches on the hypothesis that the vas deferens funnel and testes have an identical position ; it must, I think, be admitted that in two out of the three specimens the funnel lies in segment IX, and that the testes are attached to the posterior wall of this segment, while in the third specimen the funnel and testis are in segment X.

This difference appears to coincide with a difference in the position of the gizzards, and possibly means that I am dealing with two distinct species.

I do not see how any distortion produced by growth or even by action of reagents can alter the position of the testes to so great an extent as is indicated in the two figures (figs. 8, 9) ; in one case the base of the testis is directed posteriorly, in the other case anteriorly.

*Vas Deferens*.—There are a single pair of these ducts which open into the atrium ; the funnel lies either in the same segment as that which carries the external aperture, or in the one in front (IXth) ; I have already remarked, in describing the testis, that this is probably a specific difference.

The most important point to be noted about the funnel is the extreme simplicity of its structure ; instead of being folded and plaited, as in earthworms generally, it is, as in the Limicolæ, a comparatively simple disc, hardly standing out from the surface of the intersegmental septum to which it is attached.

*Atrium*.—As I have already fully described the atrium with a figure [4], I need do no more here than mention the fact that the atrium as described by me, was that of the individual in which the funnel appeared to be in the IXth segment ; it is so far additional evidence in favour of the differences in the position of the funnel being specific differences, that the specimen in which the funnel appeared to be in the Xth segment, had an atrium somewhat different in structure. The groups of glandular cells surrounding the atrium are no longer distinguishable ; the lining epithelium is surrounded by a thick mass of tissue, which is partly formed of cells and partly of muscular fibres, but there is no differentiation into a distinct muscular layer surrounded by a glandular layer. On the whole, it appears to me to be more probable that the atrium is in an immature condition, and that the glandular and muscular layers are not yet differentiated out of the peritoneal investment of the epidermic invagination (in which way I suppose that the atrium originates). The atrium in this instance is in fact rather to be compared with the immature spermatheca described and figured by BERGH [7, p. 328, pl. xxi. figs. 23, 24] ; and it seems

evidence that the atrium, like the spermatheca, does not trace its muscular layer to an invagination of the body-wall muscle, but that these are formed by a differentiation of peritoneum. This view is not in accord with VERDOVSKY'S figures [4, pl. x. figs. 1, 2] of the developing atrium of *Tubifex*. The view that the atrium is immature, and not structurally different from that of the other specimen, is confirmed by the fact that the genital ducts are only represented by their funnel; the vasa deferentia and the distal portions of the oviducts were not visible in my sections.

*Absence of Penial Setæ at Atrial Pore.*—The atrial pore is situated at the junction of the Xth and XIth segments; the atrium, however, distinctly belongs to segment X, and not to segment XI. It will be seen from fig. 8 that the dissepiment which separates segments X–XI, arises on the posterior side of the atrium; this being the case, the atrium may be spoken of as opening *behind* the setæ of segment X. and not in front of the setæ of segment XI; it is therefore the setæ of the Xth segment that we should expect to find modified, if any; but perhaps as the male pore is not definitely related to either pair of setæ, and is situated so far away from them, we should not on *a priori* grounds expect to find either pair modified. At any rate the fact is that *there appears to be no modification to form penial setæ*. The fact, however, is put forward with due reservation as to its being characteristic of the species, since the specimen is perhaps not fully mature.

*Sperm Sacs.*—As I have already described, there are a pair of sperm sacs, which in some specimens would seem to lie in segment IX, in others in segment X; in both cases they are attached to the intersegmental septum between IX and X. In many specimens which I dissected the sperm sacs appeared to be traversed by the intersegmental septum, *i.e.*, to lie in both segments IX and X; in longitudinal section of one individual, this also appeared to be the case. This specimen happened to be the most poorly preserved, and as in two other cases the sperm sac was either with IXth or Xth segment, I am inclined to believe that the appearances seen in the dissection are simply due to the bulging of the septum. The cavity of the sperm sac is simple—*i.e.*, it is not divided by trabeculæ; in this it resembles the sperm sacs of the lower Oligochaeta; each sperm sac encloses the testis and vas deferens funnel of its own side.

