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The Habits and Structure of *Arenicola marina*.

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With Plates 1—5.

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1. Distribution : Varieties: Habits.

THE common lugworm and its coiled castings of sand are familiar objects on almost all the sandy and muddy shores of Western Europe, but the exact geographical range of the species is doubtful. It has been recorded from the shores of North Siberia, Spitzbergen, Iceland, and Greenland (Wirén, 1883; Levinsen, 1883). On the north-east coast of America it has been found from the Bay of Fundy to Long Island

(Verrill, 1881). On both sides of the Atlantic, latitude 40° N. marks approximately the southern limit of *Arenicola marina*. South of this it is replaced in the Mediterranean by *A. Claparèdii*, Lev., and by *A. cristata*, Stimps., the latter also ranging on the west side of the Atlantic from Cape May (N. J.) to the Caribbean Sea. Its reputed occurrence on the north coast of Alaska (Murdoch¹), at Vancouver Island (Marenzeller, 1887), Coquimbo, and South Africa requires confirmation.

An abundant, widely ranging, and undoubtedly old form such as *Arenicola*, might be expected to vary considerably in its habits and structure, though it has not hitherto been ascertained how far this is the case. Having paid special attention to this point, we have found that there are (at least on the Lancashire coast) two varieties of *A. marina*, differing in habits, structure, and times of maturity, and that there is, in addition, considerable individual variability.

(1) From high-water mark down to the beginning of the Laminarian zone, the common shore lugworms (or "lugs," as fishermen call them, in contradistinction to the second variety, or "worms") sink their U-shaped burrows to a depth of from one to two feet below the surface. One end of the burrow is marked by a casting, the other by a "countersunk" hole, through which the head of the lugworm is protruded when the tide comes in. The size and colour of the animal vary with the amount of muddy organic matter in the sand. Where there is comparatively little mud, the *Arenicola* average about seven inches in length and are somewhat transparent, so that the superficial blood-vessels can be clearly seen through the thin body-wall. The gills, which are not very strongly developed, are composed of nine to eleven branches, each provided with three to five pairs of short lateral twigs (Pl. 1, fig. 3). The proboscis and prostomium are only slightly pigmented, and being very vascular, appear red in colour.

Where, however, the amount of organic matter is considerable, the worms are usually about ten inches long, and their

¹ 'Proc. U. S. Nat. Museum,' Washington, vol. vii, 1884, p. 522.

prostomium, proboscis, gills, and epidermis are black. The gills are better developed than those of worms living in purer sand. These differences are probably due to more abundant nutrition. The time of maturity of both these forms of the littoral variety on the Lancashire coast is the summer, while at St. Andrews they are found mature from February to September.

(2) The second variety occurs on the Lancashire coast at the upper part of the Laminarian zone. Almost all the *Arenicola* from this zone (which can accordingly be obtained only at low spring-tides) are of this kind, which when fully mature, as it is from February to May, is probably one of the largest Polychæts of our shores, measuring as much as fifteen inches in length and three in girth. It is almost black, the prostomium, proboscis, and the base of the gills being markedly so. The tail is shorter in proportion to the length of the body than in the littoral variety. The burrows are of considerable length, three feet or more, and are not U-shaped, but simply vertical. Like those of the littoral variety, they are lined by a greenish coating of mucus. The dark "worms" appear to keep nearer the surface of the sand in cold weather than in summer,—at least, during the winter of 1893-4 large numbers were thrown up on the beach at Blackpool.

The most distinctive character, however, of this "Laminarian" variety is the gill (Pl. 1, fig. 2), which presents a structure hitherto only known in *Arenicola cristata*, Stimps. Instead of the somewhat simple gill seen in the shore lugworms, there is in the "Laminarian" variety a highly developed pinnate structure, consisting of about twelve branches united by a connecting membrane at their bases, and bearing ten or more pinnules on each side of the main axis. Such a gill is undoubtedly a much more efficient respiratory organ than the gill of a shore lugworm, though it does not appear to possess the same power of contractility as the latter, and hence probably does not contribute so much to the movement of the blood. In some old specimens the gills lose many of their finer branches, perhaps owing to friction or to the

attacks of enemies,¹ and in such cases there is an approximation to the type of gill seen in the littoral variety, though a certain amount of difference is always observable.

Thus there appear to be two varieties of the common lugworm on the Lancashire coast, distinguished by their habits, external features, and periods of maturity, but there are no important structural points of difference.

The habits of *Arenicola marina* at the breeding season are still to a large extent unknown, and developing eggs have not hitherto been obtained. It has been stated that, when mature, the animal is in the habit of swimming freely (Ehlers, 1892, *a*), but we are unable to confirm this. The post-larval stage, however, appears to be, for a short time, pelagic (Benham, 1893).

The curved burrow of the shore lugworm is formed by the combined action of the proboscis, the swollen anterior region of the body, and the waves of muscular contraction which pass along the body from behind forwards. When the proboscis is everted and pressed into the sand, the prostomium is slightly retracted into the body. The proboscis is withdrawn full of sand, again everted, and the body is thrust forward, partly by contraction of the longitudinal muscles, partly by a peristaltic wave produced by the circular ones. The anterior end is in this way rendered swollen and tense, and is able to enlarge the burrow, and thus a passage is gradually eaten through the sand, smoothed by contact with the skin, and lined by the mucous secretion of the epidermis. The gill region being narrower than that which precedes it, is thus, to a certain extent, protected from friction, while, as if to ensure this, the notopodial pencils of bristles are directed so as to protect the gills. After burrowing vertically downwards for a depth of from one to two feet, the worm forms a horizontal or oblique gallery, and then a second vertical one which ends at the "countersunk" hole, through which the anterior part of the worm may protrude, and so bathe the gills in fresh sea water.

¹ See the curious account of the ravages of *Corophium longicorne*, by d'Orbigny, 'Journal de Physique,' 1821.

The amount and value of the work done by lugworms has been estimated on the shore of Holy Island by Mr. Davison (1891), and has also been adverted to by Mr. Hornell under the name of "cleansing of the littoral." Mr. Davison finds that the castings are larger and more numerous above than below half-tide; and as the result of several estimates and measurements he calculates that on the Holy Island Sands, the entire layer of sand, to a depth of two feet, passes through the bodies of the lugworms which live in it, once in twenty-two months, and that in a year the average volume of sand per acre, which is brought to the surface in the form of castings, is 1911 tons, representing, when spread out, a layer of thirteen inches in thickness over the surface of the sands.

2. External Features.

Segmentation.—The body is divided into an anterior chætigerous portion, a middle branchial one, and a posterior caudal region or tail. The first region begins with the prostomium, and is followed by a short achætous portion (fig. 1, *MET*), which in many specimens appears to be composed of four annuli, divided, however, by secondary circular markings. The first chætigerous annulus is produced into a strongly marked ridge, just behind which the notopodial setæ (*Chn.*¹) are inserted, the corresponding neuropodia (*Nm.*¹) being very short and containing only a few setæ. The intervals between the chætigerous annuli are subdivided into rings, of which there are, in the "Laminarian" variety, 2 2 4 4 4 . . . , and in the littoral variety 2 3 4 4 4 . . . respectively.

The chætigerous annuli do not mark the true somites into which the body is divided. From a consideration of the internal anatomy (see p. 10) we have reasons for believing that, in the middle region of the body, the second groove behind each chætigerous annulus marks the boundary between the somites. A somite is, therefore, composed of a chætigerous annulus together with three annuli in front of, and one behind, it. The parapodia are not situated at the beginning, but slightly behind, the middle of the somites to which they

belong, thus confirming Benham's observations on the post-larval stage (1893).

The anterior region of the body is thus composed of the prostomium, six chætigerous somites, and a region between these, made up probably of two somites, but the exact number is somewhat doubtful. (See Plate 1, fig. 1, and explanation, p. 39.)

The second or branchial region of the body is composed of thirteen somites, and is distinguished by the presence of gills, a pair of which are attached to a slight fold of the skin just behind the notopodia. The first gill is variable, usually fairly well developed, but always smaller than the rest and sometimes absent. The gills about the middle of the branchial region are frequently, but not always, the largest. Both the gills and notopodia are very sensitive, and are retracted from time to time on the application of stimuli, such as a strong light. This contraction of the gills proceeds sometimes as a wave down the body, and as Milne Edwards (1838) pointed out in his classical paper, considerably assists the circulation of the blood. The neuropodia in the branchial region extend towards the mid-ventral line, so as almost to meet, and are only separated by a groove which marks the line of the nerve-cord. This groove is continued on to the prostomium by a pair of diverging arms ("Metastomial grooves") underlying the circum-oesophageal nerve connectives (Pl. 4, fig. 19, *C. Mt.*).

The tail, which is devoid of setæ and gills, is marked by a large number of secondary annuli, crowded together at first, but arranged in distinct somites of about five each, towards the hinder end. The caudal region varies much in length; some specimens have about thirty somites, but the number is not constant, possibly owing to the tendency of the worm to throw off the last few segments when irritated.

There is no change in the internal organs to mark the somite which bears the first gill, but the transition from the branchial to the caudal region is accompanied by the loss of parapodia, oblique muscles, and branchial vessels.

External apertures.—The mouth (Pl. 4, fig. 19, *C. MO.*),

when the proboscis is withdrawn, is a slightly crescentic transverse slit, bordered by papillæ and somewhat overhung by an upper lip. The anus, which is terminal, is often protruded, and the thin vascular swollen lips of the aperture project behind the last caudal segment.

The opening of the "nuchal organ" is a fairly wide slit on the upper and hinder border of the prostomium (Pl. 4, fig. 19, *A* and *B*, *NV.*). Through this aperture, sea water (or a mixture of sea water and the secretion of the surrounding glandular cells) is probably introduced.

The openings of the otocysts are difficult to see. They lie behind the prostomium on each side of the anterior end in the position marked *OT.* (Pl. 4, fig. 19, *A* and *B*). Each is placed at the point of intersection of the first transverse groove following the prostomium, with the oblique "metastomial" groove which marks the position of the nerve commissure.

The nephridial openings (fig. 1, *NO*), six in number on each side, though not so distinct as in some species (e. g. *A. Claparèdii*), are not difficult to find. The first is placed behind and at the upper edge of the fourth neuropodium, and the other five in corresponding positions on the succeeding somites. They are minute slightly oblique slits, sometimes exhibiting tumid lips.

Skin.—The skin is subdivided into raised polygonal areas separated by corresponding shallow grooves, and is noteworthy in being devoid of special glands. Wirén (1887) has shown that the grooves are composed of columnar cells containing pigment granules, the raised areas being made up partly of larger cells containing still greater quantities of pigment granules and partly of clavate mucus-forming cells, which produce the slimy covering of the animal with which the burrow is lined.

The 5 per cent. formalin solution of the epidermal pigment is fluorescent, but does not yield any absorption bands, merely cutting off the rays at the blue end of the spectrum. In successively thicker layers of this solution, first the violet, then

the blue, and lastly the green portions of the spectrum were cut off.

MacMunn (1889), however, has shown that the alcoholic extract of the integumental pigment shows a band in the blue and green (λ 503—468); that the residue of this solution if dissolved in ether or chloroform yields two bands, λ 503—474, and λ 465—446; and that the residue of this solution again being dissolved in nitric acid gives two bands, λ 500—468, and λ 472—443, so that a chlorophan-like lipochrome is present. It is probable that the pigment (melanin) of the skin is derived from the lipochrome of the yellow "glandular" tissue of the stomach, since the alcoholic extract of the latter yields a similar absorption spectrum.

Further investigation will be required to show in what way the transference of the pigment from the yellow peritoneal cells to the epidermis is brought about, and whether the dark-coloured, hairy-looking investment of the ventral vessel and its branches (Pl. 2, fig. 5) contributes to the melanin of the skin. In this connection the intermuscular extension of the cœlom, bringing it almost into contact with the epidermis at certain points, must be borne in mind (see p. 29).

Setæ.—The notopodial setæ are long capillary structures averaging 6 mm. in length, and bearing several rows of minute free and pointed hair-like processes (Pl. 3, fig. 10). The neuropodia in the anterior somites, which at first contain few setæ, gradually extend by addition of new ones at their ventral edge, so as to almost reach the mid-ventral line (Pl. 1, fig. 1). By isolating the entire band of the setæ the different stages in their development may be seen. The youngest setæ are always at the lower end of the series; the point of each seta is formed first, then the toothed ridge, and lastly the shaft. The fully-developed ventral seta is frequently almost smooth, owing to the wearing down of the teeth behind the apex. The middle of the shaft is straight, the inner end bent ventrally, and the outer end bent slightly dorsally, ending with a finger-shaped process bordered on the convex side by a toothed ridge, while on the concave side it is slightly produced at one

point into a minute process (Pl. 3, fig. 12, *proc.*). This process is more constant in the Laminarian than in the littoral variety. It appears to correspond, in position, to the characteristic tuft of hairs on the ventral setæ of the Maldanidæ.

According to the age of the specimen the ventral setæ differ in shape, and in the development of the toothed ridge. In setæ from a small specimen (17 mm. long) the apex was bent more sharply on the shaft than in old examples, and the teeth were very prominent (Pl. 3, fig. 9). Apparently the production of fresh ventral setæ goes on slowly throughout life, and the form which they assume before being cast out of the body, varies at different ages. Their size of course varies with the age of the worm to which they belong (see Pl. 3), but in a worm of average size their length is about .5 to .8 mm.

3. General Anatomy of the Internal Organs (Pl. 2).

In opening the body-cavity by a dorsal incision, the middle part of the alimentary canal is usually forced out through the cut by the pressure of the somewhat viscous cœlomic fluid. Normally this portion of the canal, being longer than the section of the cœlom in which it lies, is swung to and fro by the movements of the body. This freedom of motion is ensured by the absence of mesenteries, by the absence of any vessels running from the body-wall into the dorsal vessel, and by the length and flexibility of the branchial and nephridial vessels, which are the only connection between the stomach and the body-wall.

