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XIX.—Notes from the Gatty Marine Laboratory, St. Andrews.—No. XL

Prof. M'Intosh M.D. LL.D. F.R.S. ^a

^a Gatty Marine Laboratory, University, St.
Andrews

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XIX.—*Notes from the Gatty Marine Laboratory, St. Andrews.*—No. XL. By Prof. M'INTOSH, M.D., LL.D., F.R.S., &c., Gatty Marine Laboratory, University, St. Andrews.

[Plates VII.–XII.]

On the Nervous System and other Points in the Structure of Owenia and Myriochele.

SINCE the remarks on *Owenia* and *Myriochele* were made in the volume on the British Marine Annelids lately issued by the Ray Society, a few observations on both types were carried out, though, unfortunately, no living forms could be obtained; yet *Owenia* formerly was cast on the beach at St. Andrews in hundreds, whilst *Myriochele* is not uncommon on the west coast of Ireland, and in certain foreign localities it occurs in swarms. Such blanks, which may stretch over many years in the British area, are in the case of the fishes often regarded as evidence of serious diminution; but, so far as observed during a long period of years, neither in the case of the fishes nor in the case of the invertebrates is there much of a basis for this supposition. The two forms above mentioned are of interest especially as regards their nervous system, which differs from that in the majority of the Polychæts in having the cephalic system as well as the

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nerve-trunks wholly hypodermal. The latter arrangement of the ventral cords is that characteristic of most Polychæts—yet about ten families have their great ventral nerve-trunks enclosed by the muscular tissues of the body-wall, besides the basement-layer, hypoderm, and cuticle, showing how uncertain any single factor is in the classification of this group. In the Archiannelid *Protodrilus* the nervous system agrees with that in *Owenia* and *Myriochele* in being mainly hypodermic, and in *Saccocirrus* and *Sternaspis* (though this is not a Polychæt) the cerebral ganglion is similarly situated and the ventral nerve-cord is not segmented into ganglia. They contrast thus with the Nemerteans, in which the cephalic ganglia are internal and the longitudinal cords either enveloped in the muscular walls of the body or entirely within them. It is further interesting, in comparing the Nemerteans with the Polychæts, that no Polychæt possesses the proportionally large nerve-supply to any organ—a supply, moreover, more bulky in its distribution than in its origin, and which undergoes remarkable changes of form, both in contraction and dilatation—as that of the Nemertean proboscis. Hence its lattice-like arrangement gave rise to the term “elastic layer” in the early memoirs. This feature is as noteworthy as the passage of the proboscis between the dorsal and ventral commissures of the cephalic ganglia. Some consider that this arrangement of the nerves causes it to be an organ of sensation; but it is often thrown off when brought into contact with foreign bodies, and, though renewed, its functions for the interval are in abeyance. In the Ammonocharidæ under consideration what appears closely allied to nervous matter is distributed as a continuous layer beneath the hypoderm of the gullet—a condition much more primitive than the elaborate system of the Nemertean proboscis or than the proboscis of a typical Polychæt such as *Nereis*.

In glancing at the literature of the subject, it is found that the acute and accomplished Claparède, familiar as he was with the ordinary nervous system of the Polychæta, failed to find the central nervous system in *Owenia* “qu’il m’a été parfaitement impossible d’en trouver la moindre trace chez l’*Owenia fusiformis* sur les coupes d’individus conservés”*, and he even had difficulty in discriminating the ventral cord in the fresh animal. Yet he had described and figured a similar condition to that of *Owenia* in *Telepsavus costarum*, one of the Chætopteridæ, in which the central nervous

* Annél. Sédent. p. 129.

system forms a subhypodermic band resting on the basement-tissue, and which Claparède interpreted as a transverse commissure between the ganglia*, yet to be considered as the representative of the cerebral ganglia, and the two eyes in *Telepsarus* rest on it. The ventral cords, moreover, show no ganglia and are wide apart. He does not allude to the minute structure of the nerve-tissue.

In 1885 von Drasche † gave a careful account, with figures, of the structure of *Owenia* “*filiformis*” as it occurred at Trieste, dealing in the first instance with the external characters, and especially the “Lippenorgan” at the oral aperture, the hypoderm and nervous system, the musculature, alimentary canal, coelomic cavity, and long mucous glands. So far as he goes, the structure of these organs is correctly described, with accompanying figures. He could not satisfy himself as to the “nephridia” and the mode of exit of the genital products. He observed no nerve-cells in the minute structure of the central nervous system or in the ventral cord, only a fibrillar structure and Leydig’s punctate substance. The ventral cord showed no ganglionic enlargements. Below the epithelium of the alimentary canal a strand similar in structure to the central system is briefly mentioned, but nothing definite is recorded concerning the nerve-supply of the internal organs nor concerning the nephridia.

In looking around for analogous relations of the central ganglia, it is found that in *Phoronis* Caldwell ‡ observed that the central nervous system remained in the epidermis, and therefore represented the primitive condition. In the adult the central system is in the form of a post-oral ring, the anus lying outside it. In *Phoronis buskii* of the ‘Challenger’ § the nerve-centre rests on a broad plate of basement-tissue, with the hypoderm externally extending from the nephridia forward to the centre of the whorl of tentacles on each side, and it agrees precisely in minute structure with that in *Cephalodiscus* and *Owenia*.

The central nervous system in *Cephalodiscus dodecalophus* || occupies an area of considerable proportional size at

* Annel. Sédent. p. 127.

† ‘Beiträge zur feineren Anatomie der Polychaeten,’ Zweites Heft, Wien, pp. 1–22, 2 plates.

‡ Proc. Roy. Soc. vol. xxxiv. p. 372.

§ Zoology, vol. xxvii. part 75, pp. 18–21, pl. ii. figs. 1 & 2, pl. iii. figs. 1–3.

|| ‘Challenger,’ Zoology, vol. xx. part 62, p. 23, pl. vi. fig. 3, and pl. vii. fig. 3.

the base of the plumes external to the median space, and is bounded externally by the thick coat of hypoderm and internally by the basement-layer. It extends laterally in the hypoderm along the basal region of the plumes and for some distance along the dorsal side of the buccal shield. In microscopic structure it is minutely cellular and granular, intermingled with fibres, and corresponds generally in position with that in *Owenia* and *Myriochele*.

Benham * (1896) described the central nervous system of the "Archiannelida" as in contact with the epidermis, and pointed out that in some Polychæta it holds a similar position in the epidermis; but he does not mention this condition in the Ammocharidæ, which he associates with his Spioniformia, nor in the Chætopteridæ included by Levinsen and himself under the same group or suborder.

Gilson (1897-98) devoted much attention to the structure and function of the various parts of *Owenia*. Besides a careful account of the remarkable secreting glands †, which form such prominent organs, he has furnished an extended description of the "valves septales" ‡ and of "cellules musculo-glandulaires" in the body-wall §. Perhaps the most important contribution is that connected with the "valves septales," wherein he gives a systematic description of each septum, with its functions, one of the most striking being the second septum (*i. e.*, between the fourth and fifth segments), his sphincter muscle being in the position of the ordinary oblique muscle at its insertion over the nerve-cord. The muscular arrangements of this septum are specially connected with the cœlomic fluid and the branchiæ. After describing the special apertures in the septa and their mechanism, he shows that apertures at several of these connect the cœlom with the exterior; that in the sixth segment two zigzag cutaneous canals springing from funnels at the septum between the sixth and seventh segments perform the function of genital ducts, since nephridia are absent—a feature of a peculiar character in a Polychæt. In his paper on the musculo-glandular cells he states that a peritoneal membrane or cœlomic coat proper is absent in *Owenia*, thus resembling such forms as the Nematodes, Acanthocephali, many Annelids and Archiannelids. The body-wall is formed by a combined musculo-glandular coat—that is, it cannot be separated into a muscular and a glandular layer. The inner

* Camb. Nat. Hist., Worms, Rotifers, and Polyzoa, pp. 243, 255, & 325.

† 'La Cellule,' t. x. fasc. 2.

‡ *Ibid.* t. xii. fasc. 2.

§ *Ibid.* t. xiv. fasc. 2.

region of this coat secretes albuminoid substances, fat, and urinary products. As will be shown subsequently, such is a misapprehension of the structure of the peritoneal surface, probably owing to the condition of the accomplished Belgian author's material.

In connection with Gilson's opinion, for it is nothing more, that the hypodermic canals in the sixth segment are genital ducts, it is noteworthy that Arnold Watson observed the reproductive elements in *Owenia* issuing from two pores, to the right and left of the anus, a portion of the posterior end of the body projecting from the anterior aperture of the tube. Thus Gilson's theory of the advantages of the anterior opening of the hypodermic tubes (his genital ducts) lapses, were it only by the thrusting out of the much more delicate tail anteriorly.