*Oviduct.*—I have nothing to say about the ovary, as I have been entirely unable to discover the least trace of this organ; it lies, however, probably in segment XI. In any case, the oviduct opens into this segment; in two out of the three specimens, which I studied by means of longitudinal sections, I discovered an unmistakable oviduct. In one specimen I have already figured and described this organ [4], the figure being largely a "restoration," as I could not find the entire organ, but only a portion—in fact, only the coelomic funnel. It appeared to me as if the entire oviduct lay in the XIth segment; if this be so—but I cannot be certain about it—there is a curious resemblance to the very anomalous form *Plutellus heteroporus* [PERRIER, 11]. In another specimen the oviducts had not this position; they opened into the cavity of the XIth segment, by a funnel which was closely attached to the dissepiment dividing this from the XIIth segment. I did not succeed in following the oviduct to its external pore; indeed, I do not think that



this portion of the oviduct was as yet developed in the specimen, which I have already shown some reasons for regarding as very immature. The relations of the oviducal funnel are illustrated in fig. 8. It is important to notice that the position of the funnel does not agree with that of the vas deferens funnel.

### III. AFFINITIES AND SYSTEMATIC POSITION OF *MONILIGASTER*.

The first question which arises is, Are all the species which have been described under this name congeneric? This question is raised in consequence of the suggestion of Dr ROSA [14], that *M. Deshayesi* of Perrier "is not only specifically but generically distinct from the other species." Dr ROSA does not state in this paper his reasons for this view, with which I am myself inclined to disagree; of course, if Dr HORST and I are wrong in regarding the anterior pair of testes and vasa deferentia of PERRIER's species as spermathecæ, *Moniligaster Deshayesi* is not congeneric with *M. Houteni* and *M. Barwelli*, but this does not appear to me any more than to Dr ROSA to be likely; accordingly, I consider that this group of worms consists of only one genus—*Moniligaster*.

The next point is, Does the genus *Moniligaster* agree more closely with the "Terricolæ" as defined by ROSA than with any other group of Oligochæta, and is this agreement sufficiently close to warrant its inclusion in the family Terricolæ? or should it rather be regarded as a family equivalent to Terricolæ?

The Terricolæ are defined by ROSA [14] as follows:—\*

1. Two pairs of testes in 10 and 11 (first sometimes wanting).
2. One to four pairs of sperm sacs formed by outgrowths of dissepiments 9/10, 10/11, 11/12.
3. Vasa deferentia generally two on each side, only one if the testes are single, opening by funnels into segments containing testes.
4. A pair of ovaries in 13.
5. A pair of oviducts opening internally into 13.
6. Generally [? always] a pair of receptacula ovarum produced by an outgrowth of dissepiment 13/14.
7. A various number of spermathecæ (except in *Criodrilus*).†

With some apparent exceptions in various points, such as *Microchæta* (in position of vas deferens funnels), which ROSA is inclined to doubt will prove to be real exceptions when submitted to reinvestigation, all earthworms are stated to conform to this definition.

I would remark, in the first place, that the above definition hardly excludes *Phreoryctes*. Add another pair of ovaries and oviducts opening into 12th segment (which sometimes are present in earthworms), and *Phreoryctes*, becomes at once one of ROSA's "Terricolæ." But surely the organisation of the reproductive system in *Phreoryctes* does not point to

\* I only give a condensed epitome, to save space.

† And some few other species, as ROSA and I have lately shown.

its being more nearly allied to the "Terricolæ" of ROSA than to, for example, the Lumbriculidæ?

Does *Moniligaster* find a place among the Terricolæ as thus defined?