The cœlom is exceedingly spacious, and continuous from one end of the body to the other. In front it is divided transversely by the origins of the buccal retractors (*B. Sh.*), which form a sheath round the proboscis, and by three septa or diaphragms (Pls. 2 and 3, figs. 5 and 6). The first of these septa (*Dphm.*) is placed obliquely, arising below behind the level of the first neuropodium, and being inserted dorsally in front of the first notopodial sacs. The result of this arrangement is that between the first and second diaphragms two pairs

of setal sacs occur, caused by the forward shifting of the upper edge of the first diaphragm (fig. 5). The second and third are inserted both above and below, opposite the second groove behind the second and third chætigerous annuli. Between the first and second diaphragms, dorsal and ventral mesenteries occur, supporting the corresponding vessels; and it will be noticed that the dorsal mesentery ends in front, exactly where the first diaphragm would be inserted if it corresponded with the other two. The third diaphragm is perforated by the funnels of the first nephridia. There are, then, three diaphragms and not, as so often stated, four, and, while affording valuable evidence of the extent of the first and second chætigerous somites, they do not help in determining the number of segments which compose the achætous portion following the prostomium.

Behind the last diaphragm the body-cavity is unsegmented up to the base of the tail. The segmental arrangement of the organs, however, can be recognised by taking the funnels of the nephridia as marking the anterior ends of the somites. The slight amount of connective tissue supporting the long afferent and efferent vessels (segmental vessels) (Pl. 2, fig. 5) of the nephridia and gills, may be regarded as the remains of the septa. Allied species of *Arenicola* fully confirm this view.

At the level of the thirteenth pair of notopodial sacs, the segmental afferent and efferent blood-vessels, which have hitherto run nearly parallel across the cœlom, diverge. At the base of the tail, the connective tissue between them increases slightly in amount, septa forming which are continued down to the end of the body (fig. 5, *C. Sp.*).

4. Musculature.

The muscles of the body-wall are arranged in (1) an outer circular sheath, subdivided in the anterior and middle regions of the body into hoops, which cause the annulation of the skin; and (2) an inner longitudinal sheath of considerable strength and thickness divided by the nerve-cord and lines of

insertion of the notopodial sacs into three parts, two ventro-lateral and one dorsal (Pl. 4, fig. 23). The intermuscular spaces are filled by cœlomic fluid, and are probably lined by a delicate peritoneum.

In the anterior region of the body there are a few circular muscle-bands which are stronger and more obvious than the rest (fig. 5, *M. Circ.*).

The oblique muscles, which divide the cœlom longitudinally into three compartments, commence behind the third diaphragm, and disappear at the base of the tail. These muscles are arranged in thin broad bands, arising at the sides of the nerve-cord, and are inserted right and left into the body-wall at the level of the notopodial sacs. They partly cover the nephridia, and in some specimens a muscle-band is attached to each nephrostome.

The musculature of the buccal mass consists of a strong sheath of fibres derived from the longitudinal layer just behind the first diaphragm. This sheath, which is loosely attached to the proboscis by slips which run through the cœlomic space between the two structures (Pl. 3, fig. 6, *B. Sh.*), is inserted into the anterior part of the proboscis. Pressure of the cœlomic fluid at this point causes eversion of the buccal mass, which is withdrawn by the contraction of its muscular sheath.

The prostomium is retracted by a small sheet of muscle which arises partly from the longitudinal layer dorsally, and partly from the muscular covering of the circumœsophageal connectives ventrally, and it is inserted into the ventral surface of the brain, and the ventral and hinder edge of the nuchal organ (Pl. 3, fig. 6, *Nu. Tr.*).

The parapodial muscles are modifications of the longitudinal layer. One, the retractor of each notopodium, is remarkably long, reaching to the side of the nerve-cord (Pl. 3, fig. 13, *Rn.*). The protractors (*Pn.*) of the notopodia are six to eight in number, three to four being placed in front of, and three to four behind, the setigerous sac. They arise from the body-wall just below the dorsal longitudinal vessel, and are inserted into the base of each sac.

The position and relations of the three anterior septa or diaphragms, of the dorsal and ventral mesenteries between the first two of these, and the presence of regularly arranged septa in the tail region, have already been noted. It may be added that a pair of outgrowths from the first diaphragm lie under the œsophagus, opening anteriorly into the cœlomic space in front of the first septum. They are very vascular, and contract rhythmically every three or four seconds during life, and are doubtless of use in everting the proboscis (Pl. 2 and 3, figs. 5 and 6, *Dph. Ph.*).

In the caudal region the intestine is attached both above and below to the body-wall by mesenteries, in which the dorsal and ventral vessels lie.

5. Alimentary Canal (Pl. 2).

This consists (1) of an eversible buccal mass (*Bucc. M.*), of a pinkish or greenish-brown colour, which lies in front of the first septum; (2) of an œsophagus, of a light brown colour, provided with a pair of glandular pouches behind the third diaphragm; (3) of a gastric region, with yellow glandular walls, extending from the level of the heart to about that of the twelfth or thirteenth notopodium; and (4) of an intestine, of a dark brown or almost black colour, folded in a concertina-like manner by the caudal septa, and opening at the terminal anus.

During life the buccal mass (or "proboscis") is constantly being everted and withdrawn, carrying sand into the œsophagus. During eversion several rows of curved, pointed, vascular papillæ (*B. Pap.*) are first extruded. These papillæ (Pl. 3, fig. 7) in old specimens are tipped with chitin, and recall the armature of the proboscis in certain Sipunculids (e. g. *Phascolion collare*¹). Then the more globular portion of the buccal mass, covered with minute rounded processes, is protruded. Finally, when fully everted, the buccal aperture is surrounded by a few pointed pigmented papillæ, which are continuous with the lining of the first part of the œsophagus.

¹ Selenka, 'Die Sipunculiden,' 1883, pl. vi, fig. 74.

The œsophagus¹ itself is slightly looped behind the second diaphragm. It is a thin-walled distensible tube, the first part of which is lined by non-ciliated mucus-forming cells. The middle portion is lined by a cuticle, and the posterior part by cells resembling those of the stomach in bearing cilia. The œsophageal pouches (*Oe. Gl.*) are somewhat flask-shaped, and open into the cavity of the œsophagus by a short tubular stalk. They are usually greenish in colour, but have a slight reddish tinge on account of their very large blood-supply. Their blood-vessels are connected with the lateral œsophageal and dorsal vessels. The cavity of the pouch is subdivided by twenty-five to thirty incomplete partitions, produced by infolding of the wall of the pouch, and therefore covered on each side by the epithelial lining of the pouch (Pl. 4, fig. 22). Between the epithelial lamellæ is a blood-sinus, which is slightly enlarged at the inner end and slightly thickened at the edge of each partition. The œsophageal pouches are lined by ciliated epithelium, covered with a fairly stout cuticle, and contain glandular cells. The walls of the œsophagus are marked by longitudinal and circular muscular impressions.

The stomach, marked out by the patches of yellow tissue on its walls, extends from the level of the heart to about the twelfth notopodial setæ. As we have already stated (p. 9), the stomach is bent upon itself and loosely attached to the body-wall. The patches of "chlorogenous" tissue are at first arranged in symmetrical oval areas right and left of the dorsal blood-vessel, while more ventrally they are placed in two or three less regular series, and are separated from one another by a network of blood-vessels.² About the level of the tenth setæ these yellow areas all become subequal and arranged in a spiral manner, ending at the level of the fourteenth setæ.

Stomach and Intestine.—The muscular wall of the

¹ The histology of the alimentary canal has been carefully investigated by Wirén (1887, p. 31). Our results agree very closely with his.

² This network is considered by Wirén and others to be parts of a continuous sinus. We are not convinced, however, that this is really the case, and our reasons will be found on p. 17 infra.

gastric region is exceedingly thin, and composed purely of circular fibres, which appear to confer very slight powers of peristalsis upon the stomach.

The mucous lining is strongly folded, and is composed of several kinds of cells. Some of the cells in all parts of the stomach are ciliated, others are apparently digestive, and a large number appear to secrete a mucus similar to that of the œsophagus, the cells themselves being discharged into the mucus which they help to form.

Commencing about the middle of the stomach (that is between the ninth and tenth segments) is a ventral groove formed by a couple of folds of its inner and lower surface. This groove¹ (Pl. 4, fig. 23, *Gv.*) is provided with specially long cilia, which produce a current of mucus from before backwards. There are other smaller grooves on the side walls of the stomach and the anterior part of the intestine, whose general direction is downwards and backwards, and which open into the median ventral groove. The direction of the current in all these is from before backwards. The ventral groove is continued back to the anus. The intestine is dark brown or nearly black in colour externally. Its mucous lining is somewhat similar to that of the stomach, but is covered by a thin cuticle, and is not ciliated.

The process of digestion in the lugworm has not been at all fully investigated, but the series of events appear to be somewhat as follows. The sand or mud is mixed with the mucous secretion of the œsophagus, and is slowly carried backwards by peristaltic contraction. At the junction of the stomach and œsophagus the secretion of the œsophageal pouches is poured upon the sand. Wirén regards the contents of these pouches as acid and digestive. In several cases we have found the fluid neutral. In the stomach several changes occur. The secretion of the gastric cells proper is probably digestive, and this, together with a further amount of mucus, is mixed with the sand, and shaken together by the swing of the loose gastric loop. In this way the food, which apparently consists of the

¹ This groove has only hitherto been noticed by Wirén (1887).

organic substances¹ in the sand, is brought into contact with the digestive secretion. The ciliary action of the lateral and ventral grooves probably separates the digested substances from the sand and carries them slowly downwards and backwards. The lining of the stomach is very thin, and the lateral and ventral grooves are in specially close contact with the blood-plexus, in which the flow is, probably, slowly forwards, more rapidly in the sub-intestinal vessels. It seems probable, therefore, that the blood in the visceral plexus conveys the nutritive material to the hearts, which pump it along the ventral vessel to the various parts of the body.

The action of the chlorogogenous tissue round the stomach, and particularly of that in the neighbourhood of the ventral vessel and its branches, is uncertain.

6. Vascular System (Pl. 2, fig. 5).

The blood-vascular system of *Arenicola* attains a high degree of perfection. The large size of the chief vessels, the great development of the capillary system (especially on the walls of the alimentary canal), and the mechanism for promoting the flow of the blood, are features that distinguish it.

There are two chief vessels running, one above, and the other below, the alimentary tract from end to end,—the dorsal vessel, which contracts fairly rhythmically from behind forwards; and the ventral vessel, which is feebly, if at all, contractile. The walls of the gastric and intestinal portions of the gut are enclosed in a blood-plexus, and the œsophageal region is supplied by lateral vessels. The gastric vessels are connected with the ventral vessel by a pair of "hearts" placed a short distance behind the œsophageal pouches (fig. 5, *V.*). These hearts drive the blood from the gastric vessels into the ventral vessel.

The dorsal vessel (*DV*) arises near the anus, and as it runs along the intestine gives off in each somite a pair of branches

¹ Saint Joseph found in an *Arenicola* a whole *Nereis* almost digested. 'Ann. Sci. Nat.,' series vii, t. xvii, 1894, p. 127.

which are attached to the anterior face of the caudal septa, and which run downwards and forwards to open into the ventral vessel (Pl. 2, fig. b). Of these there may be twenty-seven to thirty pairs. In front of the caudal region each of the last seven pairs of gills returns an efferent branch to the dorsal vessel, and between these there are three or two pairs of smaller branches which run round the alimentary canal from the ventral vessel to open into the dorsal one. From the level of the twelfth setæ to the œsophageal pouches the dorsal vessel does not receive any segmental vessels from the gills or nephridia, nor does it open directly into the heart (fig. 5). It merely receives numerous branches from the gastric plexus. In front of the heart it receives on each side a branch from the third nephridium and the fifth setigerous sac; a branch from the œsophageal pouches; and one from the second nephridium and fourth setigerous sac. It then runs on and, piercing the third diaphragm, receives a branch running on the anterior face of the diaphragm from the first nephridium and third setigerous sac. On reaching the second diaphragm it receives a branch from the second setigerous sac, and after piercing the first diaphragm receives a branch from the muscles forming the buccal sheath. Thence the dorsal vessel breaks up into capillaries around the buccal musculature, prostomium, and otocysts. From these capillaries the ventral vessel takes its origin. It gives off a small unpaired branch running in the first diaphragm and to its pouches; a paired branch arising about midway between the first and second diaphragms to the neural vessels and second setigerous sac; a single small vessel supplying the second diaphragm and the neural vessels; an unpaired vessel to the third diaphragm, to the neural vessels in that region, and to the first nephridia; a pair of branches to the neural vessels and second nephridia; and lastly, a pair to the neural vessels and third nephridia. From this point onwards the ventral vessel supplies the setigerous sacs, body-wall, nephridia (if present), and gills by large segmental vessels. The ventral vessel is very large and turgid in the gastric region, and is surrounded by tufts of dark brown chlorogogenous tissue,

which are also found in older specimens on the vessels running to the body-wall. This chlorogogenous tissue is first seen on the ventral vessel about the level of the eighth pair of setæ. In the tail the ventral vessel ends in the obliquely placed intestinal vessels which encircle the intestine, and which form, along with the capillaries from its median terminal portion, the commencement of the dorsal vessel.

Visceral Plexus.—Wirén (1887) maintains that the intestine and stomach are enclosed in a blood-sinus, thickened along certain lines which have been called the dorsal, gastric, and subintestinal "vessels." We are, however, of the opinion that the so-called sinus is a close plexus of vessels, some of which appear to have a distinct cellular lining. The dorsal vessel is, at any rate, a perfectly distinct structure with proper walls.

The subintestinal vessels (fig. 5, *S. V.*), which commence just behind the heart and run backwards, are moderately large up to the level of the thirteenth setæ, but then taper rapidly and gradually disappear. They each receive seven segmental vessels. The first of these comes from the fourth nephridium, the second from the fifth nephridium and the first gill, the third from the sixth nephridium and second gill, and the other four from the third, fourth, fifth, and sixth gills. The subintestinal vessels open through the plexus into the lateral gastric ones, and so into the heart. The flow in these vessels is probably slowly forwards.

The gastric vessels give off from the "auricle," into which they expand, a lateral œsophageal vessel (*Oe. Lat.*), which, after giving off a stout branch to the œsophageal pouches, runs forwards to the buccal mass, supplying the wall of the œsophagus, as it does so, with numerous small branches.

Neural Vessels.—These are a pair of small vessels lying one on each side of the ventral nerve-cord, and accompanying it from one end of the body to the other. They arise round the nerve-connectives from the brain from capillaries of the dorsal vessel, and receive several branches from the ventral vessel (1) midway between the first and second diaphragms, (2) from

the vessel running in the second diaphragm, (3) from a vessel just behind the third diaphragm, (4 and 5) from the vessels to the second and third nephridia. Near the middle of each somite the two neural vessels are united by cross connections, which also supply the nerve-cord (Pls. 2, 3, fig. 13, *N. V.*, *N. C. V.*).