Ogneff* (1899), working at the Naples Station, took up the subject of Gilson's "cellules musculo-glandulaires" in *Owenia*. In his preparations he found within the muscular layer of the body-wall a protoplasmic and cellular layer which lined the cœlom. In the muscle-fibres of the longitudinal coat themselves were spindle-shaped cells with nuclei, as Schwalbe first described in the muscles of worms and lamellibranchiate mollusks, and also on the surface of the muscles in a protoplasmic layer. Over these, however, is a layer of peritoneal cells, which are cup-shaped, with rounded inner or deeper surfaces and flattened surfaces toward the cœlom, with an oval nucleus, fat, and granules like the white of egg in the protoplasm. A fine protoplasmic network stretches from these amongst the muscle-cells. He thought there were as many as fifteen to twenty peritoneal cells to one muscle-cell. He did not consider that Gilson's "muscle-gland-cells" existed in *Owenia*, the misapprehension being due to the less elaborate methods of preparation and section-making.

In 1900 a very interesting paper on *Owenia fusiformis* was communicated to the Linnean Society by Mr. Arnold Watson†, whose observations on the living animals are noteworthy. His description of the lip-organ and its functions, the occurrence of a prostomial pore, the discovery of the emission of the sexual elements through two cœlomo-ducts (anal pores), the structure and repair of the tubes, and the rearing of the ova to the *Mitraria*-stage are the chief features of this contribution to the life-history of the species.

* Biol. Centralblatt. Bd. xix. p. 136.

† Journ. Linn. Soc. vol. xxviii. p. 259, pl. xxii.

One of the latest contributions is a histological paper on *Owenia* by Zürcher *, who enters into the minute structure of the muscles, showing that the long spindle-shaped muscle-cells have a spiral character (formerly noted by Ogneff), which in transverse section give them a barred aspect. A circular muscular coat occurs only at the second dissepiment and forward to the branchial lobes. This also has spindle-shaped cells with nuclei. He combats Gilson's view, as Ogneff had previously done, that there is no line of demarcation between the muscular coat and the peritoneum, that the nuclei are rare in the muscular fibres and by-and-by vanish, and that it is impossible to distinguish the nuclei of the muscles and those of the gland-cells. He points out that the peritoneal nuclei are generally rounded, whereas the nuclei of the muscles are oval and flattened, with the long axis in the line of the muscle-cell. He goes somewhat fully into the histology of the circulatory system (his hæmocœl), the main trunk consisting of a dorsal vessel carrying the blood forward and a ventral trunk carrying it backward. The dorsal forms a blood-sinus round the gut to the second septum, then breaks up into a network over the canal, the trunks fusing at the first septum and sending forward a series of vessels to the branchiæ, the returning vessels uniting to form the ventral trunk below the gut. The walls of the vessels have a fine epithelial coat and a delicate circular muscular layer with minute nuclei in their spindle-shaped cells. The author also objects to Gilson's statement that no special constrictor to the alimentary canal occurs at the septa, and points out that at the third septum an efficient constrictor apparatus exists both for the canal and the blood-sinus, the muscular apparatus showing the large muscle-cells at the outer ends of the fibres. Posteriorly also the alimentary canal is moniliform from its constrictions. He is inclined to think that Drasche's bladder-like tissue on the ventral mesentery is part of the reproductive apparatus. The ampullæ on the ventral blood-vessel, which Drasche observed to be rhythmically contractile, are confined to the genital region of the body, and bear the reproductive elements on their outer surfaces, and, though they have muscular walls, Zürcher would attach more importance to their nutritive capacity. The red blood contains rounded or lenticular corpuscles with nuclei, and some corpuscles undergo mitosis. He found them in the ampullæ and less

* *Jenaische Zeitschr. für Naturwiss.* Bd. xlv. pp. 181-220, pls. xv.-xx. (1909).

frequently in the vessels and sinuses. There is a mixture of venous and arterial blood in the branchiæ. The author does not touch on the structure of the nervous system of *Owenia*, the topography of the alimentary canal, the hypodermic canals of the sixth segment, and other features subsequently to be described, and his main points are histological. The illustrations are chiefly in outline.

No trace of a central nervous system is observed in *Owenia fusiformis* till the folds of the mouth are cut in the transverse sections*, and the first definite appearance of a layer similar to nerve-tissue is the presence of a pale band external to the stained basement-layer of the inner border of a lateral flap of the mouth. It resembles a differentiated stripe of hypoderm from which cells and pigment are absent, but the fine striæ are continued through it to the basement-tissue, the whole being minutely fibrillar like the nerve-tissue, and generally dotted with minute granules. It fades away before reaching the free or ventral edge of the lateral flap, and disappears similarly at the dorsal edge of the fold. Then (for it is difficult to cut exactly on the same level) a corresponding band appears on the opposite labial fold. This pale belt is considered by some, *e. g.*, Zürcher, to be basement-tissue, but it seems to be somewhat different. In any case, the contrast between it and the condition, for instance, in the proboscis of the armed Nemertean with its large strands of nerves and their reticulations is marked, yet

* Whilst many advantages are gained by the use of paraffin, celluloidine, and other substances for imbedding, the old plan of fine sections made directly from carefully prepared spirit-specimens is not without value in checking the proportional thickness of the muscular layers and other parts. Thus, in the case of *Owenia* the great thickness of the longitudinal muscles of the body-wall can only be appreciated in this way, and so with the proportional size of the mucous glands and the tough nature of the basement-layer. In such preparations more than forty years old the delicacy of the hypodermic¹ layer has caused most of it to be removed in the manipulations before and after preservation, but in every case the nerve-cord firmly adheres to the basement-tissue in the mid-ventral line, thus demonstrating its comparatively tough nature in contrast with the hypoderm. In such sections the gut fills the entire area, with the exception of the mucous glands, though, of course, in life the coelomic space was larger. The term hypoderm in the structure of the Polychæta refers to the glandular and granular layer, often areolated, beneath the cuticle. It is an ectodermic structure.

¹ I am indebted to Mr. E. W. Shann, B.Sc., now Captain in the Northumberland Fusiliers, Mr. J. W. Pryde, M.A., now Lieutenant in the Black Watch, and to Miss Harvey, of Edinburgh, for aid in making the various sections.

the functions of both are equally well performed. The Nemertean brain, as in many Polychæts, is distinctly isolated from the tissues outside it, and the same may be said of the main trunks in that group. Here, in what is considered to be a higher series, the opposite condition prevails, the nerve-centre and main trunks being hypodermal, as are the cords in the majority of the Polychæts. In *Owenia* this belt agrees in minute structure with that surrounding the central system, and occupies a corresponding position.

With the disappearance of a central fillet in the dorsal arch of the body-wall a slightly pale band is noticeable in the hypoderm of the region, yet that layer passes to the basement-tissue (which stains) uninterruptedly, a series of the ends of severed fibres being grasped in spaces bounded by reticulations between the basement-tissue and the adjoining circular muscular fibres. Then the pallor of the inner portion of the hypoderm becomes more pronounced, and in the next section or two (Pl. VII. fig. 1) a distinct nervous layer, as in *Cephalodiscus*, stretches along the mid-dorsal arch. It shows both fine transverse and vertical fibres or striæ, and minute granules occur next the basement-tissue (Pl. VII. fig. 2). It fades on each side into the ordinary cells and areolæ of the hypoderm, which likewise continues to the surface externally without evident break. The nerve-tissue, in short, is marked by no hard-and-fast line from the hypoderm, but is traversed by its fibres, and the neuropile, nemoglia, and neurilemma of the ordinary Polychæt ganglia are not distinguishable. From end to end in section the tissue has a uniform structure, and where, for instance, it is separated from the basement-layer only projecting vertical fibres and granules appear. Certain granules occur at its outer border next the deeply stained cells and granules of the hypoderm, but these could not be associated with the nerve-band, the finely fibrillar edge of which coursed evenly along. In succeeding sections this great nerve-band stretches downward at the sides, becomes more distinctly differentiated from the hypoderm externally and the basement-tissue internally, and then a slight narrowing of the mid-dorsal arch takes place, the lateral extensions being thicker. The mouth is still divided ventrally in these sections, and the nervous expansion extends over the entire arch of the body-wall with the exception of a comparatively short region of the ventral edge of the lateral lip, the thickest layer being lateral, for the dorsal is now diminishing. A narrow layer, apparently of basement-tissue, occurs, as indicated, simultaneously in the sections external to the hypoderm lining the mouth, and

at this level all round, though it is thickest ventro-laterally, and it was this layer which was first encountered in front. The structure of this lateral band of so-called basement-tissue closely resembles that of the central system, and it is possible that it may perform functions of a sensory kind in connection with the lateral flaps of the vestibule. The flaps gradually unite to form the lower half of the vestibule, the thicker band of pale tissue still being retained ventrally with a thin connecting-band dorsally. Proceeding a little backward the main nervous band disappears from the dorsum and is confined to the lateral regions of the body-wall, from which it gradually thins off dorsally. Finally, when the lip-organ appears in the section over the oral gap, a large nerve-cord alone is left at the lower limit of the former nerve-band (Pl. VII. fig. 3, *nc.*), all the hypodermic layer dorsad of it having assumed the usual condition. In sections of *Saccocirrus* near the mouth Dr. Goedrich* found the lateral cords (his "oesophageal commissures") in a similar position. This limited nerve-area presents in section pale, finely granular, transverse striation, through which delicate fibrils from the hypoderm external to it pass to the basement-tissue. When the circle of the body-wall is complete—that is, immediately behind the oral gap (Pl. VII. fig. 3),—the large nerve-cords are situated a little below the middle line of the body-wall, and have a blood-vessel in the muscle to their inner side. The central region is still lined by hypoderm, and the thick pale band of the inner layer is infero-laterally conspicuous. Then the hypodermic layer of the vestibule passes into the gullet, and sections of the lip-organ (*lp.*) appear, whilst the hypodermic inner lining of the dorsal region is shut off by a deep fold with a narrow layer of hypoderm from the vestibule, the rest of the large arch above having a thick coat of the same tissue. Externally, again, a change has occurred in the mid-ventral line, for the thick lateral coat of hypoderm in which the nerve-cords lie has thinned off ventrally, leaving a considerable area with just a trace of it; but this appears to occur only for a short distance. With the termination of the vestibule lined by hypoderm, and the increase of the lip-organ in section, the ventral hypoderm of the body-wall again gradually thickens from the middle line outward. Moreover, the narrow pocket formed by the first septum lies on each side of the lip-organ (Pl. VII. fig. 4), and then is quite shut off from the upper cavity (vestibule) lined by hypoderm, and which represents the