ROSA points out that there is a serious discrepancy between the statements of Dr HORST and myself with regard to the position of the various organs of the reproductive system. "It is a remarkable fact that in the description by BEDDARD of *M. Barwelli* it is possible to reconcile the positions assigned by him to the various parts of the reproductive system with that given by HORST, by moving the first two segments further back. The spermathecæ open, according to BEDDARD, in the intersegmental groove 6/7; according to HORST, in 8/9. The male pores are for BEDDARD in the intersegmental groove 9/10, and for HORST in that of segments 11/12. The sperm sacs, according to BEDDARD, depend from dissepiment 8/9, and according to HORST from dissepiment 10/11. Is it possible that in two related species there is such a difference? Is there not rather in one of the two cases an error of enumeration? In that case I shall regard as exact the data of HORST, as they do not demand the admission of any exceptional fact." Dr ROSA omits to mention that PERRIER's data are exactly midway between those of HORST and myself; on *a priori* grounds, I should have considered it more probable that the mean would be correct; in any case (with no prejudice to Dr HORST's statements of fact, which, however, it is very desirable that he should re-examine), PERRIER, I have convinced myself, is right as to the segments upon which the spermathecæ (his anterior vasa deferentia) and atria open; BOURNE also [6] mentions the same segments as bearing the generative pores in all of the seven species described by him. This point may therefore, I think, be regarded as settled. But this correction of my own error, as well as of ROSA's, does not so far invalidate his conclusions—at least not seriously. The statement that "the first pair [of testes] is sometimes wanting" will have to be changed to "the second pair," &c. This point may be conceded. But the position of the ovaries and oviducts will not agree with his definition. Both PERRIER [10] and BOURNE [6] speak of a sac containing ova occupying segments XII–XV; this must surely be *not* ovary, but receptaculum; hence in all probability the ovary does not lie further back than in segment XI. No one has as yet found the ovaries of *Moniligaster*. The oviduct has been partly described by HORST and by myself [4]. I have referred briefly to an organ in segment XI, which is probably the oviducal funnel; I have since traced this through septum XI/XII, but not as far as to its external orifice. This structure may conceivably be a second pair of vas deferens funnels, but it does not seem at all likely that this is so. It is therefore a fair assumption that the ovaries are in segment XI.; but in any case it seems extremely probable that the oviducts have been so far correctly described, and that therefore in this particular *Moniligaster* does not conform to ROSA's definition of the Terricolæ. While therefore, at any rate for the present, I abstain from examining into the naturalness of this group Terricolæ, I feel obliged to oppose the relegation of *Moniligaster* to this group.

Dr ROSA defues his group Terricolæ entirely in terms of the modifications of the re-

productive system; no one will probably find fault with this, as the reproductive system in the Oligochæta generally is most useful for systematic purposes.

From the point of view of its reproductive organs, *Moniligaster* does not agree with any family of Oligochæta. The *clitellum*, which has at present only been described in *M. sapphirinaoides* [BOURNE, 6], probably occurs also in other species, though it is very remarkable that none of the examples studied by PERRIER, HORST, and myself showed any traces of it. It is possible that the explanation of this is that the worm only develops the clitellum during a very short breeding season, as in many of the Limicoline genera. In any case, the forward position of the clitellum (segments X–XIII, inclusive, in *M. sapphirinaoides*) is a remarkable point of resemblance to many aquatic genera—e.g., *Phreoryctes*; it is quite unlike anything that has been recorded among earthworms. I have already dwelt sufficiently upon the resemblance of the atrium to that of the Lumbriculidæ and I may add of *Iliodrilus* (STOLC, 9, Tab. iii. fig. 1); the presence of a single vas deferens on either side only occupying a single segment is not met with elsewhere among the Oligochæta, except in the Naidomorpha.

The simplicity of the vas deferens funnel is also a point to be noted in this connection.

The egg sacs are stated by BOURNE [6] in *M. minutus* to "occupy segments XII–XV at least;" HORST [8] found that in his species *M. Houteni*, the egg sacs extended through segments XIV–XVI. (? XIII–XV). The large size of the egg sacs is clearly an important point of difference from earthworms, where these bodies are so minute as to be often only with great difficulty recognisable.

Briefly to recapitulate.

*Moniligaster* differs from all other earthworms in the following points:—

1. Clitellum occupies segments X–XIII.
2. Male pores in intersegmental groove X/XI.
3. Female pores in intersegmental groove XI/XII (?).
4. Vas deferens only occupies one segment; atrium with a glandular investment, formed by peritoneal cells.
5. Ovary in segment XI (?).
6. Egg sacs occupying a large number of segments, XII–XV (or XIII–XV ?).
7. Spermatheca with an immensely long duct.