Behind the third diaphragm the neural vessels supply the oblique muscles by branches which run the whole length of the bands, and are connected with the outer longitudinal parietal vessel (fig. 13).

Vessels of the Body-wall.—This parietal system of true vessels is highly developed in *Arenicola marina*. It consists of two longitudinal vessels, (1) the nephridial longitudinal vessel (fig. 22, *N. L. V.*) running just below the level of the nephridiopores, and (2) the more important dorsal longitudinal vessel (fig. 13, *D. L. V.*), which runs just above the level of the insertion of the notopodial setal sacs. Both arise just behind the first setæ, and increase in size as they pass backwards. The former receive vessels from the nephridia, just behind which they taper and disappear. The latter, which may be traced to the anus, and are largest in the branchial region, receive branches in each somite: (1) from the segmental vessels; (2) from its fellow of the opposite side. The body-wall in the dorsal and lateral regions derives its blood-supply from the nephridial and dorsal longitudinal vessels, and in the ventral region from the neural vessels. These parietal vessels (*Par. V.*) run just within the layer of circular muscles in almost every groove between adjacent longitudinal muscle-bands of the body-wall, are chiefly longitudinal in direction, but at frequent intervals there are cross connections. Branches from these vessels ramify between the bases of the epidermal cells, and are accompanied by extensions of the cœlom.

Hearts.—The hearts are a pair of muscular bulbous swellings connecting the visceral plexus with the ventral vessel on each side. Each commences with the thin-walled expansion of the gastric vessel ("auricle," fig. 5, *A. v.*) which, after giving off the lateral œsophageal branch, opens into the ventricle

(*V.*). The cavity of the ventricle is small and broken up by a spongy mass of cells. The ventricular walls are muscular, and contract from above downwards, forcing the blood into the ventral vessel. (We have sometimes seen an apparent reversal of the heart's action.) The spongy cardiac body arises by ingrowths from the wall of the ventricle, chiefly in the middle and ventral regions. It gradually encroaches on the blood space, so as to reduce it considerably (Pl. 5, fig. 36, *Card. B.*) in an old specimen. The cardiac body in a young specimen (fig. 38) is much smaller, and extends obliquely across the heart, its general direction being downwards and backwards. The cells of the cardiac body in an old specimen which we have examined are loosely arranged, so as to cause the formation of a large number of intercellular spaces, some of which are of considerable size, and which are in life filled with blood (Figs. 36—38, *B. S.*). Between the cells there are numerous fibres, which are probably muscular. The cells are apparently of two kinds, which, however, merge into each other: (1) cells whose protoplasm has a very vacuolated appearance, and which contain few or no granules (*Vac. C.*); (2) cells which contain a large number of yellowish granules in the protoplasm (*G. C.*). These latter cells are possibly glandular, and correspond to those found in the cardiac body of other *Polychæts*. The function of the cardiac body may be, as *Schæppi* (1894) suggests, to prevent regurgitation of the blood from the ventral vessel into the heart when the diastole commences. The "cardiac body" of *Polychæts*, as hitherto described, is an unpaired structure lying in the dorsal vessel. That of *Arenicola*, however, is paired and in no way connected with the dorsal vessel. Hence a strict homology is scarcely probable.

Blood.—As Professor Lankester was the first to point out, the blood of *Arenicola* is strongly impregnated with hæmoglobin, but there has been no thorough investigation of the constituents of the plasma. *Krukenberg* (1882), it is true, made some experiments which led him to believe that there were no coagulable albumens in the blood of his specimens; but as they

were in a starved condition, a fresh examination is very desirable. A large quantity of albumen is certainly present, which when the specimens are fixed becomes very hard and brittle.

We have seen small cells (4μ in diameter) in the blood-vessels of the nephridia, but it is doubtful if these are the blood-corpuscles, which we have not been able to demonstrate.¹

General Remarks on the Circulatory System.—No other system of organs shows the true segmentation of the body of *Arenicola* so well as this. The lines of demarcation between the somites from one end of the body to the other are marked by the segmental vessels passing from the ventral to the dorsal vessel and breaking up on their way in the body-wall, nephridia, or gills. Throughout the gastric region, however, this arrangement is somewhat disguised, owing to the loss of the connection with the dorsal vessel, an alteration caused probably by the necessity for leaving this part of the alimentary canal freely moveable.

Wirén evidently believes that there is no capillary system except in the gills and the alimentary canal. He suggests that the assimilation of food and oxygen by the tissues is effected chiefly through the mediation of the cœlom, which he points out is parcelled off in the intermuscular spaces, by a channelling out of the subepidermic connective tissue, into "perihæmal canals." Though this suggestion is a valuable and correct one, we have found a very perfect system of capillaries in the skin in all parts of the body, and in the nephridia and septa the same is the case. The extension of the cœlom into the intermuscular and subdermal spaces has, however, all the appearance of acting as the equivalent of lymph-spaces of higher forms. The transformation of the constituents of the blood into cœlomic fluid takes place in all probability with especial rapidity in the neighbourhood of the dark chlorogenous processes of the ventral vessel (cf. Cuénot, 1891).

¹ Since writing this we have discovered that these small cells are the blood-corpuscles.

7. The Gills (Pl. 1, figs. 2—4).

The general characters of these organs have been mentioned in the introductory part of this paper, and little remains to be added.

There are thirteen pairs of gills from the seventh to the nineteenth chætigerous somites inclusive. The shape varies from the short dendritic type of the littoral form to the delicate, richly-branched gill of the Laminarian variety. The gills are hollow, being outgrowths of the body-wall enclosing an extension of the cœlom, and what little evidence we have of their development (see Benham, 1893) points to their being independent structures, and not modified dorsal cirri.

The walls of the gills, though thin, are muscular, and there are also muscular bands stretching across the cavity of the gill (fig. 23); and Milne Edwards has pointed out that the contraction of the gills, which often proceeds like a wave from before backwards down the sides of the body, must exert a powerful influence in propelling the blood partly into the efferent vessels, and partly to the parietal capillaries.

The ventral vessel supplies all the gills with their afferent branches. The first seven pairs return the blood to the sub-intestinal vessels, and so to the heart; while the efferent branches of the remainder open into the dorsal vessel.

8. Nervous System and Sense-organs.

This system is composed of the brain, the œsophageal connectives, the ventral nerve-cord, and the nerves arising from these. We have not been able to demonstrate a visceral nervous system.

The brain (Pl. 5, figs. 25, 26) is placed in the prostomium, of which it forms the chief part, being only separated from the epidermis by blood-vessels lying in extensions of the cœlom. It is a small elongated structure, measuring $\cdot 75$ mm. in length in ordinary shore lugs, and 1 mm. in the large "Laminarian" variety. At its anterior end the brain is divided into two stout cornua (*A. Cr.*), separated by a cleft containing blood-vessels. About the middle of the brain the cornua unite, but only for a

very short distance, a second connective-tissue partition dividing the smaller posterior cornua (*P. Cr.*), which gradually taper off and end at the hinder edge of the nuchal organ (Pl. 5, fig. 25).

Sections of the prostomium of the littoral variety of *Arenicola* (immature specimens, 4" long) exhibit a thick covering of ganglion- and glia-cells, forming the dorsal surface of the brain (fig. 24); a central fibrous portion; and a strong ventral membrane, into which the greater part of the prostomial muscles are inserted, though a few fibres are attached in front of and between the anterior cornua (Pl. 5, fig. 25). In older specimens, and particularly in mature examples of the "Laminarian" variety, the ganglion-cells are more scattered, and in other ways the brain shows greater differentiation. The anterior cornua, for example, are not only deep and thick, but give off from their dorsal surface short stout branches, along which the ganglion-cells are scattered, and which supply the prostomium. The central fibrous part of the brain also grows out ventrally in these large examples, separating the hitherto compact layer of cells and carrying them outwards or leaving them in clumps, and not evenly arranged as in young *Arenicola*.

From the anterior cornua a large nerve arises on each side, in front of the origin of the œsophageal connectives. It passes out to the under surface of the epidermis, and supplies the papillæ on the upper surface and the sides of the mouth. The epidermis of the prostomium itself is in close contact throughout its whole length with the ganglionic covering of the processes arising from the dorsal and lateral surfaces of the brain. The posterior cornua seem to be specially connected with the nuchal organ, against which they lie and terminate (Pl. 4, fig. 21).

The most remarkable histological feature of the brain is the close contact between the large ganglion-cells of its upper surface and the sensory epithelium of the prostomium (figs. 20 and 24). *Racovitza* (1896) has figured (Pl. 5, figs. 48 and 49) a similar condition in *Clymene*. It is only at this point

that the nervous system of the adult *Arenicola marina* can be said to have an epidermal position. Elsewhere it is separated from the epidermis by the circular musculature.

The circum-œsophageal nerve-connectives arise from the large anterior cornua in the form of two thick cords, covered on their outer surfaces by ganglion-cells (figs. 20, 21, 25, *Oe. Comm.*). From them a pair of short nerves (fig. 26, *OT. N.*) arise supplying the otocysts, and several longer ones are distributed to the oral papillæ of the ventral region of the mouth. The line of the connectives is marked externally by the "metastomial groove" (Pl. 4, fig. 19, *C.*), and the commencement of the ventral cord by the junction of these grooves, which occurs on the ventral surface just in front of the first chætigerous annulus. The nerve-cord is protected by a delicate connective-tissue sheath, a thin sheath of circular muscle, and a thin layer of epidermis. Though nearly circular in section it is somewhat flattened from above downwards, but exhibits scarcely a trace of segmentation externally or internally. The ganglion-cells are arranged in two ventral groups, while the fibrous portion of the cord is dorsal. In the tail the ganglionic masses increase in size, and are separated from the skin by a thicker layer of circular muscle-fibres. Two "giant-fibres" are present in the branchial region, a single one only in the anterior and tail region.

From the cord a paired series of nerves is given off with great regularity, one opposite each groove separating the annuli of the somites, so that there are five nerves on each side of the body in each somite. These lie in the body-wall just beneath the circular layer of muscle, and, in some places where this layer becomes obsolete, they lie just under the epidermis. Dorsally these nerves thin out and become very difficult to trace.

Sense-organs.—There is no doubt that the prostomial lobes, the nuchal organ, and the otocysts are sense-organs; but there are, in addition, certain other structures, such as the *setæ*¹ of the notopodia and some of the buccal papillæ, which,

¹ *Retzius* has described free nerve-endings on these *setæ*. 'Biologiska Föreningens Förhandlingar,' Bd. iii, Hefte 4—6, 1891, p. 85.

on account of their position, movements, and the nerves ending in them, may be considered as probably belonging to this category.

Professor Ehlers' (1892) account of the nuchal organ and otocysts is an almost exhaustive description of these organs in *Arenicola*. We have worked over the whole subject again, however, and are able to add a few points to this important paper.

The nuchal organ belongs to the prostomium, whereas the otocysts belong to the metastomium. The prostomium and the nuchal organ are found, in varying degrees of complexity, in nearly all Polychæts; the otocysts, however, occur in few and widely separated families.

The general appearance of the prostomial lobes and the opening of the nuchal organs have already been described. Seen from the dorsal surface the former consists of a small median papilla and two larger lateral prominences (Pl. 4, fig. 19), which together correspond with the single prostomial papilla of allied forms (cf. Racovitza's figure of *Leiocephalus*, 1896, pl. v, fig. 5). In young *Arenicola* these lobes are transparent, and therefore red from the underlying blood-vessels. In old specimens they become dark-coloured and opaque from the deposition of pigment in them. In no species of *Arenicola* have eyes been discovered, although they are known to occur on these lobes in many related genera.

The prostomial epithelium is a complex of several distinct kinds of cells,—unaltered columnar elements, fusiform sense-cells, each ending in a conical prominence, glandular cells, and apparently also "wandering cells" from the body-cavity. Underneath the epithelium is a connective tissue continuous with the supporting tissue, the neuroglia of the brain, which binds together the large ganglion-cells of the cornua of the brain. The prostomial sensory structure thus formed is very sensitive to light, but what function it subserves has not been determined with accuracy.

Nuchal Organ.—To the outer side of the lateral prostomial lobes is a depression guarded externally by a fold (just

above *Nu.*, Pl. 4, fig. 19, *B.*). These two pits form the beginning of the nuchal organ and indicate its paired origin. Further back they unite to form a transverse groove (bordered by the hinder edge of the prostomium), which is continued inwards as a deep pit to the hinder margin of the brain (Pl. 5, fig. 25). From the posterior cornua of the latter the nuchal organ is innervated.

In its paired form and under the names "Wimperorgane," "Wimpergrübschen," the nuchal organ is well known in almost all families of Polychæts, and a similarly placed organ is found in Sipunculids,¹ not to mention other more distantly related groups. It is always associated with the posterior lobe of the brain, and arises as a pair of pits from the surface of the prostomium. Of its development in *Arenicola*, however, we have no evidence, but the two depressions in front of the main part of the organ, together with the paired nerve-supply, point to its double nature.

The epithelium of this deep, pigmented pit (Pl. 4, fig. 21, *Nu.*) is composed of long columnar ciliated cells, glandular cells which secrete the mucus in which the cilia work, and slender sense-cells. It seems probable that the whole organ is olfactory in function.

Otocysts.—The otocysts of *Arenicola marina* are a pair of flask-shaped structures projecting into the body-cavity close to the outer edge of the œsophageal nerve-commissures. They open externally by a couple of apertures (Pl. 4, figs. 19, *A* and *B*, *OT.*), at that point on the "metastomial groove" where the latter is crossed by the first groove of the body following the prostomium. The body of the flask is placed at an angle with the "neck," and contains the otoliths. It is lined by non-ciliated columnar sense-cells and supporting cells, which are surrounded by the nerve-fibres and connective-tissue fibrils, figured by Ehlers (1892, pl. xii). The neck of the otocyst is made up of a columnar epithelium covered with a thick cuticle, which gradually merges into the epidermis of the external surface, and ciliated cells only occur in its lower portion. A

¹ Ward, 'Bull. Mus. Harvard,' vol. xxi, 1891, p. 143.

short nerve from the œsophageal commissure supplies the otocyst.