* Quart. Journ. Micr. Sci. n. s., vol. xliv.

gullet proper (which may have complex functions), surrounded by a tough (muscular) investment, from which various strands radiate to the body-wall amongst the blood-vessels of the region. The body-wall at this part has a thinner coat of hypoderm both mid-dorsally and mid-ventrally, its thick layer being lateral. The longitudinal muscles form a somewhat thin layer of fasciculi all round, and the lip-organ shows a thick mass of modified vertical cells with nuclei, each mass probably rubbing against the other. The massive lip-organ then forms a thick-walled tube in section, with a central cavity (Pl. VII. fig. 5) and an external muscular investment, whilst the œsophagus has a thick mucous layer, continuous with the hypoderm, to subserve its special functions, the radiating strands and numerous blood-vessels still continuing. These radiating fibres show that the movements of this thick-walled region (Pl. VIII. fig. 18) must be more or less restricted, yet the longitudinal bands, especially on its dorsal wall, would point to protrusion and retraction. Externally the hypoderm—thickest laterally at and above the nerve-cords, which are descending—has increased in depth dorsally, but is thin ventrally. Behind the forego the lip-organ loses its central cavity (a fold) and diminishes in size, but its complex muscular coat is proportionally thicker, and in the surrounding area the blood-vessels are larger. Finally, the muscles of the lip-organ alone are visible, and then disappear, showing that it is, in short, attached by a muscular stalk, first hollow and then solid, though the sections would indicate that the muscular fibres (retractor) are fixed to the body-wall close behind and for some distance backward. Moreover, a fan-shaped arrangement (Pl. XII. fig. 17) occurs anteriorly where the fibres spread into the lip-organ. Besides, various oblique and transverse fibres act on the folds and give complexity to the movements (Pl. XI. fig. 16). A double layer of muscular fibres, further, lies beneath the basement-tissue bounding the gland-cells—the one the reverse of the other,—so that in sagittal section the cut ends of one series abut on the thick inner (*i. e.* toward the cœlom) belt. Gland-cells also occupy considerable areas internally at the edge of the organ. The whole structure of this organ therefore differs from mere labial folds of the vestibule, as more clearly seen in vertical sections (Pl. VII. fig. 6), the densest part of the cellular layer being toward the middle of the ventral fold and thinning off dorsally and laterally. The lip-organ, in short, is a highly differentiated apparatus, both secretory and manipulative, for the tube-formation and other

functions. It is interesting that Dr. Goodrich* found a similar organ (his "muscular pad") in *Saccocirrus* and *Protodrilus*. The body-wall at this level again presents a change in its hypoderm (which throughout has a firm exterior film or cuticle), since, though somewhat diminished dorsally, it is now of a considerable thickness mid-ventrally, its densest part being at the nerve-cords, which have moved downward, so that they are separated by about a sixth of the circumference of the body (Pl. VIII. fig. 7). The œsophagus has special fasciculi of muscles laterally and dorsally, besides the radiating fibres.

The next important change is the merging of the œsophageal region of the canal, with its boldly arranged coat continuous with the external hypoderm, into the stomachal region at the third septum, with its granular glandular surface (Pl. VIII. fig. 7) and its external muscular coat, the whole internal surface of the stomach being by-and-by thus transformed.

At the commencement of this region of the gut at the third septum a complex muscular sheath connected with the lip-organ occurs ventrally, with thickened muscular pillars at each side—abutting on a membranous space to the exterior and just over the nerve-trunks, certain of the fibres, moreover, a little further back being attached to the basement-tissue over the outer part of the nerve-cords. Blood-vessels occur in the large space which is thus soon formed below the alimentary canal, and the vessel in the median mesentery (which is attached to the upper border of the mass of muscle stretching from side to side over the area above the nerve-cords—a little behind the section figured in Pl. VIII. fig. 7) is distinct, the special mesenteric area still being visible externally, though much reduced in size. Between the basement-tissue of the body-wall and this transverse muscular mass lie the ventral longitudinal muscles (*vm.*). The great cavity appears to contain coelomic fluid and corpuscles, and is shut off by a shelf of septal tissue (Pl. VIII. fig. 7, *bt.*) continuous at each side with that of the body-wall, whilst the upper area on each side of the alimentary canal is occupied by elastic connective-tissue strands and by the muscular fasciculi along the dorsal wall of the canal. The body-wall at this region has dorsally the longitudinal muscles (*dm.*), which may be held to cease at the junction of the transverse platform of septal tissue a little below the middle, of longitudinal muscular fibres

* Quart. Journ. Micr. Sci. n. s., vol. xlv. p. 415, sections 18 & 20.

ending at the junction of the ventral transverse band, and, lastly, of the median (ventral) longitudinal fibres (*vm.*) beneath the latter (Pl. VIII. fig. 7). The nerve-cords at this part are separated by fully a sixth of the circumference of the body-wall. The transverse septal plate above the ventral longitudinal muscles has a central structureless part—apparently of a homogeneous nature (pale and elastic), the muscular fasciculi fraying out especially at the dorsal surface and ends (Pl. VIII. fig. 7 A). In its progress backward a change in the diminishing area between the nerve-trunks is inaugurated, the homogeneous central region of the transverse band, the anterior part of which is indicated in Pl. VIII. fig. 7, being shortened transversely and increased vertically, so that it pushes as a lozenge-shaped and then wedge-shaped area into the centre of the ventral muscular mass, whilst the upper muscular fibres externally become defined as more or less independent masses, bounded externally by sloping muscular fibres which simulate the oblique in certain sections—at least, at their insertion. The lozenge-shaped area of the homogeneous (for it can scarcely be called “tendinous”) tissue thins off on each side to a plate, to the upper edge of which fasciculi of muscular fibres are attached, whilst ventrally processes pass into the median ventral longitudinal muscles. The whole thus forms a complex muscular apparatus attached to the central tough tissue, which gradually in its progress backward shrinks, leaving the fused muscular fasciculi to form the massive ventral longitudinal muscles as shown in Pl. VIII. fig. 8, *vm.* By the gradual diminution of the tough central area of the before-mentioned transverse band to which the median mesentery from the gut is attached, and by the grouping of the several longitudinal ventral muscles into a mass on each side, the typical ventral longitudinal muscles are formed, and at this part they exceed in bulk the dorsal muscles. This evolution of these continuous ventral fasciculi out of the elements in front is probably connected with a change in the function of the contents as well as in the body-wall itself.

The disappearance of the longitudinal muscular fibres and the radiating strands from the dorsal wall of the gut leaves the two halves of the upper division of the cœlomic space for cœlomic fluid only, and it is separated from the two much larger spaces inferiorly by strong muscular bands at each side of the transversely enlarged alimentary canal; yet the appearance of the canal beneath—to which the median mesentery is attached ventrally—apparently leaves a gap by

which the two cavities communicate superiorly under the transversely enlarged canal.

The anterior end of the stomach is a narrow tube as seen in Pl. XI. fig. 23, and in the various transverse sections. It further presents a bifid border ventrally, a narrow process of the cavity ending in a dilated rim on each side below, the ventral blood-vessel and the mesentery occupying the gap, whilst a spacious sinus surrounds the stomach. This bifid condition gradually disappears, the organ assuming the outline shown in Pl. X. fig. 30.

A mesentery with the dorsal blood-vessel in the centre passes from the upper arch of the gut to the dorsal wall, and another mesentery, with the ventral blood-vessel, goes to the mid-ventral tissues, the coelom being thus divided into halves. Then a process from the wall of the stomach above the rugose and somewhat triangular ventral arch appears, and a little behind is tacked to the ventral portion, and thus cuts it off as a separate canal with folded mucous membrane internally, the longer upper chamber having its inner surface smooth and symmetrically folded. The inferior and somewhat pear-shaped chamber (Pl. VIII. fig. 8, *st.*, stomach) is surrounded by blood-vessels, which form a vascular plexus around it on their way to the branchial region, and from its apex inferiorly a mesentery passes to join a mid-ventral homogeneous (pale tough) area arching over a special muscular region which terminates on each side over the outer edge of the nerve-cord, now approaching that of the opposite side.