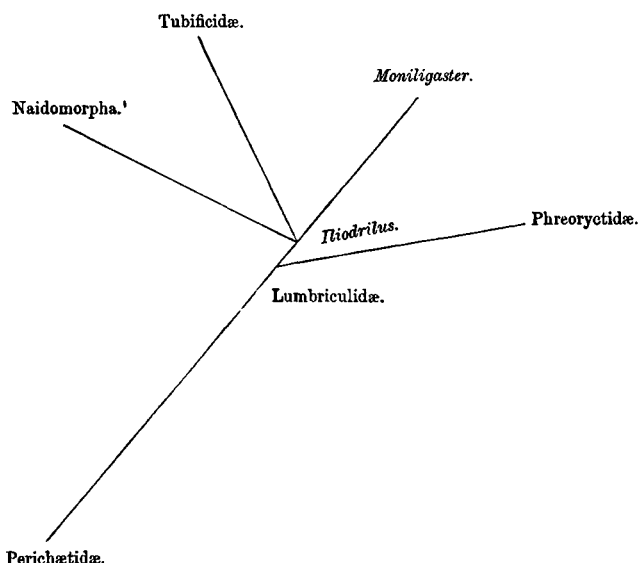
The structure of the body-wall, septa, alimentary tract, and nephridia is on the whole like that of earthworms, except that there seem to be no calciferous glands.

The characters of the reproductive organs are such that *Moniligaster* cannot be referred to any group of *Oligochæta*, though it agrees in particular points with several families. The clitellum is near that of *Phreoryctes*, and I believe the Lumbriculidæ; with these groups the absence of genital or penial setæ is another point of agreement; the structure of the atrium affines the genus to the Lumbriculidæ, but the characters of the vas deferens are more like those of the Naidomorpha. The egg sacs, from their large size, agree with those of many Limicoline families; but in being paired and the sperm sacs also, the

resemblances are rather with earthworms, though among the *Enchytræidæ* paired sperm sacs are met with (see MICHAELSEN, 15, plate, fig. 3), but not paired egg sacs.

The genus in fact must be regarded as forming a distinct group related to the *Lumbriculidæ*, *Phreoryctidæ* (?), and *Lumbricidæ*, but coming closer to the two former than to the latter. Its resemblances to earthworms, in fact, are almost entirely confined to those structural features which are in direct relationship to the mode of life of the worm; *i.e.*, gizzard, vascular supply, thickened body-walls, septa, and setæ. If I were compelled to adopt CLAPARÈDE's divisions of *Terricolæ* and *Limicolæ*, I would refer *Moniligaster* to the latter.

As it is, the following phylogenetic diagram seems in the present state of our knowledge to express the relationships of this remarkable Annelid :—



The principal facts in the anatomy of *Moniligaster Barwelli* are the following :—\*

†1. The setæ are strictly paired; the distance between the two pairs of each side is considerably greater than that between the ventral pair and the ventral median line, and considerably less than that between the dorsalmost pair and the dorsal median line. The setæ differ greatly in size, but are not peculiar in shape, being like those of most earthworms.

†2. *Dorsal pores* are present.

†3. The *prostomium* is very small, and does not extend over the peristomial segment.

4. The dissepiments separating segments V/VI, VI/VII, VII/VIII, VIII/IX, are very much thickened.

\* I do not attempt to discriminate between what are generic and what are specific characters; there are not sufficient data to do this with much probability of success.

† The dagger indicates that the statement to which it is prefixed is made for the first time in the present paper.

†5. The *hearts* are in segments VI–XIV, and are of large size.

†6. The *alimentary tract* begins with a buccal cavity, which occupies the first three segments; the *pharynx* is apparently restricted to a single segment, the IVth; the *oesophagus* lying in segment V is very narrow, afterwards it widens and extends through seven segments; the *gizzards* (three in number) occupy segments XIV–XVI; in an other specimen, probably not *M. Barwelli*, they are further back. There are *no calciferous glands* (?).

†7. The *nephridia* commences in segment V; each has a saccular diverticulum; the funnel opens in the segment in front close to nerve cord.

†8. The *testes* are either (*M. Barwelli*) in segment IX, attached to the posterior wall of this segment, or else in segment X, attached to the front wall.

9. The *sperm sacs* (one pair) are in segment IX or X, in correspondence with the position of the testes; their cavity is undivided.