If the otocyst of a fresh shore lugworm be rapidly dissected out under sea water and mounted, the sand-grains will be seen to execute a most extraordinary movement. Each one is rotating slowly and jostling its fellows, so that the whole contents of the flask are in a state of commotion. The fluid in which the otoliths move is slightly viscous, and is a secretion of the walls of the otocyst, mixed with a little sea water. The sand-grains are covered with a distinct layer of some chitinous substance soluble in boiling potash. Acids have no appreciable effect upon these grains, and under the polariscope they react as quartz does. Hence it seems clear that the otoliths of *Arenicola marina* (the other species of the genus differ most remarkably in this respect, as well as amongst themselves) are quartz grains covered by an organic film, and surrounded by a fluid which is not merely sea water.

Large specimens of the "Laminarian" variety were examined without being opened under sea water, and the otocysts were mounted by us in cœlomic fluid. No movement of the otoliths was observed even in specimens which were perfectly healthy in all respects. The otoliths sometimes filled the expanded part of the organ, and it is possible that they had no room to turn round. But it appears to us more likely that if we assume the cause of the rotation to be the diffusion caused by liquids so different as sea water, in which the preparation was first mounted, and the somewhat viscous, perhaps albuminous fluid inside the otocyst; then if we mount the otocysts in the same kind of fluid which they contain, no movement should occur; and the experiment showed that in these cases no movement did occur. The whole matter is one of very great interest, especially in view of the probable functions of such an organ as the otocyst. Ehlers has suggested that the movement is due to the cilia at the bottom of the neck of the otocyst; but the same extraordinary movements are seen in the otocyst of *A. Grubii*, which is closed and has no cilia. We quite agree with Ehlers that there are no cilia in the expanded part

of the otocyst where the movement has been noticed, but we are of the opinion that the quivering motion of the otoliths is not a normal phenomenon, but is due to diffusion currents.

9. Nephridia.

There are six pairs of nephridia, belonging to somites 4 to 9. Of these the first pair seems to be unrepresented in any other species of *Arenicola*, and its variation in *A. marina* points clearly to a gradual degeneration which it appears to be undergoing at the present time. It is not only the smallest of the series, but is sometimes represented merely by a funnel or by the secretory and terminal portions. Very rarely both the first nephridia are mere funnels, and again one may be fully developed and the other rudimentary, but they are never absolutely wanting. Their small funnels, which are of a bright pink colour, are placed on the anterior face of the third diaphragm with the long axes vertical (Pl. 2, figs. 13 and 14). One lip (the outer) is produced into processes corresponding to the dorsal lip of the other nephridia. The secretory portion is elongated, narrow, and usually brownish in colour, and the terminal portion opens just above the fourth neuropodium (Pl. 1, fig. 1) at a decidedly lower level than is the case in the succeeding nephridiopores.

The remaining five pairs are always in adults fully developed. They are attached to the body-wall partly by connective tissue, partly by the broad bands of oblique muscle which obscure them at first sight (Pl. 2, fig. 5). The nephrostomes are very long, and bent upon the rest of the organ. The narrow slit-like aperture has a dorsal vascular lip bearing finger-shaped or spatulate ciliated processes, and an entire ventral one. The cilia just within the mouth of the funnel are exceedingly long, and produce a current tending to carry cœlomic fluid and corpuscles into the cavity of the organ. The middle or secreting portion is brownish (in old worms almost black), owing to the excretory granules which are formed in its cells. The terminal rosette-shaped bladder, which is slightly lighter in colour, opens by a minute slit-like aper-

ture through the body-wall, which thins out at this point (Pls. 1 and 4, figs. 1 and 22, *NO.*).

The blood-supply to the nephridia (Pl. 4, fig. 18) is derived from the ventral segmented vessels, which divide, one branch going to the funnel of the nephridium and the other to the body-wall. The former traverses the funnel, sending a vessel into each of the ciliated processes, and giving off numerous small branches to the lips of the funnel. After traversing the funnel the vessel runs over the secreting portions of the nephridium, supplying the genital strand in its course, and finally ramifies on the terminal portion. The blood is collected again into small vessels, which open into the dorsal longitudinal or nephridial longitudinal vessels of the body-wall, from which it is returned largely to the dorsal or subintestinal vessels, but in part passes into the parietal vessels.

In young specimens the funnels are naturally simpler, but have similar positions and relations, as may be seen in figs. 16—18, which show nephridia from worms 29.5 and 44 mm. long, in which the processes on the dorsal lip are being formed. In the post-larval stage (Benham, 1893) the nephridia have no funnels, the development of which has still to be investigated.

10. Cœlom.

The cœlom of *Arenicola* is well developed, and continuous in all its parts. Not only does it form the space between the alimentary tract and body-wall from one end of the body to the other, but it is carried along with the blood-vessels into the intermuscular spaces. Thus the blood-vessels of the prostomium, of the buccal sheath, and of the body-wall generally, are accompanied by cœlomic canals which very probably serve as lymphatic spaces from which nutritive matters can be absorbed by the surrounding tissue, and into which waste nitrogenous substances may be excreted.

The segmentation of the body-cavity is very faintly marked. Anteriorly three diaphragms, perforated just above the nerve-cord, are present, whose position and relations are indicated

in fig. 5, and Pl. 3, fig. 6. The whole middle region of the body is devoid of septa, which, however, reappear on the last two somites of the branchial region, and are present throughout the tail in a complete form, though they are perforated to allow of the more thorough circulation of the cœlomic fluid.

Arenicola fresh from the sand exhibits a series of peristaltic waves of the body-wall from behind forwards, which can be easily seen if the gonads are sufficiently developed to cause slight swellings, which each wave carries forwards. These waves of fluid are probably of considerable physiological value. They assist the circulation of the fluid, the cœlomic cells, and the developing reproductive cells. They indicate the anterior digging part of the worm, and thus assist in burrowing. By their action the contents of the gut will tend to travel slowly backwards, the weak visceral musculature being probably insufficient by itself to cause the requisite amount of movement of the sticky sand: while in defecation the main agent is doubtless the pressure of the cœlomic fluid on the intestine, brought about by violent contractions of the body-wall.

The cœlom is lined by a very thin layer of flattened cells, which undergo remarkable changes in certain parts of the body, resulting in the formation of (1) chlorogenous tissue, (2) ova or spermatozoa, (3) cœlomic corpuscles.

The cœlomic fluid is a mixture of sea-water and globulins, among which only paraglobulin has hitherto been detected (Krukenberg, 1882, p. 87). We find that the specific gravity of the fresh fluid (including corpuscles) varies slightly, but is on the average 1.0288.¹

On exposure to air this fluid coagulates, and a delicate fibrous network is formed, binding the corpuscles together. If carmine is injected into the cœlom, it is removed by the cœlomic corpuscles, by the cells lining the cœlom and by the

¹ It was found to be least (1.0270) in specimens which had been kept for some time in sea water, and greatest (1.0311) in those which had been kept for thirty-six hours in moist seaweed only. The specific gravity of the sea water used was 1.0264.

nephridia, and there is no trace of carmine in the coelom after forty-eight hours.¹

Cœlomic Corpuscles.—These abundant cells occur in two chief forms, which probably pass into one another. The first varies from 8 to 20 μ in length, is amœboid, and usually contains yellow or brown granules of a very highly refractive character. The pseudopodia are often grouped at the two ends of the cell (Pl. 5, fig. 24). The longer forms of this kind of corpuscle pass into the second or spindle-shaped cells of the coelom, which measure as much as 50 μ in length, and contain no coloured granules. These fusiform elements are most abundant, and constitute the most characteristic features of the cœlomic contents.

The chlorogogenous tissue of the ventral vessel and its branches in the body-wall consist of groups of cells about 20 μ in length, full of large slightly yellow or deep brown granules, which are not highly refractive. The tissue in old black worms is immensely developed, so as to completely cover the vessel by the masses of hair-like threads, each thread consisting of a small blind diverticulum of the vessel surrounded by the chlorogogenous cells.

11. Reproductive Organs.

Thanks to the researches of Cosmovici (1880), Cunningham (1887), Kyle (1896), and others, the true ovaries and testes of *Arenicola marina* are now known to arise by proliferation of the peritoneal covering of an extension of the blood-vessel supplying the funnels of the nephridia. It is not certain that there is a corresponding gonad on the first pair of nephridia, but on each of the following five pairs the gonads are present during the breeding season. In both sexes the organ is a mass of cells, from which the ova or spermatoblasts break away at a very early stage, to ripen in the coelom. The rachis is continuous with the posterior angle of the nephrostome, and is developed around a backwardly projecting process of the

¹ Schneider, 'Arbeit. Naturf. Gesellschaft,' St. Petersburg, Bd. xxvii, Heft 1, 1890.

nephridial vessel which comes off segmentally from the ventral vessel (Pl. 4, fig. 18, *G. V.*).

In large *Arenicola*, at certain seasons, the vascular process has no gonad, and it is possible, as Cuénot (1891) suggests, that a formation of the amœboid corpuscles of the coelom takes place at this point when the animal is not breeding.

After passing through the earliest stages of their development in the genital rachis, the young reproductive cells may be found at the breeding season in all stages of development in the coelom. The ova do not exhibit any considerable changes except in size in attaining maturity. They are nourished either directly from the cœlomic fluid, or possibly (Cuénot, 1891) by the amœboid cells acting as follicle-cells, though we have seen nothing to support this view. Extrusion of a polar cell (?) has been observed by us in an ovum only about half the definitive size (Pl. 5, fig. 35, A and B). In the spherical ripe ova (which measure .16 mm. in diameter) a distinct but very thin vitelline membrane is present, and a small quantity of food-yolk in the form of very small granules in the protoplasm. The production of ova by the fertile vascular processes of the nephrostomes must be extraordinarily great, since the spacious body-cavity of a large worm is eventually filled to bursting with them by the end of February.

We have not followed the development of the spermatozoa in great detail. The youngest stage which we have found in the coelom contained eight spermatoblasts arranged round a vesicular-looking blastophore (Pl. 5, fig. 30). Further division and elongation of the outer ends of the cells to form the tails of the spermatozoa produces the stages seen in figs. 31 to 34. The masses of spermatids are not spherical, but disc-shaped, their thickness being only about one quarter of their long diameter. They contain a cavity, the remains of the blastophore, together with a small quantity of a slightly fibrous coagulum in the centre of the cavity. Curiously enough, perfectly ripe males were comparatively rare in March and May of this year, when mature females were abundant. In most cases the body-cavity was full of spermatids in great bundles,

as in fig. 31. The ripe spermatozoa closely resemble those of *A. Grubii*, which have been accurately figured by Claparède.¹ They measure .058 mm. in length, and possess a curiously shaped head, .004 mm. in length, and an extremely long slender tail (.054 mm. long). The head (figs. 28 and 29) is divisible into three regions,—a rounded disc-like cap (*S.*) at the anterior end, which is partially divided by a median groove; the nucleus (*N.*), which is large and oval in shape; and the “middle piece” (*M.*), which bears posteriorly a depression into which the tail is inserted. This depression is formed only at the time when the spermatozoa are fully ripe. The tail (*T.*) in the specimens which we have been able to obtain appeared to be a somewhat stiff filament, which could only be bent to a comparatively small extent.

The breeding season of the “Laminarian” variety of *Arenicola marina* lasts from February to May on the Lancashire coast. The large black “worms” which may be dug out during the great spring tides of these months are then distended with ova or spermatozoa. Males and females are not distinguished by external characters, but owing to the slight discharge of gonads from the nephridiopores consequent on the tense condition of the body, it is often possible to distinguish the sex of an example without dissection. It is at present impossible to state how long these *Arenicola* live and how many times they breed.

The ordinary littoral lugworms of the Lancashire coast and of the Isle of Man are not mature in the spring, and contain at most a few very small eggs. In the summer (August) of 1896 we found mature specimens, and we believe that this variety breeds through the summer, commencing at about the time when the deeper water form has ceased.

Relation of the Nephridia to the Reproductive System.—As is well known, the ova and spermatozoa escape by the nephridiopores, but it does not seem to have been noticed before, that in both males and females the bladders of the last five pairs of nephridia are specially enlarged (Pl. 3, fig. 15, *Bl.*),

¹ ‘Annélides de Naples,’ 1863, pl. xix, fig. 2, *C.*

and contain mature ova or spermatozoa, so that upon irritation a simultaneous discharge through all these apertures may occur. In one worm only eight inches in length the bladder of the nephridium was swollen with ova so as to measure 14 mm. in length and 6 mm. in width. During the discharge of ova from the female the eggs are caught by the slimy mucus covering of the body, and, owing to the movements of the animal, collect in strings round the body. We have not observed the formation of gelatinous capsules in which the eggs may be laid, since we have not worked at the oviposition of this species, about which nothing is at present known. At certain times of the year, chiefly in the spring, the nets used by shrimpers on the sandy coast near Lytham are almost choked by the balls of eggs, each moored by two “cables” to the sand. Whether these eggs belong to *Arenicola* remains to be seen, but their form differs from that of *Phyllodoce* found so commonly in early spring.

It has generally been assumed that the number of nephridia and gonads occurring in *Arenicola marina* is typical or fairly typical of the genus, and it is usually stated that the number of both these organs is a small one (five or six). An investigation of several other species of *Arenicola*, the results of which we hope shortly to publish in full, have shown that *A. Grubii* and *A. Claparèdii* have five pairs of nephridia, and apparently the same number of gonads, whereas *A. ecaudata* has no less than thirteen pairs of nephridia, twelve of which bear large and complicated gonads of a size and complexity which is scarcely equalled by any other *Polychaet*. What relations exist between *A. marina* and the other species of the genus cannot be discussed here, but it may be stated generally that the genus exhibits greater variety in the development of several systems of organs than has been hitherto suspected, and that it is no longer possible to exemplify the characters of *Arenicola* as a genus by using their particular grade of development in *A. marina* as a type.

12. General Summary.

The following is a recapitulation of the new points which we have found in *Arenicola marina*.

1. On the Lancashire coast, and probably elsewhere, two well-marked varieties of *Arenicola marina* occur, differing, as the following table shows, in general appearance, in their habits, in the structure of their gills, and periods of maturity.