At this level the body-wall has thin hypoderm in the mid-dorsal line, then it increases in depth laterally, again becomes thinner, and then swells out ventrally at the nerve-cords. Within are the basement-tissue and circular fibres, then the dorsal longitudinal muscles (*dm.*), which end below the attachment of the upper canal on each side, and the ventral longitudinal (*vm.*), which are more massive, and have the differentiated region with the arched fibres in the middle line, such, indeed, forming the only separation between them. This differentiated region is probably in connection with the movements of the alimentary canal. The nerve-cords in section show a granular and fibrillar aspect, and they are much better differentiated than in front. The occurrence of bristle-tufts makes the separation between the dorsal and the ventral longitudinal muscles more pronounced, and below the tuft is a well-defined pore of the mucous gland with large nuclei in its cellular wall (Pl. VIII. fig. 9, *mp.*), one side abutting on the hypoderm, the other

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having muscular fibres from the bristle-tuft attached to it; and the hypoderm is thinned at the tuft and has an incurvation at its upper edge, whilst it rapidly thickens above it. Moreover, a distinct muscular slip (*mc.*) occurs in the mid-ventral line, the remnant of the complex condition in front.

The next change is the infolding of the stomachal wall (Pl. VIII. fig. 10, *st.*), the loss of its lateral connections, and the termination of its cavity; whilst the intestine enlarges, its folds become more prominent and alter their character, resembling, indeed, the œsophageal hypodermic lining. The intestine still shows a plexus of vessels, about seven, for instance, being cut on each side, and they resemble buds from the investment of the gut, though they are only sections of longitudinal trunks with their internal and external investments. The dorsal mesentery and its enclosed vessel now pass upward from the gut-wall, and inferiorly are the ventral mesentery and its vessel, the membrane trending to a fissure between the more massive ventral longitudinal muscles, since the special median muscular area and its fibres (shown in Pl. VIII. fig. 7 A) have disappeared. The nerve-cords are separated only by their own breadth from each other, and they are, perhaps, more distinctly granular than before. The mucous glands, with their secretion rendered fibroid by preparation, are now prominent, each placed above the ventral muscle of its side. The cœlomic spaces (Pl. IX. fig. 11, *c.*), reduced to one on each side, have a translucent coagulum with granules.

When the nerve-cords touch and fuse (Pl. IX. fig. 11, *nc.*) it is seen that the glandular tubes in the cœlom approach each side of the ventral vessel, and slope outward as they go forward to the excretory duct below the bristle-tuft. The gut has become pear-shaped, the narrow end being below with its mesentery, whilst two mesenteries pass from the dorsal arch and join before reaching the dorsal blood-vessel. This arrangement makes an additional supra-intestinal chamber.

The hypoderm still presents a symmetrical enlargement just above the bristle-tuft on each side, this thickened region being differentiated by the narrow layer immediately above it, for it gradually deepens dorsally and again becomes narrow as it reaches the mid-dorsal line. From the lower edge of the bristle-tuft it gently increases to the nerve-cords in the mid-ventral line. The dorsal longitudinal muscles are thinner than the massive ventral, but they extend over a larger area of the body-wall.

A little further back (Pl. IX. fig. 12) the gut increases in

vertical diameter, forming a long flattened organ extending from the dorsal to the ventral region in section, and the cellular lining is thrown into rugæ. Both dorsal and ventral short mesenteries are double, and the wall of the dorsal vessel is more muscular. The gut has the same vascular investment as just mentioned, and the vessels lie outside the mesentery just alluded to. At the next bristle-bundle a pore similar to the first gives issue to the secretion of the second pair of glandular tubes. The ventral longitudinal muscles retain their more massive outline.

After an interval the body (Pl. IX. fig. 13) increases in bulk proportionally, but the hypoderm becomes thinner all round, the thickest part being that situated ventrally on each side of the nerve-cords. The ventral longitudinal muscles pass far upward, and encroach on the dorsal, which occupy only the upper arch of the body, and each pair has a distinct median notch into which the mesentery fits, the ventral mesentery having the ovaries or spermaries attached to it laterally, and the contents of which are shed into the cœlom. Two mucous glands in section occupy the upper half of the cœlom on each side, and the nuclei of the cells forming their walls are regularly arranged. The gut stretches nearly from dorsal to ventral arch, held in position by the median mesenteries and also by the septa at intervals. The double attachment superiorly forms a blood-channel, which communicates with a sinus (*sin.*) surrounding the gut, so that here, instead of the isolated though reticulated vessels, there is a continuous blood-channel—a development in all probability attained only in the adult or nearly adult condition. The nerve-cord still has numerous hypodermic fibres passing from the outer to the inner (ventral to dorsal) or *vice versa*, and, in addition, fine reticulations and granules, some of which are probably nuclei. Usually a slight ventral furrow and a median peak dorsally indicate the double nature of the area. The second pair of glandular tubes is situated to the exterior of the first pair in transverse sections.

The sixth segment is distinguished by the presence of Gilson's epidermal tubes, which stretch from the septum between the sixth and seventh segments to that in front. They are readily recognized by their position in transverse sections, viz., dorsad of the groove (Gilson's "*gouttière de la soie*") which runs along the dorso-lateral region. They are canals of considerable size, and are separated from the basement-layer by a stratum of cells, the cavity in section being also bounded externally by an arch of hypodermic cells. Gilson supposed that these hypodermic canals served

for the transmission of the reproductive elements, and possibly also for an interchange between the cœlomic cavity and the exterior as in certain Oligochaets. True nephridia, at any rate, are absent in *Owenia*. Whatever the function of these canals may be, Arnold Watson has shown that sperms and ova escape by different channels.

In front of the tail the hypodermic coating of the surface is of moderate thickness. The massive muscular investment is conspicuous, and it is difficult to distinguish where the dorsal longitudinal muscle ends and the ventral begins, though a fold above the mucous gland seems to indicate the separation. The nerve-cords have shrunk to a small lenticular area, which in minute structure has the same fibrillar and granular character as in front. The intestine, held in position by a dorsal and a ventral mesentery, is considerably less, but it has large vessels or sinuses on each side, the ampullæ from the ventral vessel passing into the large gonad below the gut. Two mucous glands are still in evidence under the dorsal wall, and they have the same character as in front. Moreover, their ducts open above the long line of hooks in the space between these and the bristle-tuft, which is now dorsal in position, and so leave the entire lateral wall to the hooks; thus the restricted area occupied by the dorsal longitudinal muscles is defined. The whole lateral and ventral regions are covered by the ventral longitudinal muscles, which, however, are much thinner than the dorsal, the reverse of the condition in front. The conspicuous development of the gonads in this region and the ampullæ of the ventral vessel are noteworthy. The mucous glands have now ceased (Pl. IX. fig. 14).

One of the interesting features toward the tail is the occurrence of the septa (Pl. IX. fig. 15). Their first appearance is indicated by the envelopment of the intestine and its blood-sinuses by a sheath which springs from each side of the vertical mesentery under the dorsal blood-vessel, and stretches to the mid-ventral mesentery considerably below the ventral blood-vessel. In such a view it might be supposed that the middle of the septum has been sliced, leaving the upper and lower attachments; but such will not explain all the outlines of these posterior septa.

Reproductive elements occur in the spaces outside the septum as well as within it and its areas. Then the upper and lower arches separate, each having a zigzag outline as it passes to the body-wall. The cœlom is thus divided into six areas—two dorsal, two ventral, and the lateral with the gonads inferiorly on each side of the gut.

The first appearance of the septum in the sections is heralded by a tuft of muscular fibres attached to the exterior of the gut-wall and the ventral septum; then the muscular ring (the ventral septum and the gut being free) loosely envelops the gut and its vessels, besides the ventral blood-vessel and its mesentery, almost to the ventral longitudinal muscles, but leaves the dorsal blood-vessel for the most part free. The septum, indeed, springs on each side from the lower wall of the vessel, and encloses that part of the mesentery between the vessel and the sinus around the gut, whilst the distal part of the mesentery passes freely to the gap between the dorsal longitudinal muscles. This muscular sheath or tubular chamber by-and-by swells out into a large area, its upper arch or roof being attached on each side to the body-wall between the dorsal and ventral longitudinal muscles, and its floor stretches from the median ventral mesentery to the wall of the body a considerable distance below the attachment of the roof. This chamber encloses the alimentary apparatus and the gonads, but the more advanced sperms lie in the two coelomic chambers outside its roof—that is, between the latter and the body-wall (Pl. IX. fig. 15). It is difficult to explain the exact nature of these septa—whether they are modifications of the ordinary septa, which extend far backward in the caudal region, or only the ordinary septa sliced so as to present these characteristic appearances,—for it is unlikely that two septa would fall into the line of section. These septa seem to differ in disposition and aspect from those in front, and are probably associated with the special functions of the caudal region—respiratory, purely intestinal, or otherwise.

On viewing the animal externally from the dorsum, a broad fillet passes from each side of the collar anteriorly and slopes obliquely inward and backward on the dorsum to the constriction behind the third bristle-tuft, then bends a little outward, and is continued along the dorso-lateral region posteriorly. A groove exists at the collar just below the anterior end, and which apparently is functional also for the median ventral ridge and groove, so that, if ciliated, it may send a current outward and forward to it. These ridges apparently are those which show the remarkable pennate arrangements in the hypoderm in the preparations (Pl. IX. fig. 20).