†10. The *vas deferens funnels*, in accordance with the varying position of the testis open into the IXth or Xth segment.

11. The *atrium* open between segments X/XI; it has precisely the structure of the atrium of *Rhynchelmis*.

†12. There are no *genital* or *penial setæ* (?).

†13. The *oviducts* are in segment XI; in the individual which probably belongs to a species distinct from *M. Barwelli*, the oviducal funnel is spread along the anterior face of the septum separating segments XI/XII.

14. The *spermathecae* are a single pair situated in segment VIII; each consists of a small oval pouch, with a very long contorted duct.

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#### EXPLANATION OF PLATE.

- Fig. 1. Ventral surface, showing distribution of setæ. *pr*, prostomium; ♂, atrial pores.
- Fig. 2. Setæ. *a*, of posterior, *b*, of anterior, segments.
- Figs. 3, 4. Section through posterior and anterior region of body-wall to show relative thickness; the blood capillaries in fig. 4 are shown penetrating the epidermis.
- Fig. 5. Dissection to illustrate gizzards. *sp.*, septa; *g*, gizzards.
- Fig. 6. Transverse section of gizzard, drawn to scale.
- Fig. 7. Longitudinal section through mouth and anterior segments. *m*, mouth; *pr*, prostomium; I, II, III., 1st, 2nd, 3rd segments; *ce*, supra-oesophageal ganglion; *s*, setæ.
- Fig. 8. Section through genital segments of an individual, in which the gizzards are situated further back than in *M. Barwelli*. IX, X, XI, segments numbered; *t*, testis; *v.d.*, vas deferens funnel; *ss*, sperm sac; *od*, oviduct; *at*, atrium.
- Fig. 9. Section through male genitalia of *M. Barwelli*. *t*, testis; *ss*, sperm sac; *sp*, septum separating segments IX and X; *vd*, vas deferens connected with funnel close to attachment of testis; *at*, atrium.
- Fig. 10. Diagrammatic longitudinal section to illustrate positions of different parts of alimentary tract. *m*, mouth; *b*, buccal cavity; *nc*, nerve cord; *ph*, pharynx; *æ*, narrow region of oesophagus; *æ'*, wider region; *g*, gizzards. The segments are numbered.

## POSTSCRIPT ADDED JUNE 2, 1890.

Since the foregoing was written, I have received an important paper from Dr ROSA\* dealing partly with the anatomy of the Moniligastridæ.

As I have already pointed out, Dr ROSA was inclined to doubt in some particulars the accuracy of my description of the reproductive organs of *Moniligaster*. He now describes a species, which he has done me the honour to dedicate to myself, which agrees very closely in structure with *M. Barwelli*.

It is gratifying to me to read this description; the doubts which were thrown upon my work by so able an investigator of the group as Dr ROSA has proved himself to be, caused me some anxiety.

In *Moniligaster Beddardii* the position as well as the structure of the genitalia appears to be precisely as in *M. Barwelli*. Dr ROSA describes the funnel of the vas deferens as being flattened out, and not projecting much into the interior of the sperm sac; the testes also are attached to the funnel itself. The figures published in the present paper are quite in accord with those of ROSA. I have ventured (*vide supra*) to suggest that the ovary is in all probability contained in the XIth segment; I also identified a ciliated funnel-like structure attached to the hinder wall of this segment as the oviducal funnel. These identifications are rendered practically certain by ROSA's very clear diagram of the genitalia of *M. Beddardii*. A second interesting species is referred to a distinct genus—*Desmogaster*. *Desmogaster Doriae* has two pairs of atria opening on to the intersegmental grooves XII/XIII and XIII/XIV, all four apertures being distinct; as in *Moniligaster*, the vasa deferentia open into the atrium; the vasa deferentia, funnels, testes, and sperm sacs are as in *Moniligaster*, though, of course, four in number. The structure of the atria is rather different; there is the same central epithelium and annular layer of muscles; outside this are the groups of glandular cells that are met with in *Moniligaster*, but they are interspersed with muscular fibres; there appears to be also a delicate peritoneal investment. Dr ROSA considers that the resemblances of the atrium here are rather with other earthworms, though possibly the organ is to be regarded as intermediate in character, connecting such a form as *Eudrilus* with *Moniligaster*.