Name.	Habitat.	Colour.		Gills.	Breeding Season.
		Adult.	Young.		
"Shore lugs," or littoral variety, 6—8" long, exceptionally 10"	The sandy and muddy shores of bays, estuaries, and harbours, extending from high water mark to and sometimes beyond low tide level Burrow U-shaped	Greenish brown or reddish black	Semi-transparent, yellowish or brown	Moderately developed. Branches with 3—5 pairs of gill-plumes	July, August.
"Worms," or Laminarian variety, 8—15" in length	The sandy shore exposed at extreme low spring tides, occasionally extending above this. Burrow a vertical shaft	Black or very dark brown	Dark red, opaque	Very well developed. Branches with usually about 12 pairs of dichotomously arranged plumes	January to May.

2. The cilia lining the central or gastric region of the alimentary canal are specially arranged (1) on the sides of a ventral groove which is continued to the anus, and (2) on curved shallow grooves running downwards and backwards into the former. The current caused by the action of these cilia carries a stream of mucus and of digested food slowly backwards and away from contact with the mass of sand in the gut. As these grooves are in close connection with parts of the visceral plexus, absorption may take place from them.

While the ventral groove is morphologically equivalent to the similar structure of *Oligognathus* (described by Spengel¹),

¹ "*Oligognathus Bonellii*," *Mitt. Zool. Stat. Neapel*, iii, 1882.

and probably to the "siphon" of Capitellids, we have seen no reason for regarding it or any other part of the alimentary canal as "respiratory" in function.

3. In the circulatory system the two hearts each contain a cardiac body. This structure is composed of masses of granular and vacuolated cells, projecting into the cavity of each ventricle. Functionally they may be regarded as glandular valves preventing the reflux of blood into the gastric sinuses. While previously unknown in *Arenicola*, the "cardiac body" has been long known in allied genera (*Ophelia*, *Trophonia*, *Chlorhæma*), but as an unpaired structure in the dorsal vessel (Schæppi, 1894). Hence, though histologically similar, it is very doubtful whether the paired structure of *Arenicola*, which has no connection with the dorsal vessel directly, is homologous with the unpaired organ of other Polychæts.

Contrary to Wirén (1896), we regard the dorsal vessel as a distinct structure, the gastric blood-system as a plexus, and we find that the nephridia and body-wall, as well as the gills, are well supplied with capillaries.

4. Both the large pinnately-branching, and the smaller dendritic, types of gill occur in *A. marina*. The usual statement that the latter type of gill characterises this species, and that the former type is characteristic of *A. cristata*, must therefore be modified.

5. The brain is divided by a narrow cleft throughout the greater part of its length. The anterior cornua supply the prostomium, the buccal papillæ, and give off the œsophageal nerve-connectives. The middle region of the brain supplies the upper part of the prostomium, and the posterior cornua innervate the nuchal organ.

In young specimens the almost uniform covering of ganglion-cells of the brain is in close contact with the peculiar and complex sensory epithelium of the prostomium, but in old specimens of the "Laminarian" variety fibrous outgrowths from the dorsal and lateral surfaces of the brain scatter this ganglionated covering.

6. The nuchal organ, though apparently single, shows traces

of a double origin. It is probably an olfactory organ, and is developed from the posterior region of the prostomium.

7. The otoliths consist of quartz grains surrounded by a delicate chitinous film, as Ehlers stated. The peculiar commotion observed in otocysts mounted in sea water was not noticed in others examined in coelomic fluid. Hence the motion is probably a result of diffusion currents.

8. The first pair of nephridia are in process of reduction. In the others the form of the funnel at an early stage is described and figured. In adult examples the terminal portions of the nephridia act as receptacles for the ripe ova or spermatozoa.

9. The specific gravity of the coelomic fluid varies slightly, but is on the average (including the corpuscles) 1.0288, thus being only very slightly denser than sea water (1.0264).

10. The general analogies of *Arenicola* with certain other limnivorans Chaetopods are very striking. With the Sipunculids the Arenicolidae agree in the chitinous spines tipping the proboscis papillae, the buccal papillae, the strong retractors of the "proboscis," the capacious and largely unsegmented coelom, the general character of the musculature, the thin-walled looped alimentary canal with its ciliated ventral groove, the action of the body-wall in producing waves of coelomic fluid auxiliary to the process of burrowing and defecation, and lastly, the pigmented nuchal organ. If we acknowledge the many points of agreement, which have for the most part arisen independently, between these two distantly related families under similar conditions of life, the true relationship between *Arenicola* and other genera of Polychaets can only be ascertained by exercising the greatest caution in not confusing convergent adaptational characters with true genetic resemblances.

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EXPLANATION OF PLATES 1-5,

Illustrating Mr. F. W. Gamble's and Mr. J. H. Ashworth's paper on "The Habits and Structure of *Arenicola marina*."

LIST OF REFERENCE LETTERS.

A. Cr. Anterior cornua of the brain. *An.* Anus. *Au.* "Auricle" of the heart. *Bl.* Bladder or terminal part of the nephridia. *Blph.* Blastophore of spermatoblast. *B. Pap.* Papillæ of the buccal mass. *Br.* Gills. *Br. Aff.* Branchial afferent vessels. *Br. Eff.* Branchial efferent vessels. *BR.* Brain. *B. S.* Blood spaces in the heart. *B. Sh.* Sheath of retractor muscle enclosing the buccal mass. *Bucc. M.* Buccal mass. *Card. B.* Cardiac body. *Chl. Tiss.* Chlorogogenous tissue on the stomach and ventral vessel. *Chn.* Notopodial chæte. *C. F.* Cardiac fibres. *C. Sp.* Caudal septa. *D. L. V.* Dorsal longitudinal vessel. *D. Nph.* Dorsal lip of the nephrostome. *Dph. Ph.* Diaphragmatic pouch. *Dphm.* ¹⁻³ Diaphragms or anterior septa. *Ep.* Epidermis. *G.* Refrangent granules in cœlomic cells. *Ga.* Ganglion-cells of the brain. *Gast. Lat.* Lateral gastric vessel. *Gast. V.* Gastric vessels. *G. F.* "Giant fibres." *Gl. Op.* Opening of the œsophageal glands into the œsophagus. *G. S.* Granular cells of the heart. *Gv.* Ventral groove of alimentary canal. *G. V.* Gonidial vessel. *Int. V.* Intestinal vessels. *M.* "Middle piece" of spermatozoon. *M. Circ.* Circular muscles. *Mes. D.* and *Mes. V.* Mesenteries supporting the dorsal and ventral vessels between the first and second diaphragms. *MBT.* "Metastomium," or achætoutous portion of the body immediately following the prostomium. *M. Long.* Longitudinal muscles. *MO.* Mouth. *M. Ob.* Oblique muscles. *M. Par.* Parapodial muscles. *M. Pr.* Retractors of the prostomium. *N.* Nucleus. *N. Aff.* Afferent vessel to the nephridia. *N. C.* Ventral nerve-cord. *N. Cap.* Nephridial capillaries. *N. Eff.* Efferent vessel from the nephridia. *NLV.* Nephridial longitudinal vessel. *Nm.* ¹⁻¹⁰ Neuropodia. *No.* ¹⁻⁶ Nephridiopores. *NPH.* ¹⁻⁶ Nephridia. *NPHH.* Nephrostomes. *NS.* Nervous elements and connective tissue round otocyst. *Nu.* Nuchal organ. *Nu. Tr.* Retractor muscle of nuchal organ. *N. V.* Neural vessels. *Oe.* (Esophagus. *Oe. Comm.* Circumœsophageal nerve-connectives. *Oe. Gl.* (Esophageal glands. *Oe. Gl. V.* Vessel of œsophageal glands. *Oe. Lat.* Lateral œsophageal vessel. *O. Ot.* External opening of otocyst. *OT.* Otocysts. *OT¹.* Neck of otocyst. *Oth.* Otolith. *OT. N.* Nerve to otocyst. *Par. V.* Parietal vessels. *P. Cr.* Posterior cornua of brain. *Pz.* Protractor of notopodium. *Pr.* Prostomial lobes. *Rz.* Retractor of notopodium. *S.* Cap of spermatozoon. *S. V.* Sub-intestinal vessels. *T.* Tail of spermatozoon. *V.* Ventricle of the heart.

Vac. Vacuole. *Vac. C.* Vacuolated cells of the heart. *V. Nph.* Ventral lip of nephrostome. *V. V.* Ventral vessel. *I. II. III. IV. &c.* Somites beginning with the first chætigerous.

PLATE 1.

FIG. 1.—The anterior end of a large specimen of the "Laminarian" variety seen from the left side, to show the external features, the segmentation of the body-wall in relation to the internal metamerism, the nephridial apertures, and the commencement of the branchial region. The achætoutous region following the fully everted buccal mass (*Bucc. M.*) extends forwards as far as the groove indicating the insertion of the first diaphragm dorsally (*Dphm.*¹). We have considered the first chætigerous annulus and the annulus behind this, as composing the first chætigerous somite (*I*), although we are fully aware that, owing to the obliquity of the first diaphragm, and the absence of landmarks in the achætoutous region in front of this septum, it is somewhat hazardous to delimit this first chætigerous somite. $\times \frac{5}{8}$.

FIG. 2.—View from the right side of two somites from the anterior part of the branchial region of a specimen of the "Laminarian" variety 7 inches long. The fourth gill is shown in detail, while the third and fifth are cut down to the base of the main branches. The large size of the spreading branches and the somewhat pinnate arrangement of the lateral twigs distinguish the gill of this variety of *A. marina* from that of the ordinary shore lugworm seen in figs. 3 and 4. The webbing at the bases of the branches is generally much more marked in old black examples than in immature dark red specimens such as the present. $\times 14$.

FIG. 3.—Fifth gill of the right side of a shore lugworm 8 inches long, to show the features characteristic of the littoral variety of *Arenicola marina*. The branches are united by extensive connecting membranes, between which the blood-vessels of the gill are faintly visible. $\times 14$.

FIG. 4.—The first gill of the right side from the same specimen as Fig. 3. The ventral branches are apparently the last to develop, and are only just budding off the secondary leaflets. $\times 14$.

PLATE 2.

FIG. 5.—Dissection of a large "Laminarian" variety, to show the general characters of the internal anatomy (conf. pp. 9 to 10). The body-wall has been cut along the mid-dorsal line, the flaps pinned back, and the alimentary canal turned over to the left side. The special features shown are the vascular system, the nephridia, the septa, and muscles. $\times 2$.

PLATE 3.

FIG. 6.—View of a vertical longitudinal section of *Arenicola marina* taken somewhat to the left of the middle line. The thickness of the body-wall is exaggerated. The stomach has been cut away behind the heart, to show the oblique muscles and the second nephridium. The main blood-vessels only are indicated, the object of the figure being to show the exact position of the three diaphragms (*Dphm.*¹⁻³), of the buccal or proboscidal sheath (*B. Sh.*), and the relations of these to the external segmentation. $\times 3$.

FIG. 7.—Glutinoid spines covering the buccal papillae of that part of the proboscis which is first protruded during eversion. They may be compared with the figures of "hooks" from the proboscis of Sipunculids (e.g. *Phascion*) shown in Selenka, 'Die Sipunculiden.' Caustic potash preparation. $\times 50$.

FIG. 8.—Papillae in situ on the base of the proboscis of young worm. $\times 6$.

FIG. 9.—A group of neuropodial setae from a very young *Arenicola marina* 16 mm. long. The shape and strongly-toothed ridge distinguish these setae from those of the adult (figs. 11 and 12). The youngest setae are on the left side of the figure. $\times 300$.

FIG. 10.—Notopodial seta 6 mm. long. $\times 16$.

FIG. 10A.—The tip magnified. $\times 50$.

FIG. 10B.—The toothing on the notopodial seta highly magnified. $\times 450$.

FIG. 11.—Neuropodial seta ($\times 20$), and enlarged ($\times 120$).

FIG. 12.—A group of developing neuropodial setae in situ in the neuropodium (*Nu.*) of a "Laminarian" specimen. $\times 76$. *Proc.* is referred to on p. 9.

FIG. 13.—The fourth and fifth chaetigerous segments of the left side of a large mature "Laminarian" specimen. The first two nephridia are shown. The figure is a study of the blood-vessels of the nerve-cord, of the oblique muscles, and of the connection between the nephrostomial and the dorsal longitudinal vessels (*D. L. V.*). $\times 3\frac{1}{2}$.

FIG. 14.—The first nephridium from the specimen shown in fig. 13, seen from the dorsal surface, to show the gonidial vessel (*G. V.*¹) bearing blind, vascular processes. The gonidial vessel on this nephridium is sterile. $\times 4$.

FIG. 15.—Fifth right nephridium of an adult male, to show the bladder distended with spermatozoa. The nephrostome is widely open. Seen on February 21th, 1897. $\times 4$.

FIG. 16.—The second nephridium of the right side of a specimen 29.5 mm.

long, seen from the dorsal surface, to show the gonidial vessel (*G. V.*), the commencing processes of the dorsal lip, and the position of the external opening (*No.*²) with regard to the neuropodium (*Nm.*²). The ventral lip of the oesophostome (*V. Nph.*²) is seen through the dorsal one. $\times 60$.

FIG. 17.—Funnel of the first left nephridium from the same specimen as fig. 16, seen from the right side, to show the vertical position of the nephrostome and the commencing processes on the anterior lip. $\times 90$.

PLATE 4.

FIG. 18.—The second right nephridium from a specimen 44 mm. long. Dorsal view, to show the remarkably complete capillary circulation and the extension of the vessel of the dorsal lip to form the gonidial vessel (*G. V.*). The ventral lip (*V. Nph.*²) is seen by transparency. $\times 65$.

FIG. 19.—Three views of the anterior end of a specimen 8 inches long (littoral variety), to show the prostomium, nuchal organ, openings of the otocysts, and the secondary annulation of the skin. a. From the left side. b. From above. c. From below. $\times 12$.

FIG. 20.—Transverse section across the middle of the prostomium to show the brain, the three prostomial lobes, and the rich blood-supply of this region. The brain lies in the central prostomial lobe, and its covering of ganglion-cells is closely applied to the overlying sensory epithelium. The section is cut across in the region of the posterior cerebral cornua (*P. Cr.*). $\times 65$.

FIG. 21.—Transverse section of the same series as Fig. 20, across the nuchal organ, *Nu.*, the hinder cornua of the brain, and one otocyst, with its contained otoliths. $\times 65$.

FIG. 22.—Transverse section of the body a short distance behind the third diaphragm at the level of the openings of the oesophageal pouches (*Os. Op.*). The external aperture of the second nephridium is shown on the right side. The subdivision of the body-cavity into three longitudinal portions, and the structure of the oesophageal pouches, are well seen. $\times 38$.