In certain longitudinal sections (Pl. VIII. fig. 18) the dark pigment stretches as a broad band behind the collar, a gap intervening between it and the edge of the fold behind, such probably representing a sensory groove, and its borders have

the specially modified cells. Von Drasche* figures the pigment only behind the collar, and his "ganglion" is small and considerably in front of the collar, thus diverging from the condition described here. Zürcher does not deal with this region.

In longitudinal sections a marked feature is the pennate condition of the hypoderm of the anterior region—that is, between the first and second dissepiments, as well as a little in front of the former in certain cases; and it appears to be specially developed on the dorsum. The hypoderm is there thrown into a series of ridges, which in section present a streaked granular basal region terminating externally in a pennate and symmetrical series of small granular cells, after the manner of the barbs of a feather (Pl. IX. fig. 20), the breadth of the ridge varying, whilst the processes (in section) increase in size from behind forward, culminating in the collar with the deep groove in front (Pl. XI. fig. 16, and Pl. VIII. fig. 18). Some of the ridges, springing from the continuous base, are narrow distally, so that the lateral rows of cells are close on the midrib and a few are more or less conical. The transition from the hypoderm of the succeeding segment is by a gradual modification in the arrangement of the vertical cells, which by-and-by are fan-like and then pennate. This pennate condition in the preparations of the hypoderm is apparently limited in distribution, since it is absent in most sections both dorsally and ventrally, and Von Drasche neither mentions nor figures it. Moreover, in transverse sections, so far as observed, it is not seen, and therefore may be due to the arrangement of the cells in a vertical plane after preparation. An approach to this condition of the hypodermic cells is observed in some longitudinal sections of *Myxicola*, but it is less distinct than in *Owenia*, and is probably due likewise to the effect of the preservative fluid acting on a thick glandular hypoderm. The inner edge of the collar has a series of minute cells along its anterior border, and a fan-like series of strands and cells posteriorly, whilst the tip is symmetrically pennate. The anterior curve of the furrow is furnished with a special series of granular pigmented cells, *oc.*, closely arranged at the surface, and which probably have the functions of eyes. They extend the whole length of the collar from side to side on the dorsal surface, and are partly protected by that fold (Pl. VIII. fig. 18, and Pl. XI. fig. 16).

The mucous glands (*mg.*) present either a characteristic

* *Op. cit.* Taf. i. fig. 3.

pennate aspect in longitudinal section or a series of straight or curved transverse bars, according as the long tube is cut in a median or lateral plane (Pl. X. fig. 19). In the former case a central axis of the secretion is flanked on either side by a series of plates, often slanting distally, and containing an occasional nucleated cell or a series of granules in the plate. Such a condition may be due to the action of the preservative spirit, or to the method of secretion, but it is worthy of note. The slender posterior ends of these glands are curved forward and outward. The secretion forms a lining to the tube, and attaches foreign structures such as sand-particles and foraminifera to it externally; and in many cases, so firmly do the annelids adhere to it after preservation, that rupture of the tissues accompanies their removal.

The hypoderm covering the mouth and buccal region, including the "lip-organ," differs from that on the surface of the body and branchiæ. It is bounded by a uniform and definite investment, and has a finely-granular and fibrillar structure, so that it forms a tougher, more massive, and more consistent layer, which, however, at certain parts diminishes in thickness as it approaches the branchiæ. It rests on a basement-layer having beneath it a complex series of muscular fibres. The same kind of hypoderm dips down and envelops the lip-organ, though it is more translucent in section, from the paucity of granules which stain more deeply. Then the organ forms a deep furrow (Pl. VII. fig. 6) with massive pale walls, whilst a double fold which now appears to the inner side, as well as the folds dorsad of the mouth, stain distinctly, as also do all the folds of the mouth and pharynx. The pale region thus lies in the figure between *a* and *a* in the centre of the organ, but it thins off on each side—that is to say, the middle region of the fold has thickest walls. The buccal mucous membrane is like that first mentioned in the lateral area of the cephalic region, viz., closely fibrous and granular, and it continues to the second diaphragm. It rests on a basement-membrane and a firm outer layer of both circular and longitudinal muscular fibres, the anterior or buccal region having numerous trabeculæ fixing it to the body-wall; and this is specially marked at the thick pale folds (lip-organ, *lp.*, in the various figures). The anterior buccal region is probably capable of partial protrusion. In front of the second diaphragm the folds of the canal have thick muscular walls, so that a certain amount of differentiation exists—either as proventriculus or stomach. Behind the second dissepiment the walls of the canal are

apparently uniform, and contain mud rich in organic remains.

The former or stomachal region enters the following or intestinal region by an aperture which is thrust backward as a cone. Moreover, the walls of the organ undergo a structural differentiation, for a short distance before reaching the aperture (text-fig.) they become finely reticulated and dotted as if formed of muscular or erectile tissue (*ec.*), whilst the lining of the tube consists of the same mucous membrane as in front. Further, the adjoining circular fold of the diaphragm (*spt. 3*) is provided with a similar, though thinner, layer of the same tissue (*ec.*), which likewise

Longitudinal section of the alimentary apparatus at the third septum, *spt. 3*, showing traces of the special muscular layer, *ec.*, enveloping the posterior wall of the stomach and its sinuses, and continued over the valvular region, *val.*; *hp.*, hypoderm; *cœl. c.*, coelomic corpuscles; *mg.*, mucous glands.

occurs in two of the folds of the organ in front of the foregoing. This tissue is apparently muscular, and its minute structure is interesting as showing the peculiar muscle-cells with their granular contents and nuclei which stud the free border of the muscle. Zürcher* has given a good description and figures of the structure of this tissue. It evidently controls, not only the wall of the canal but the blood-sinus on its outer surface, and thus may have considerable effect on the main trunks proceeding forward to the branchiæ. The coelomic corpuscles often form a

* *Op. cit.* p. 203, and figs. 33 & 35.

translucent mass (*cœl.c.*) behind the diaphragm and on each side of the gut.

Myriochele, the second genus of the Ammocharidæ, differs from *Owenia* in the simplicity of its anterior end, for it is broadly truncated, with a smooth margin, a deep pit or vestibule leading to the mouth, and a ventral fissure; yet it is found that, though the branchiæ are absent, the nervous system is formed much on the same plan as that of *Owenia*. *Myriochele* is even more broadly truncate than *Owenia*, and as a transparent object its large blood-vessels in front and the great longitudinal mucous glands which follow give the body a striped aspect.

The cilia covering the large funnel-shaped oral cavity of *Myriochele* are long and powerful, so that the currents they cause are probably considerable. Moreover, the oral aperture is oblique, the rim dipping backward to the notch at the ventral border, thus somewhat resembling the condition in the young of *Owenia*, though the oral gap is larger.

In the early sections of the snout of *Myriochele* the hypoderm presents more distinct elements than in *Owenia*, and it appears to be somewhat thicker, its minute cells and granules in the gelatinous matrix being conspicuous. The sections have a horseshoe-shaped appearance, the wide oral gap beneath forming the heel of the shoe, which, however, is tapered at the tip, the wall thinning off at each side. The exterior of the shoe has cuticle, glandular hypoderm, and basement-tissue resting on a gelatinoid layer which has numerous minute nucleated cells along both outer and inner borders. Basement-tissue, again, bounds the vestibular hypoderm on the inner border, which differs from that of the outer wall in having a distinct inner coat, from which cilia probably spring. The basement-layer in both cases is apparently elastic. The surface-layer of hypoderm often presents clear spaces or vacuoles—probably from rupture and extrusion of the glandular tissue. Moreover, its external surface forms a more definite cuticle, whilst its inner border rests on the basement-layer, no nervous belt appearing in the first sections; but circular fibres occur within the basement-layer, and then a well-developed longitudinal coat of muscle which stretches downward to the oral edge, from which the epithelium of the mouth passes inward (Pl. XI. fig. 22) as a thick layer of cylindrical cells with nuclei, bounded internally by a thin sheet of circular fibres and a few longitudinal strands. The space (*cœlom*) between the body-wall and the oral wall shows many

granular cells with fine connective-tissue fibres at certain parts, besides blood-vessels. Then a narrow pale belt becomes distinct within the circular fibres and basement-tissue of the oral wall, apparently corresponding to the pale sensory layer of *Owenia* in the same region. The nerve-centre appears as a narrow pale granular band in section at the inner border of the hypoderm of the body-wall, and stretching downward from the dorsum (Pl. XI. fig. 22) as it passes by-and-by into the trunks connecting it with the ventral cord. This region therefore represents the prostomium, though devoid of any external indication. The minuteness of the nerve-centre in comparison with that of *Owenia* renders its finer details obscure, and it is more transparent. No fine strands from the hypoderm could be made out, the slightly prominent cells and interstitial tissue alone appearing at the edge, whilst its inner border rested on a smooth basement-tissue. Its position and extent agree with that in *Owenia*.