The glandular cells are regarded as being referable to the lining epithelium, but a complete circular layer of muscular fibres is figured between them and the single layered epithelium. It seems to me to be still possible to refer all which lies outside of the lining epithelium to the peritoneum. Unfortunately, in this, as in so many other questions concerning the morphology of the Oligochæta, there is no assistance to be got from embryology. The development of the spermathecæ, however, offers an analogous case, which supports the view that all the structures lying outside of the lining epithelium are

\* Viaggio di Leonardo Fea in Birmania e regioni vicine xxv. Moniligastridi, &c., *Ann. Mus. Civ. Geneva*, vol. ix, 1890, p. 368 *et seq.*

peritoneal in nature; at first, as BERGH has shown, the spermatheca consists only of an ingrowth of epidermis with a peritoneal layer, somewhat thickened, lying outside it; out of this latter are formed *the muscles as well as the peritoneal layer* of the mature spermatheca; it does not, therefore, follow that a distinct peritoneal epithelium separates from the coelom structures which have had an ectodermic origin. Reference may also be made to the description of the immature atrium of *Moniligaster* contained in this paper. I am therefore not yet convinced that the glandular cells packed among the muscles in the atrium of *Desmogaster* are to be looked upon as part of the lining epithelium.

As to the position of the testes and ovaries, this point of difference must apparently be dropped, now that we have ROSA's genus *Desmogaster* added to the Moniligastridæ; the position of the gonads and of the other parts of the female apparatus is quite normal in *Desmogaster*. But we have still the remarkable fact that the vasa deferentia open on to the segment next to that which contains their internal aperture; even when they are doubled this takes place. The double condition may perhaps be regarded as the older, as it occurs in most Oligochaeta, though not to so complete an extent as in *Desmogaster*. DR ROSA, however, is not correct in implying, as I understand him (p. 369), that two external pairs of apertures is a unique feature; the same occurs in *Phreoryctes*, the atria having almost completely vanished; and *Phreoryctes* is certainly not an "Earthworm," though it is, as I have pointed out, hardly excluded from that group by ROSA's definition.

DR ROSA admits the great peculiarity of the sperm sacs in the Moniligastridæ, upon which I have omitted to lay sufficient stress in this paper. The remarkable way in which the sperm sac is, as it were, suspended in the middle of the dissepiment is unlike anything that occurs in any earthworm, though certainly not leading towards any condition observable in the "Limicolæ."

It is, moreover, impossible in sections of *M. Barwelli* to state with any certainty which segment the sperm sacs belong to; in *Desmogaster* ROSA's figure indicates the same difficulty.

The remarkable partial obliteration of a segment (the XIIIth) which MICHAELSEN has lately described in *Nemertodrilus griseus*, suggest that something of the same kind may have occurred in the Moniligastridæ, *the supposed sperm sacs may be all that is left of the coelom belonging to the segment which contains the testes*. This is of course no more than a suggestion; but the varying position of essential organs in the Oligochaeta requires, as I point out in a forthcoming number of the *Quarterly Journal of Microscopical Science*, some possibility of the intercalation or excalation of segments at the head end.

This suggestion is supported by the absence of trabeculæ in the sperm sacs of *Moniligaster* and *Desmogaster*.\*

The correspondence between external and internal metamerism in *Desmogaster* is a little difficult to follow; between the last thickened septum and the dissepiment which

\* "L'interno della vesicola seminale non presenta un intreccio di fibre, ma solo una rete lassa di sanguigni," &c. (ROSA, p. 376).



separates segments XIV/XV are five coelomic cavities ; but the same points are divided by six external furrows. Dr ROSA does not state whether the irregularity is righted further on ; in the meantime it looks as if one segment at any rate were dropped, or rather may be represented by the wall of one of the sperm sacs.

Finally, I would point out that the egg sacs are unusually large in this group, though they do not nearly reach the size of those structures in the aquatic Oligochæta. I am, therefore, still inclined to retain the Moniligastræ in a group apart, though I admit that Dr ROSA's fresh discoveries somewhat weaken my contention that they form a group equivalent to all other Earthworms. They seem to me, however, undoubtedly to lead in the direction of some of the aquatic Oligochæta.