FIG. 23.—Transverse section of the body in the branchial region at the level of a parapodium. The neuropodium is cut through its entire length on the left side. On one side of the nerve-cord a retractor muscle from the notopodium arises, on the other an oblique muscle. The vascular supply of the body-wall, setae, and gills is well seen. $\times 38$.

PLATE 5.

FIG. 24.—Amœboid and spindle-shaped cells of the coelom. $\times 1000$.

FIG. 25.—Sagittal section of the brain slightly to the left of the middle line, from a young littoral form about 3 inches long. The mass of ganglion-

and glia-cells underlying the epithelium of the prostomium is distinct; some of the cills of the latter are shown bearing sensory processes. The nuchal organ, *Nu.*, is cut at its full depth. $\times 85$.

FIG. 26.—View of a dissection of the brain, cesophageal connectives, otcysts, and the buccal sheath. The commencement of the neural vessels from capillaries of the organs just mentioned, is shown. Seen from the dorsal surface. The buccal mass, cut transversely, lies in the centre of the figure. $\times 6$.

FIG. 27.—An otcyst with the otoliths composed of quartz grains. The sensory epithelium and the surrounding nervous and supporting cells are seen. $\times 160$.

FIG. 28.—Otoliths to show the chitinoïd covering of the quartz grains. $\times 500$.

FIG. 29.—Ripe spermatozoon seen on March 10th, 1897. Length of head 4μ , length of tail 54μ . $\times 3000$.

FIG. 29A.—Head and portion of tail of an immature spermatozoon seen on February 22nd, 1897. $\times 3000$.

FIGS. 30—34.—Stages in the development of the spermatozoa.

FIG. 30.—The 8-celled stage, in which the spermatoblasts leave the testis. $\times 500$.

FIGS. 31 and 32. Later stages. $\times 500$.

FIG. 33.—Two cells from a stage much later than the preceding, showing the commencement of the tail. $\times 2000$.

FIG. 34.—Discoidal mass of almost ripe spermatozoa. $\times 500$.

FIG. 35.—Developing ova. (*a* and *b*) show a polar body (*p*) $\times 250$. (*c*) is a ripe ovum enlarged 125 times.

FIG. 36.—Longitudinal section of the heart of an *Arenicola* 250 mm. in length, to show the cardiac body. $\times 32$.

FIG. 37.—Histology of a portion of the cardiac body of fig. 36. $\times 500$.

FIG. 38.—Longitudinal section of the heart of a young *Arenicola* 65 mm. in length, to show the cardiac body at an early stage of development. $\times 50$.

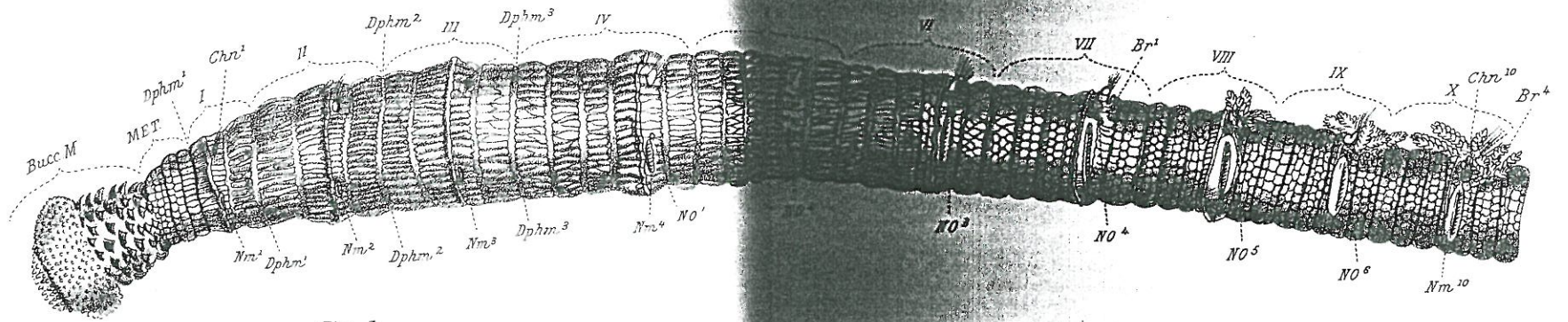


Fig. 1.

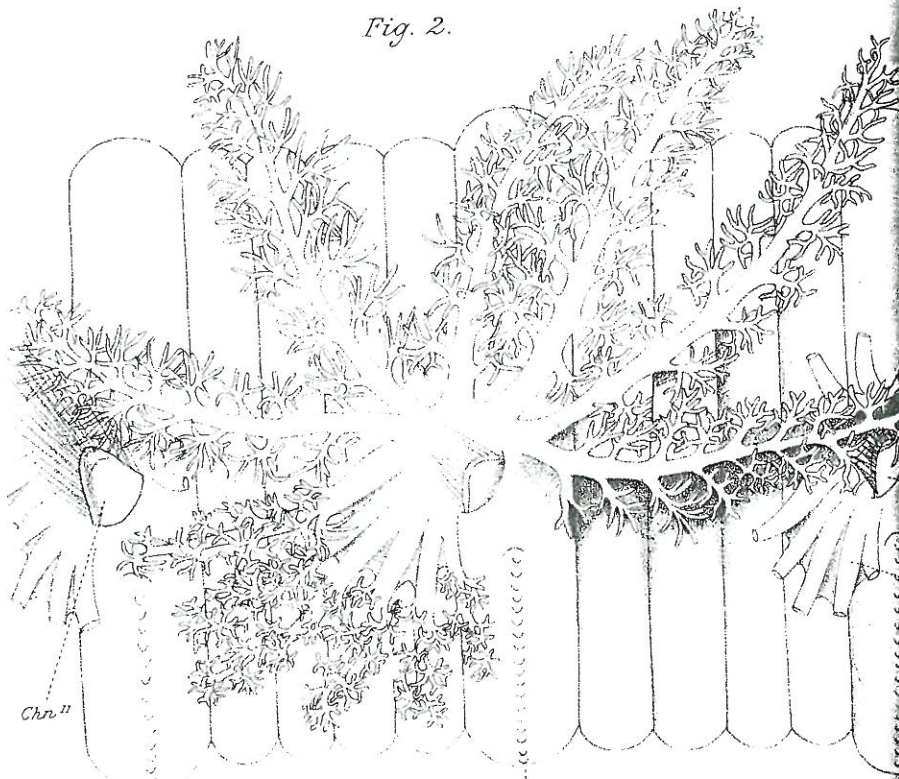


Fig. 2.

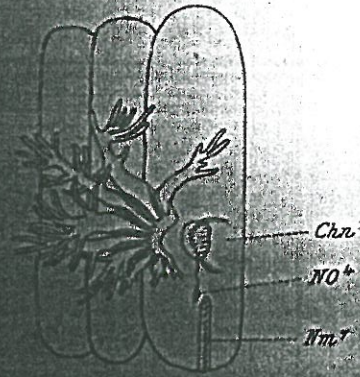
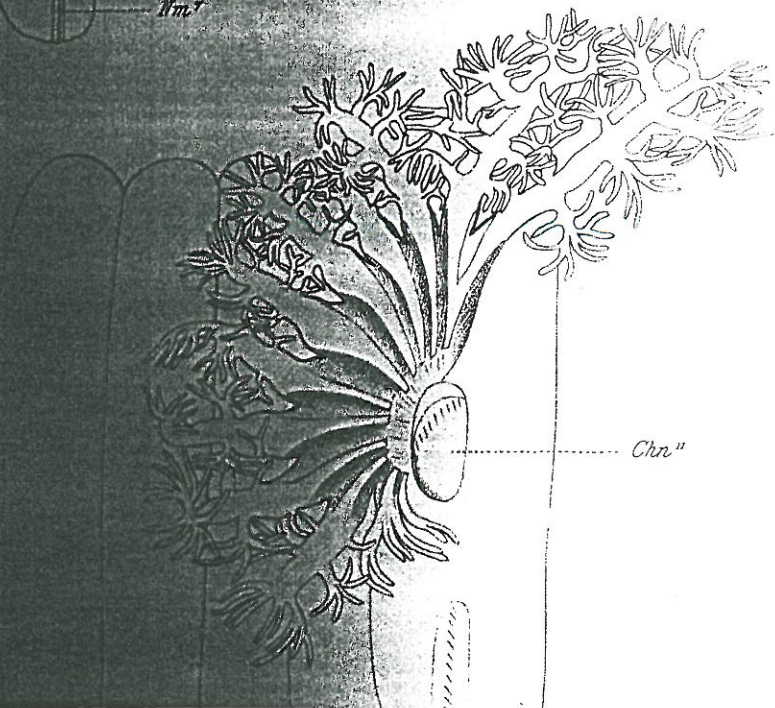
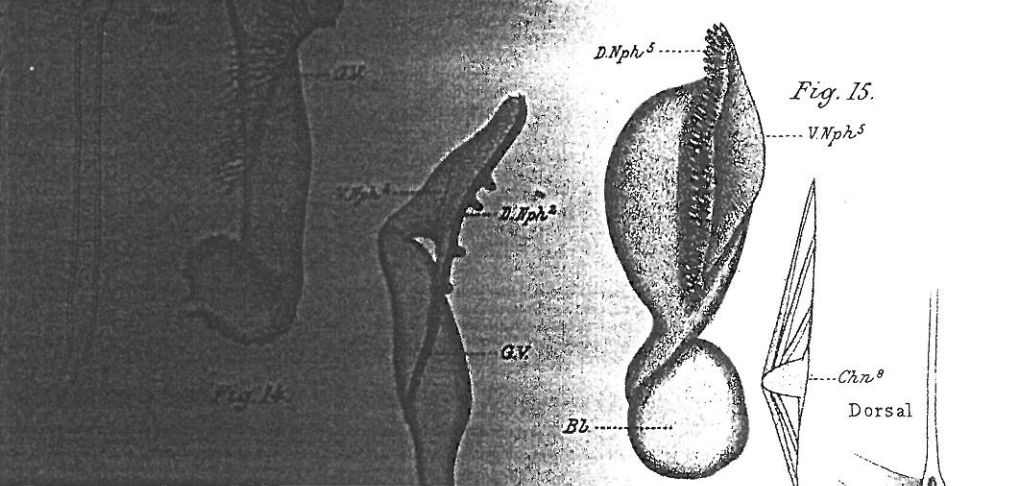
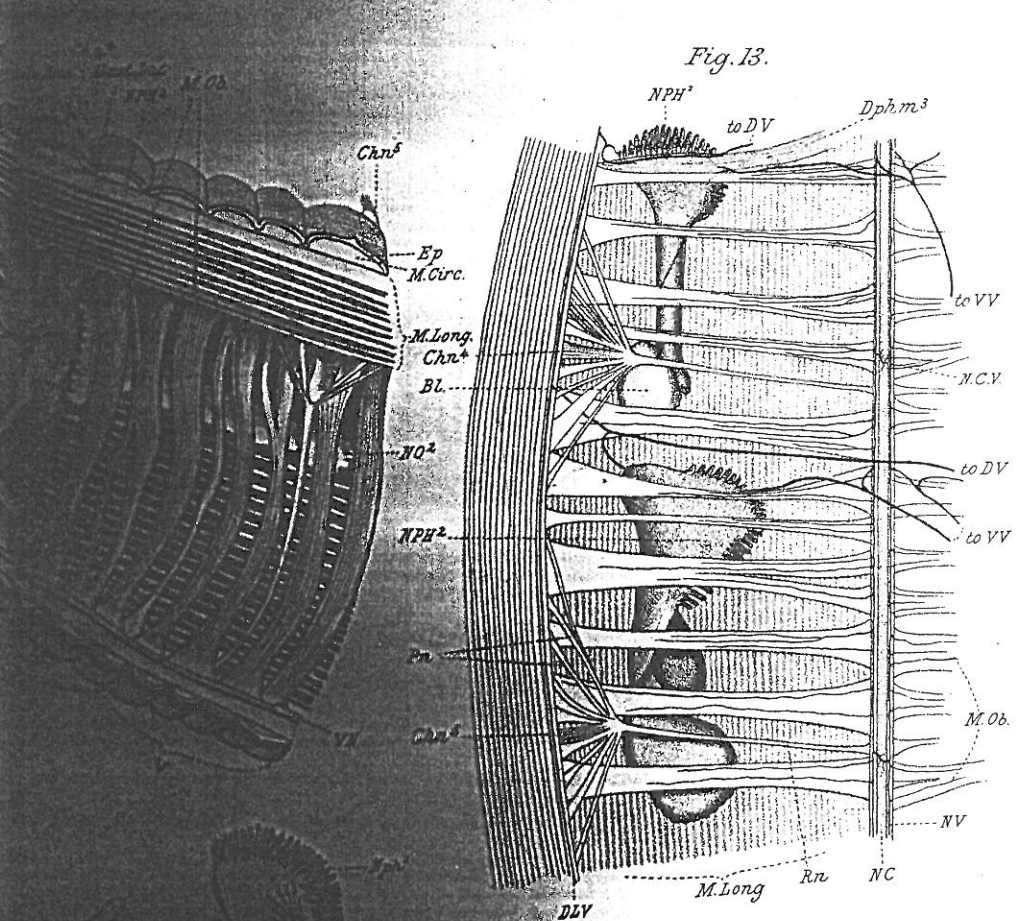
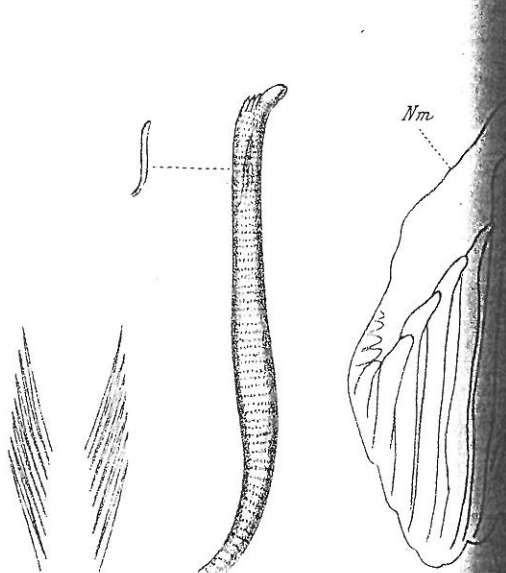
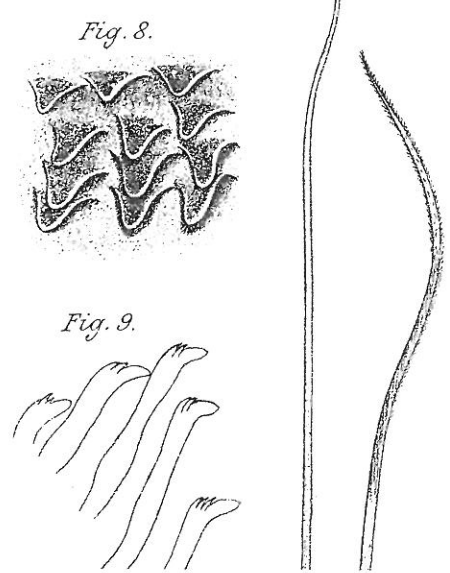
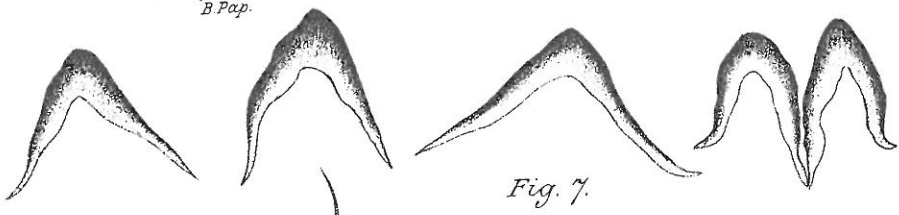
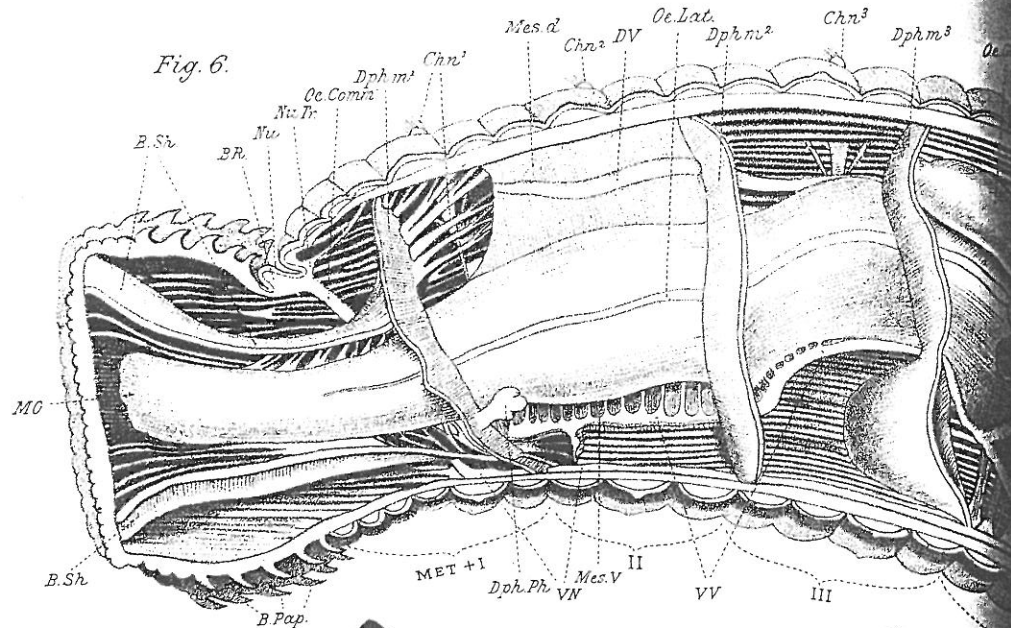