In horizontal (longitudinal) sections the central nervous system appears as an area at the inner border of the hypoderm about the point of the V-shaped oral funnel (Pl. XI. fig. 23), and its transverse breadth is shown by its appearing on each side in these sections. So far as can be ascertained in the preparations, no special sensory apparatus is present either in the form of a groove or deposit of pigment in the body-wall, but the pigment may have been removed by long preservation in spirit. Therein it differs from *Owenia* with its pigmented cells and its groove.

Then, the hypoderm, again, extends over the whole depth to the basement-layer dorsally, and the nerve-cords are differentiated laterally—at first high up, nearly on a level with the dorsal arch of the mouth (Pl. XI. fig. 25), and then gradually descending as in *Owenia*. Very soon between the mid-dorsal and the oral walls a blood-vessel appears, and one in each lateral space, the connective-tissue strands and cells which connect the walls apparently keeping them more or less in position, the vessels being proportionally large for the size of the annelid and perhaps subserving respiration (Pl. XI. fig. 25 and Pl. XII. fig. 24, *bv.*). When the body-wall becomes continuous—that is, just behind the ventral (oral) slit—the cords have reached the commencement of the lower third of the body-wall, and the median arch dorsally and the mid-lateral regions of the gullet present the thickest layer of cells, the upper angles and the lower edges being thinner. Moreover, a section of

the lip-organ (*lp.*) appears. A pale band indicates a differentiation outside the cellular layer dorsally and another laterally. The chamber by-and-by assumes a figure-of-8 outline, the section of the lip-organ occurring in the lower division; and this shows a dorsal lenticular region of firm pale nucleated cells, somewhat symmetrically arranged, the lower part still having its cavity surrounded by the softer and more deeply-stained nucleated cells of the vestibule (Pl. XI. fig. 26). The figure-of-8 outline of the chamber is now complicated by a median process on each side and by the appearance of a diverticulum (gullet) dorsally, whilst the increase in its size diminishes the space between it and the body-wall laterally and superiorly, though from the first it clings to that wall ventrally. The pale streaked dorsal region of the lip-organ is gradually increasing in size as the sections pass backward; the diverticulum joins the upper region of the canal, which is soon separated from the lower by the junction of the median processes or isthmuses, thus confining the lip-organ to a special chamber (Pl. XII. fig. 27). The upper chamber is lined by the soft cellular mucous coat; the lower has a thin lining of epithelium, with longitudinal and a few circular muscular fibres externally, the whole becoming continuous with the upper edge of the lip-organ on each side, the remains of the ventral wall with its mucous lining at first linking it to the lip-organ and then disappearing, the mid-ventral region being occupied by strong muscular fibres, probably the protractor of the organ. The nerve-cords are on each side and widely separated, and the ventral wall of the body is very thin. A blood-vessel lies on each side at the upper edge of the lower chamber; a section of a succeeding part of the canal appears at the upper border of the wall of the lower chamber, and soon stretches across the entire region. A change is also taking place in the upper chamber, the lower region of which is thickened and its cells rendered paler. In the roof of the lower chamber the cells are assuming the chordoid condition of those in the lower region, so that very soon both halves make an efficient organ for compression or manipulation. The upper chamber becomes also smaller, and the space between the two larger. Strong muscular fasciculi appear both dorsally and ventrally over the lingual organ in the lower chamber; and the nuclei in the elongated cells of the modified organ form a row nearer the outer than the inner border. In the interval between the upper and lower chambers another diverticulum of the upper chamber has

been intruding, and is easily recognized by the numerous nuclei. The halves of the lip-organ in the lower chamber are becoming continuous and, fusing, form a dense cylinder with only a chink in the centre, the nuclei of the cells being situated near the external border. The alimentary canal in the upper region occupies more than half the area within the body-wall. At this level the hypoderm is thickest laterally and has increased ventrally with the downward progress of the nerve-cords, the lip-organ is now solid in section and smaller, whilst the canal above has increased in size, and a central chamber of different cellular structure makes its appearance, whilst by-and-by only muscular fibres occupy the place of the lip-organ inferiorly, and a cœlomic space occurs at each side. The nerve-cords touch and soon fuse.

The alimentary canal now takes a median position in the body-cavity, with a dorsal and a ventral mesentery, and it occupies a large space. The thinning of the dorsal longitudinal muscles in the mid-lateral region indicates a differentiation, whilst a considerable mass over the ventral nerve-cord and a thinner layer on each side represent the longitudinal ventral muscles. The mucons glands now appear toward the lower region of the cœlom, and they seem to have the same structure (Pl. XII. fig. 28) as in *Owenia*, and to open by similar wide ducts. The dorsal and ventral blood-vessels in the respective mesenteries are large. The hypoderm at this level is thick all round, especially ventrally, where the nerve-cords are in juxtaposition, and the dorsal and ventral longitudinal muscles are thicker and better differentiated (Pl. XII. fig. 29). The alimentary canal next presents various wrinkles; and a pale band passes from each side of the nerve-cords (which are proportionally large) outside the basement-layer, as if extension were indicated. The alimentary canal is thrown into deep folds, as if a stomachal or gizzard-like part existed in the lateral regions, whilst the dorsal and ventral arches have the ordinary mucons structure; then considerable vertical constriction occurs, the dorsal and ventral arches disappear, and a vascular sinus is established laterally. Thereafter the gut is pointed above and is split into two lobes ventrally, with muscular bundles in the gap. The latter (gap) by-and-by disappears, the canal enlarges, the lumen is much filled up with the dense coating of cells, and the vascular sinus around it is continuous in the sections (Pl. X. fig. 30). Externally at this level the hypoderm is massive ventrally, thins off laterally, and again becomes thin dorsally. The longitudinal muscular coat is thinner, and fibres radiate from a little

above the duct of a mucous gland, impinging on the wall of the blood-sinus on one side, and apparently attached to the depression in the hypoderm and indicative of an opening in the mid-lateral region. The epithelium in the food-canal differs quite from that in front, being almost fibro-granular in aspect from the elongation of the cells, the nuclei of which lie toward the outer border, and at first the surface presents reticulations. The alimentary canal enlarges behind the foregoing, but the character of the mucous lining remains the same, and the ventral blood-vessel lies in the mesentery over the nerve-cord, which is large, with a median peak dorsally and a specially thickened hypodermic layer at each side. On the dorso-lateral regions of the body the hypoderm appears to be thicker than on the mid-dorsal and mid-lateral parts. No specialized dorsal blood-vessel appears in this region, for it has fused with the sinus.

In horizontal longitudinal section (Pl. XI. fig. 23) the alimentary apparatus has a similar appearance at the second septum to that shown in *Owenia*, though the details are slightly different and the scale is much less. The mucous lining is thickened as it approaches the septum, and a centro-lateral fold bulges forward into the stomachal or gizzard-like division, whilst the central opening is narrowed and enters the succeeding part of the alimentary canal as a prominent papilla. The narrow termination of this region stains more deeply than the rest; indeed, it is coloured like the muscular septum, so that it is probable that it has specially developed muscular fibres at this part so as to enable it to perform sphincter-like functions, the food being retained in this chamber for some time and then permitted to pass backward by relaxation of the muscular guard.

In vertical sections of the middle region the gut is at first flask-shaped, the wide part, with the contents, being dorsal, the narrow part ventral; and the mucous lining has again altered its character, the cells being larger, their nuclei larger, and the inner edge smooth. The cœlomic space in the female is distended on both sides with large ova having a clear nucleus, an opaque nucleolus, and granular contents, and they spring from the epithelium of the mesentery below the ventral blood-vessel, the smaller ova being inferior, the larger superior. A noteworthy change is the disappearance of the blood-sinus around the gut and the presence of a dorsal vessel in the upper mesentery, the ventral trunk remaining as before. The thick layer of hypoderm ventrally has a furrow over the median nerve-cord, and this coat is comparatively thin laterally and dorsally. The dorsal and

ventral mesenteries separate the muscles of the sides, but there is little to distinguish between the areas of the dorsal and the ventral muscles respectively.

Proceeding backward the epithelium of the gut becomes somewhat finer, the longitudinal muscles form a uniform layer all round without evident differentiation other than the attachment of the median mesenteries, and the hypoderm still remains thicker ventrally, whilst the blood-vessels and ova show no change. A gelatinoid (protoplasmic) layer envelops the longitudinal muscles internally, the representative of the coelomic epithelial layer.

Then the intestine in section shows a keel ventrally, and septal strands, apparently muscular, pass from it to the body-wall, making membranous (and partly muscular) septa to the latter, viz., one on each side of the gut. These septa, however, soon reach the dorsal region and become attached to a process from the dorsal wall of the gut on each side, the dilated (globular) region of the canal being filled with food below these, the ventral portion forming a solid apex. The septa tend to mount upward on the interior of the body-wall, leaving two great areas ventrally on each side of the canal and a narrow dorsal chamber above the septa. Finally, the septum disappears, leaving only a small vessel at the dorsal mesentery. Then a sinus again forms on the upper wall of the gut, the ova continue as in front, and the section of the nerve-cord is more or less circular.