Fig. 3.



Chr¹¹



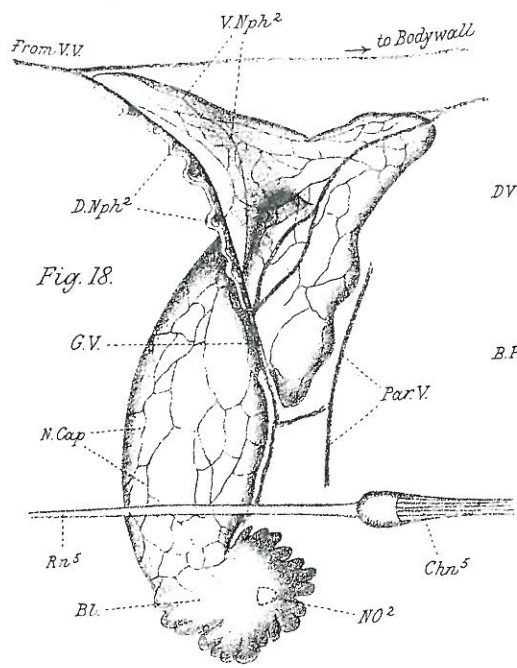


Fig. 18.

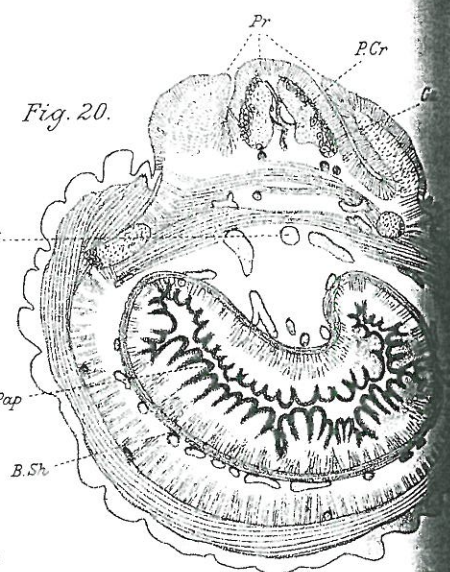


Fig. 20.

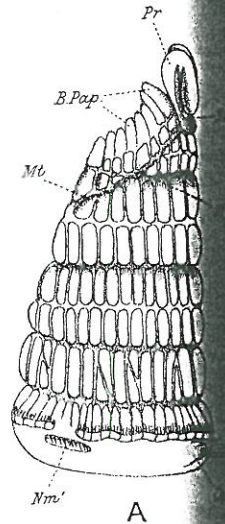
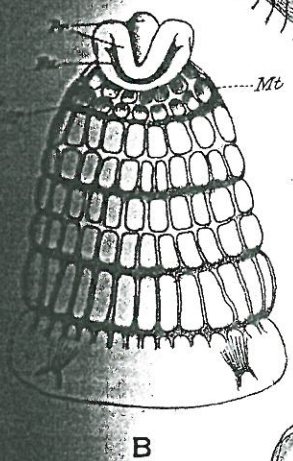


Fig. 19.



B

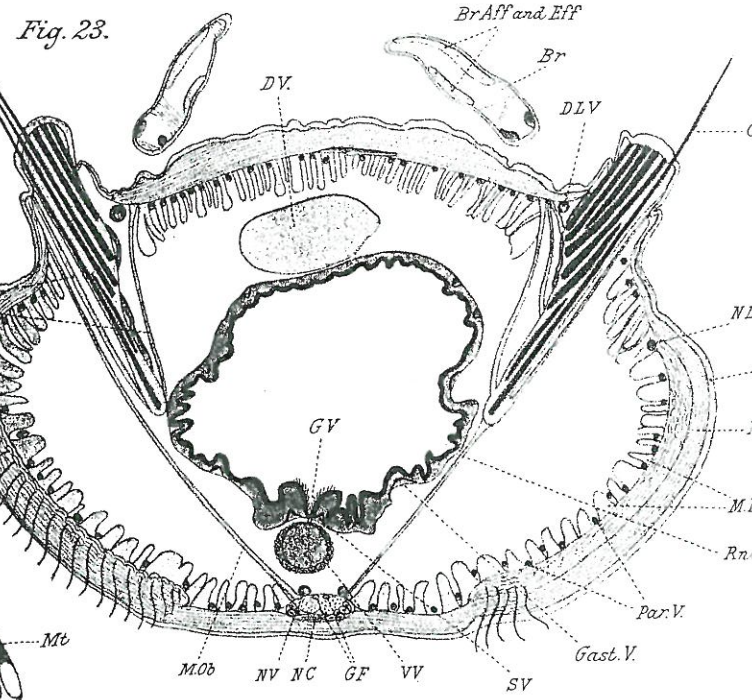


Fig. 23.

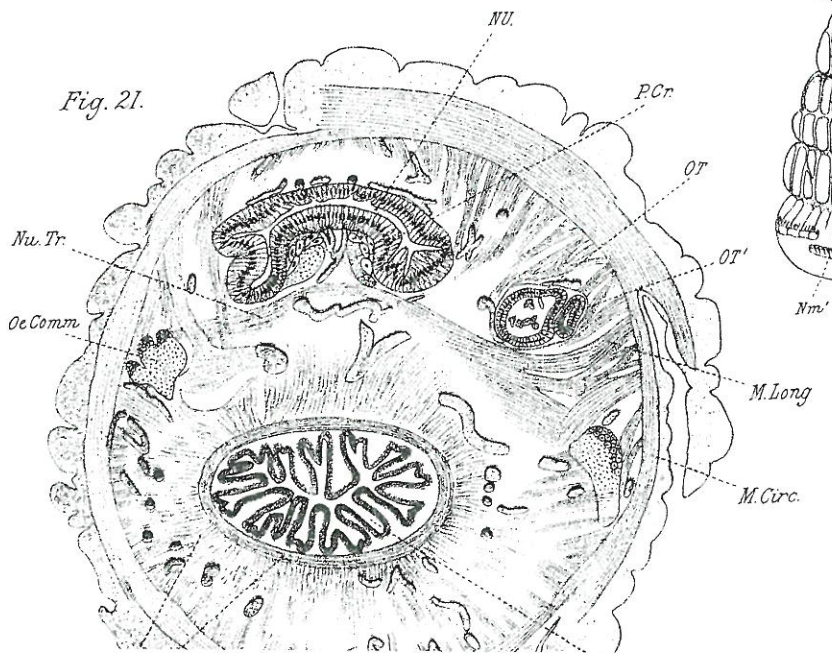


Fig. 21.

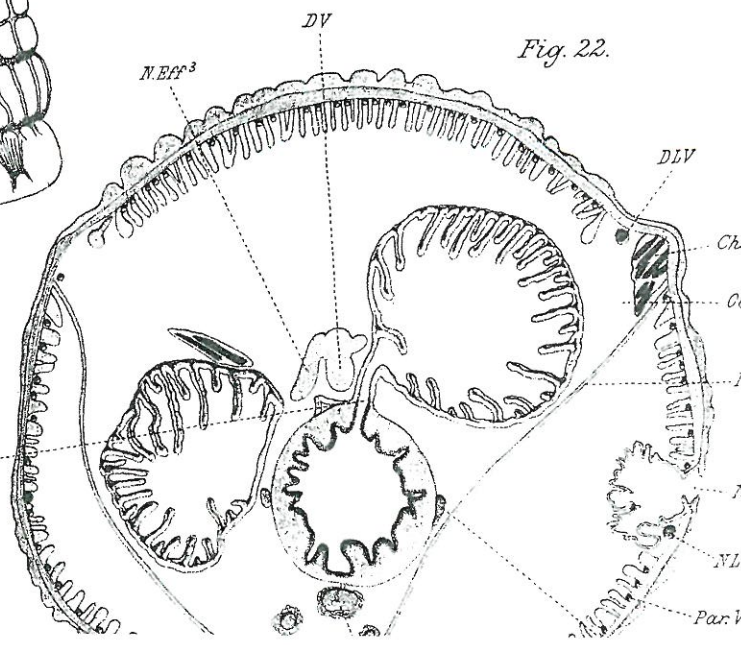


Fig. 22.

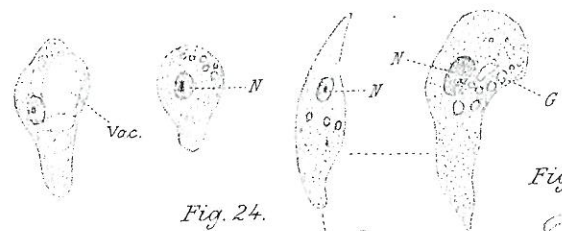


Fig. 24.

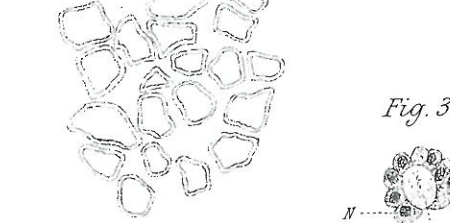
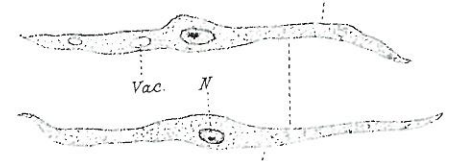


Fig. 28.

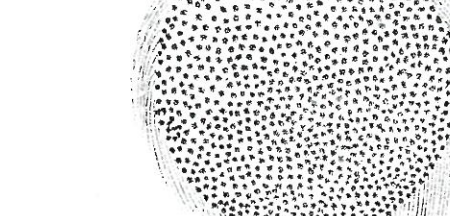


Fig. 30.



Fig. 31.

Fig. 32.

Fig. 33.

Fig. 34.

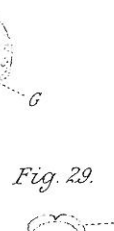


Fig. 29.

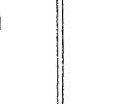
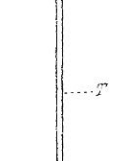
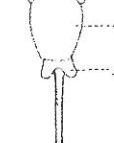


Fig. 29A.



Fig. 31.



Fig. 32.

Fig. 33.

Fig. 34.

Fig. 25.