Behind the former region the body-wall becomes somewhat thinner, the thickest region of the areolated hypoderm being the ventral. The nerve-area is comparatively large and ovoid. The basement-layer and, it may be, fine circular fibres occur internally, whilst the longitudinal muscular fibres are only differentiated by the median mesenteries dorsally and ventrally. The gut is large, with a firm external wall and a single layer of cylindrical epithelium, the nuclei being symmetrically arranged in the middle. No dorsal vessel is visible, but the frilled external wall of a sinus occurs laterally on the intestine. The ventral blood-vessel is large and the mesentery leading to the ventral wall is loaded on each side with developing ova, the larger forms distending the coelomic cavity on each side (Pl. IX. fig. 31).

The tip of the tail is bilobed, with, in addition, a ventral median semicircular lobe, and is richly ciliated (Pl. X. fig. 32), a short terminal portion of the intestine being straight, the next (in front) being indicated by a slight constriction, whilst the third is almost elliptical, from marked constrictions in front and rear. In most cases, when removed from the

tubes after preservation, the caudal region is thrown into various zig-zags or spirals, and the tufts of bristles are more conspicuous than in front. One or two of the terminal bristles are single on each side, those preceding being in groups of two, three, four, and five or more. In certain examples, in lateral view, the ventral process at the tip of the tail projects more than the dorsal, though, perhaps, irregularity of the dorsal lobes occasionally occurs. The arrangement of the septa is apparently on a similar plan to that in *Owenia*, where they are very distinct. The septa in *Myriochele* probably cause the constrictions, and the tips of the lozenge-shaped sections of the intestine are fixed by membranous attachments to the body-wall. A pinnate aspect is apparently due to the blood collecting at the septa, where it was darkened by the stain (hæmatoxylin). The reproductive elements appear to be lodged on each side posteriorly, but their mode of exit has not been demonstrated. So far as could be made out, no pores were present posteriorly.

In sagittal sections of the tail (Pl. X. fig. 33) the constriction present a short distance from the tip appears to be normal, the gut being narrowed at this point and furnished with a valvular process projecting forward (*val.p.*). The terminal region of the body thus marked off is divided dorsally into five compartments by short transverse septa, on the anterior faces of which layers of blood occur, probably from extravasation, as no walls other than the septa are visible. The continuation of comparatively large intestinal sinuses almost to the tip of the tail, in addition to the ventral trunk, indicates their importance in the economy of the annelid, probably in connection with a respiratory function.

The transverse sections of the extreme tip of the tail show a ring of hypoderm with a ventral gap (Pl. X. fig. 34), on each side of which the wall is thickened, so that it is lobate. Moreover, a differentiation occurs in this lobate part, as if an aperture existed; but such may be due simply to the more vacuolated condition of the hypoderm of this region. The cells are larger than on the dorsal surface, and after the completion of the posterior aperture they form a distinct pale area on each side of the middle line (Pl. X. fig. 35). The gut shows, almost before its closure, traces of the vascular sinus (Pl. X. fig. 35, *vs.*) on each side, the blood in which had been rendered of a deep purplish-black hue by the action of hæmatoxylin; and soon the ventral vessel appears, the lateral sinuses greatly increase in size, whilst ova are present between the ventral vessel and the body-wall, the nuclei in these being

deeply stained. The lateral sinuses leave only a small portion of the gut bare above the ventral vessel in front of the fore-going sections, and the ova occupy the lateral regions, though their position is variable, for they by-and-by appear, as the body enlarges, below the alimentary canal and the vessels.

The fine sand-tubes of this form abound in such regions as the Gulf of St. Lawrence, and occasionally one end (the caudal) is terminated by a long tapering filament of the secretion covered with sand.

The main feature in forms like the present is the partial differentiation of the nerve-tissue from the hypoderm with which it is in continuity at its centre. No sheath is evident anywhere, even in the more distinctly outlined nerve-cords posteriorly. Yet the position of the cephalic centre and its connection by two trunks with the ventral nerve-cord agree with the general type. The innervation of the alimentary canal seems to be carried out on a similar plan to that of the main system, viz., by contact with a sensitive layer rather than by special twigs, since the latter have not been met with in sections. The whole nervous apparatus, indeed, is in an elementary condition, and in marked contrast, for instance, with that of such highly differentiated types as *Bispira* and *Branchionma*, where a chordoid skeleton protects the central ganglia and the neuroglia is much developed, the whole central system being shielded by the tissues around it, and so in the brain of *Glycera* as described by Gravier*, in various types by Eisig, and in the brain of *Lagis* as shown by Nilsson†. In *Owenia* and *Myriochele* the trunks from the central system are not œsophageal, but run externally in the hypoderm to join the ventral cord. Both *Owenia* and *Myriochele* appear to have certain larval characters, as seen in the young of various polychæts, for instance, in Kleiuenberg's‡ *Lopadorhynchus*, in which, amongst other features, the nervous system of the gullet may approach that of the enigmatical pale layer in the vestibule of the present species. The structure of *Saccocirrus*, as given by Goodrich§, also presents certain analogous conditions.

The alimentary canal of both *Owenia* and *Myriochele* shows certain valvular complexities, doubtless associated with the nature of their food—viz., mud or sandy mud containing organic particles of various kinds. Carried into the

* Bull. Sc. France et Belg. t. xxxi. p. 159.

† 'Beiträge der Kennt. des Nervensystems der Polychæten,' Upsala, 1912.

‡ 'Die Entstehung des Annel. aus der Larva von *Lopadorhynchus*,' 1886.

§ *Op. cit.*

vestibule by ciliary currents, it would in the first instance be subjected to the action of the œsophagus, then passed in certain quantities into the stomach with its mobile glandular walls, and subsequently sent through the funnel-like muscular valve at the third septum into the intestine. The occurrence, moreover, of the valve-like folds towards the posterior end of the intestine in *Myriochele*, with the adjacent vascular apparatus, would seem to indicate special functions there, both in regard to the contents of the gut and respiration.

The central nervous system in *Owenia* and *Myriochele* does not conform to the typical three regions of the able investigator Racovitza—viz., the paired “région palpaire” giving branches to the palpi, the unpaired “sincipital” giving branches to the eyes and tentacles, and the paired “nuchal” to the ciliated sensory grooves; or to those of other authors of more recent date, the elementary condition, perhaps, being associated with the feebly developed and much modified prostomium, especially in *Myriochele*. Further, the contrast between the typical form with its circumœsophageal commissures is noteworthy, since the homologues of these are as much hypodermal as the central mass, for the nervous layer beneath the hypoderm of the vestibule essentially differs.

Another feature of moment is the absence of distinct nephridia in both *Owenia* and *Myriochele*, the only representative of a tube communicating with the cœlom and the exterior being Gilson's long hypodermic tube in the sixth segment, and which apparently is indicated in Delle Chiaje's* original figure as two zig-zag tubes between two bristle-tufts; and the author was also acquainted with the long mucous glands and the general arrangement of the branchiæ and their blood-supply. The addition of two eyes to one of the figures (2), with a pair of pinuate branchiæ, is, however, more or less imaginary.

Again, the general structure of *Owenia* and *Myriochele*, as representing the family Ammonocharidæ, gives small grounds for their association under the same suborder, as Prof. Benham in his earlier classifications† seemed to think, with the Spionidæ and Chætopteridæ in his group Spionoformia, which really comprehends these only, since his Polydoridæ and Magelonidæ, of which separate families are made, can without undue laxity be placed under the Spionidæ. Levisen, indeed, had previously made a separate group for

* Discriz. e Nat. degli Anim. Invert. pl. 175. figs. 1-5 (1841).

† ‘The Cambridge Natural History,’ vol. ii. p. 258 (1896).

his "Ammochariformia," keeping under his "Syllidiformia Spionina" the Spionidæ, Chætopteridæ, Cirratulidæ, Ariëidæ, Chloræmidæ (?), and Opheliidæ, an assemblage even more complex than that of Prof. Benham.

Explanation of the letters used in the figures.

- bv.* Blood-vessels.
- c.* Central nervous system.
- cm.* Circular muscular coat.
- cæ.* Cœlom.
- cæf.c.* Cœlomic corpuscles.
- dm.* Dorsal longitudinal muscles.
- dv.* Dorsal blood-vessel.
- ec.* Special layer of gut and diaphragm.
- g.* Gonads.
- hp.* Hypoderm.
- hpe.* Thickened layer of hypoderm.
- int.* Intestine.
- lp.* Lip-organ.
- m.* Mouth.
- mg.* Mucous glands.
- mp.* Pore of mucous gland.
- nc.* Nerve-cord.
- œs.* Œsophagus.
- ov.* Ova.
- spt.* Septum.
- st.* Stomach.
- val.p.* Valvular process of alimentary canal.
- vm.* Ventral longitudinal muscles.
- vs.* Vascular sinus.
- vv.* Blood-vessels.

EXPLANATION OF THE PLATES *.

PLATE VII.

- Fig. 1.* Transverse section of the anterior end of *Owenia fusiformis*, Della Chiaje, to show the central nervous system (*c.*). *m.*, mouth, the lining of hypoderm also having a pale band beneath it at *mc.* The ventral gap in the body-wall is still open. × Zeiss oc. 2, obj. A.
- Fig. 2.* More highly magnified view of the central nervous system, *c.*, as part of the hypoderm, *hp.*, *cm.* Circular muscular coat. × oc. 4, obj. D.
- Fig. 3.* Transverse section after the completion of the body-wall in front and the appearance of the lip-organ *lp.* *nc.*, nerve-cord. × oc. 2, obj. A.
- Fig. 4.* Section behind the foregoing. The vestibule is now contracting, and the lip-organ, *lp.*, is in full development, with its inner bifid region and more massive external part. × oc. 2, obj. A.

* I am indebted to the Carnegie Trust for part of these figures,

- Fig. 5.* The wall of the œsophagus, *œs.*, as the sections proceed backward, is completed, and various blood-vessels, *vv.*, including the dorsal trunk, *dv.*, are prominent. The lip-organ, *lp.*, presents a basal mass with a central chink, and a regular arrangement of its tissue. $\times$ oc. 2, obj. A.
- Fig. 6.* Vertical section of *Owenia fusiformis*. *a.*, the vestibule; *c.*, central nervous system; *lp.*, lip-organ; *mg.*, mucous gland; *spt.*, septum. The section is imperfect at *x*. $\times$ about 40 diam.

PLATE VIII.

- Fig. 7.* Transverse section behind the folds of the lip-organ and at the point where the tendinous transverse band, *bt.*, and its lateral connections occur in the ventral region. $\times$ oc. 2, obj. A.
- Fig. 7 A.* Transverse section indicating the condition of the parts of the lozenge-shaped tendinous region ventrally, as its upper and outer edges differentiate into muscular fibres and strands pass into the fasciculi beneath. $\times$ oc. 2, obj. A.
- Fig. 8.* Transverse section behind the foregoing, showing the diminishing, pale, elastic band, *bt.*, and the complete condition of the ventral longitudinal muscles, *vm.* The stomachal region is surrounded by blood-vessels, *bv.* $\times$ oc. 2, obj. A.
- Fig. 9.* Section in the line of the bristle-tufts with the opening of the mucous gland, *mp.* The stomach is still surrounded by the various vessels and their mesenteries. A trace of the elastic system is seen in the muscular differentiation, *mc.*, of the mid-ventral area. $\times$ oc. 2, obj. A.
- Fig. 10.* The thickening of the dorsal and ventral walls of the stomach is conspicuous in this section (behind fig. 9). On the left is a bristle-tuft, *br.* The median dorsal and ventral blood-vessels and their mesenteries, and the ducts of the mucous glands are seen on the way to the anterior. $\times$ oc. 2, obj. A.
- Fig. 18.* Vertical section of the region of the collar, *col.*, and the central nervous system, *c.*, with the adjoining body-wall. $\times$ oc. 4, obj. D, with 2-inch draw-tube.

PLATE IX.

- Fig. 11.* The body-wall has attained its general arrangement with the exception of the thickened lateral portions of hypoderm, *hpe.* The coelomic space is large, and the median dorsal mesentery is split inferiorly. The nerve-cords have now fused. $\times$ oc. 2, obj. A.
- Fig. 12.* In this section, which is posterior to the preceding, the vertical elongation of the alimentary canal is noteworthy, and the accompanying vessels are still separate, though in some fusion is indicated. The coelom has its corpuscles, and the mucous glands and their ducts are distinct. $\times$ oc. 2, obj. A.
- Fig. 13.* Transverse section after a considerable interval backward from the foregoing, showing the great extent of the ventral longitudinal muscles, *vm.*, and the commencement of the male gonads, *g.*, below the gut. The large area occupied by the intestine and its enveloping sinus is noteworthy. $\times$ oc. 2, obj. A.

- Fig. 14.* Section in front of the tail in a ripe male. The gut is still enveloped in the spacious sinus, *vs.*, with its dorsal and ventral mesenteries, and the coelomic cavity is loaded with sperms. The gonads, *g.*, are large, as also is their blood-supply, *bv.*, whilst the nerve-cord is smaller than in front. The arrangement of the muscles of the body-wall diverges from that in front, since the dorsal longitudinal muscles, *dm.*, are thickened on each side of the middle line, as are also the ventral above the nerve-cord; but in the figure the parts have been separated by the methods of technique. The hooks, *u.*, occur in numbers along the whole lateral region on each side, the bristle-tufts being shifted to the dorsal aspect. $\times$ oc. 2, obj. A.
- Fig. 15.* Section through the characteristic arrangement of the caudal septa, *spt.*, some distance behind *fig. 14*. The gonads, *g.*, in this region increase in size from before backward, and the free sperms lie in the chamber above the upper septa. A transverse septum is seen below the gonads. The dorsal longitudinal muscles are thickest, whilst the ventral cover two-thirds of the body-wall. $\times$ oc. 2, obj. A.
- Fig. 20.* Peculiar pennate arrangement of the gelatinous tissue and glands of the hypoderm anteriorly. $\times$ oc. 4, obj. D, with full draw-tube.
- Fig. 31.* Transverse section of the posterior region in a female with well-developed ova, *ov.*, which arise from the vascular ovigerous tissue ventrally, as in the male; some are cut and others altered by compression. $\times$ 100 diam.

PLATE X.

- Fig. 19.* Longitudinal section showing the arrangement of the mucus in the mucous glands. $\times$ oc. 2, obj. 4.
- Fig. 30.* Section through the stomach after the blood-sinus, *vs.*, around it is established. *mg.*, mucous gland; *bv.*, blood-vessels. The median ventral furrow, making the organ bifid in section, has now disappeared. $\times$ 100 diam.
- Fig. 32.* Tip of the tail of *Myriochele* protruding from a tube. Two dorsal papillæ and a slightly more prominent ventral papilla occur posteriorly. The zig-zag condition of the gut in this region is indicated. $\times$ 60 diam.
- Fig. 33.* Section of the tip of the tail of *Myriochele*, showing the valvular apparatus, *val.p.*, at the constriction of the body-wall, the septa, *spt.* The blood has been rendered opaque blackish by the hæmatoxylin used in the technique, and apparently has accumulated at the septa.
- Fig. 34.* Transverse section of the extreme tip of the tail of a female with the modified areolæ of the hypoderm, a larger area on each side being evident. $\times$ oc. 2, obj. D, with 1 inch of draw-tube.
- Fig. 35.* Section of the tail a little in front of the foregoing, showing the large areolæ of the hypoderm and the blood in the sinus, *vs.*, around the gut. $\times$ oc. 2, obj. D, with 2-inch draw-tube.

PLATE XI.

- Fig. 16.* Vertical section of one half of the anterior end of *Owenia fusiformis* cutting the nerve-centre, *c.*, across, and showing its relation to the sensory groove with its pigment-corpuses on the anterior wall, in close relation to the central nervous system. A fold of the vestibule is seen at *vt.* $\times$ oc. 2, obj. A, with 1-inch draw-tube.
- Fig. 22.* Transverse section a little behind the tip of the snout of *Myriochela* on the appearance of the pale central nervous system, *c.*, which becomes continuous with the nerve-cord on each side. The mottled condition of the hypoderm anteriorly is characteristic of this form. $\times$ about 100 diam.
- Fig. 23.* Horizontal section through the vestibule and three regions of the alimentary canal, viz., *æs.*, oesophagus, *st.*, stomach, and *int.*, intestine. *spt.*, septa; *val.*, valvular apparatus; *c.*, central nervous system; *bv.*, blood-vessels, in some cases the dark blood (coloured by hæmatoxylin) has been pushed beyond the line of the vessel. $\times$ Zeiss oc. 4, obj. A, with $1\frac{1}{2}$ -inch draw-tube.
- Fig. 25.* In this section the cords are descending, being a little below the middle line; and the sides of the vestibule are now slightly united. Dorsal and lateral blood-vessels are in a similar position to those in the foregoing figure. $\times$ 100 diam.
- Fig. 26.* The body-wall is completed, as also is the vestibule. The nerve-cords, *nc.*, are descending, and a section of the lip-organ, *lp.*, appears. $\times$ 100 diam.

PLATE XII.

- Fig. 17.* Sagittal section of the anterior end, to illustrate the complex interlacing of the muscular fibres. The collar, *col.*, and central nervous system, *c.*, are seen on the left. $\times$ oc. 2, obj. A, with 1-inch draw-tube.
- Fig. 24.* Transverse section before the completion of the body-wall. The nerve-centre, *c.*, is well shown, and probably the lower ends represent the commencement of the nerve-cords. Blood-vessels, *bv.*, occur both dorsally and laterally. $\times$ 100 diam.
- Fig. 27.* In this section the outline of the body is slightly altered, the vertical exceeding the transverse diameter. *æs.*, oesophagus with its cellular lining; *lp.*, lip-organ and its radiate arrangement of cells; *bv.*, blood-vessels. The dorsal and ventral portions of the walls are much attenuated, partly from stretching. $\times$ 100 diam.
- Fig. 28.* The diminution of the dorsal hypoderm and the increase of the ventral hypoderm are indicated in this figure, together with the great size of the oesophagus. The nerve-cords are approaching each other. $\times$ 100 diam.
- Fig. 29.* Transverse section after the union of the nerve-cords, *nc.* The succeeding region of the canal is joining the oesophagus on the right, and two mucous glands, *mg.*, are cut obliquely. $\times$ 100 diam.