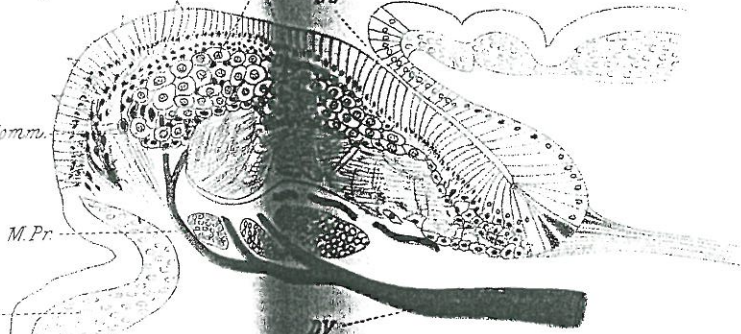


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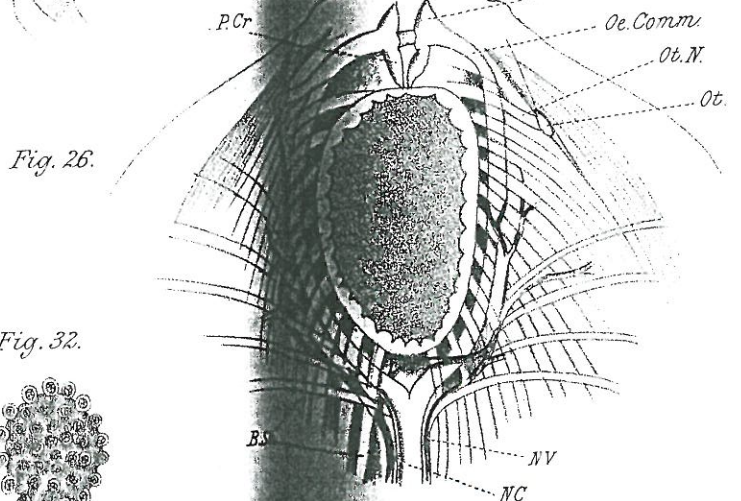


Fig. 32.



Fig. 33.



Fig. 36.



Fig. 27.

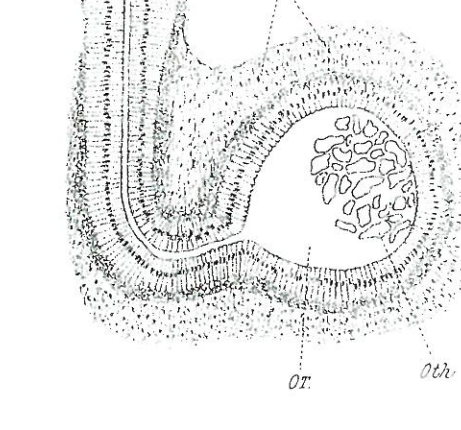


Fig. 37.

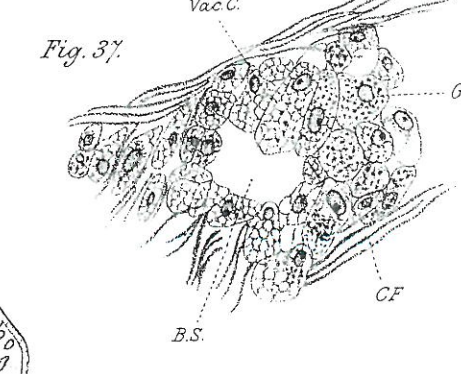


Fig. 36.

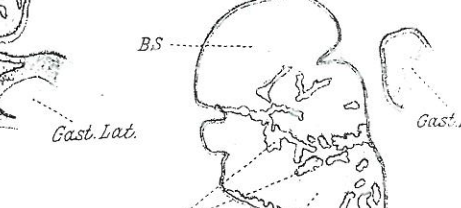


Fig. 36.

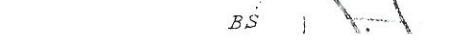
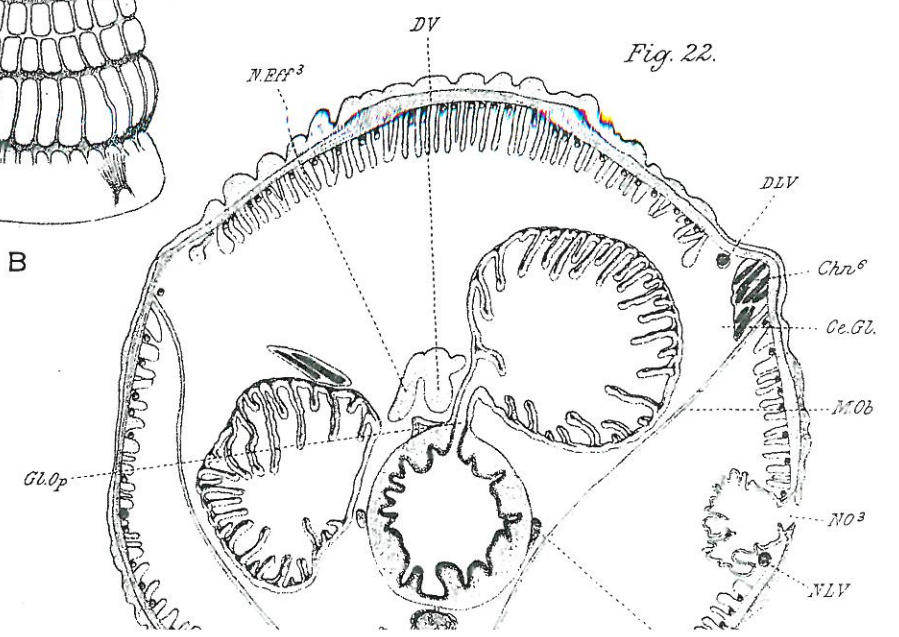
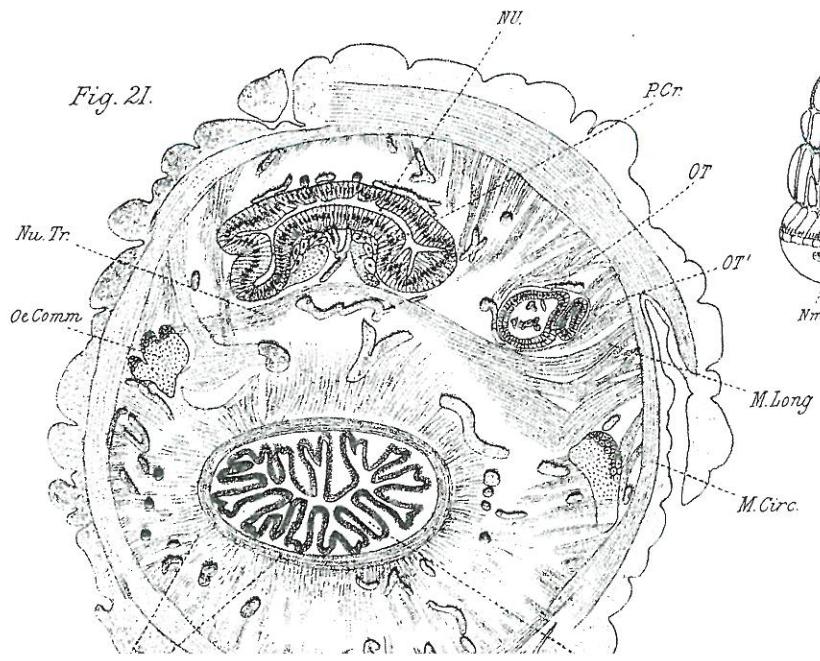
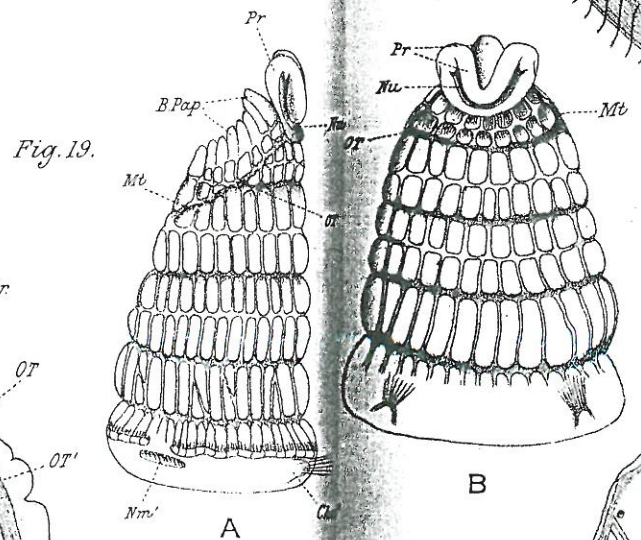
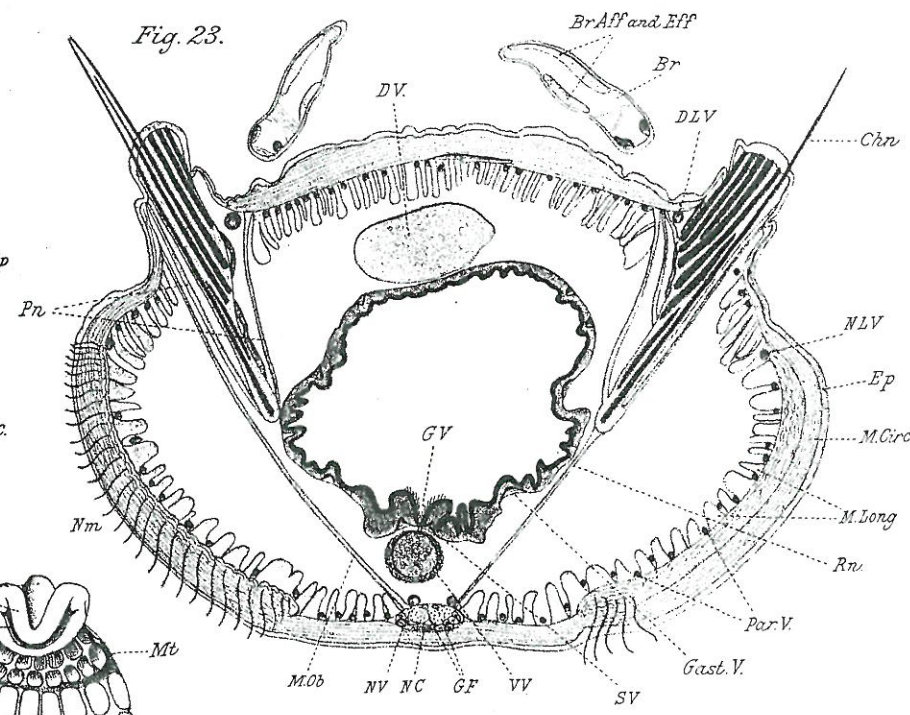
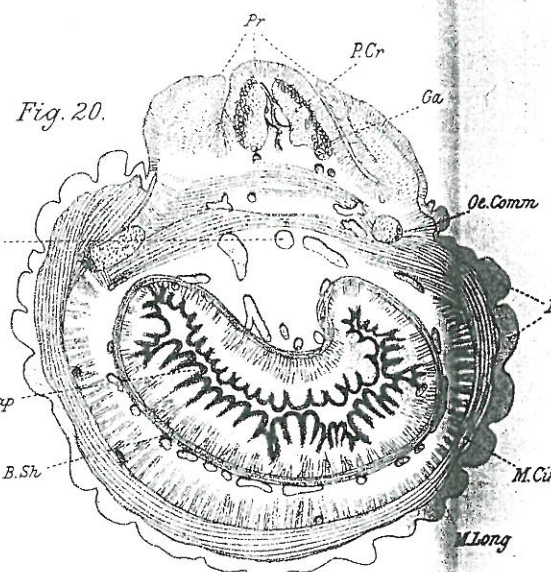
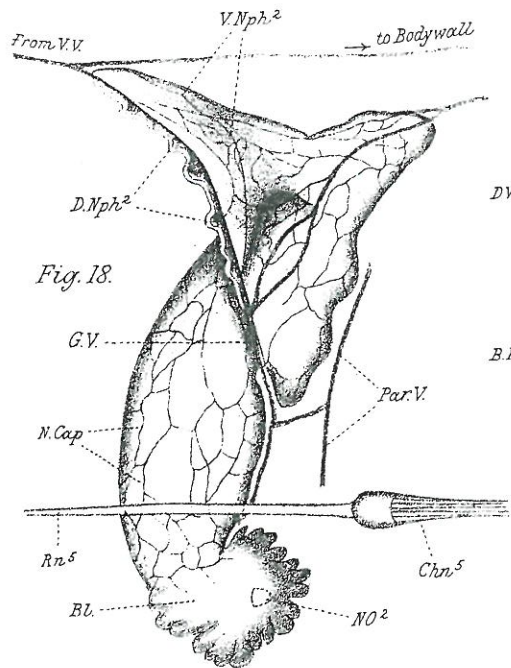


Fig. 36.



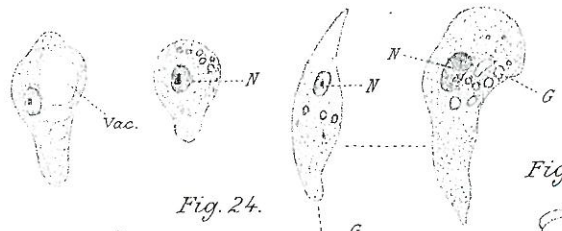


Fig. 24.

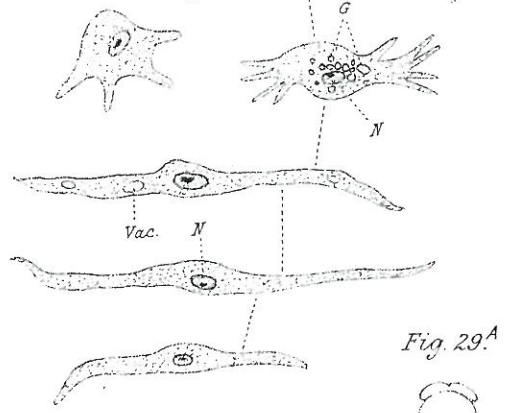


Fig. 29A



Fig. 28.

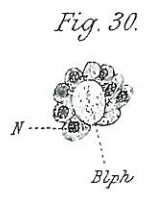


Fig. 30.

Fig. 31.

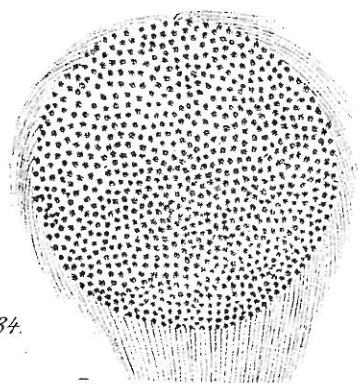


Fig. 34.

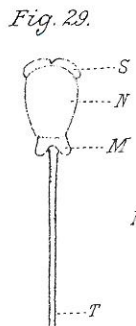


Fig. 29.

Fig. 25.

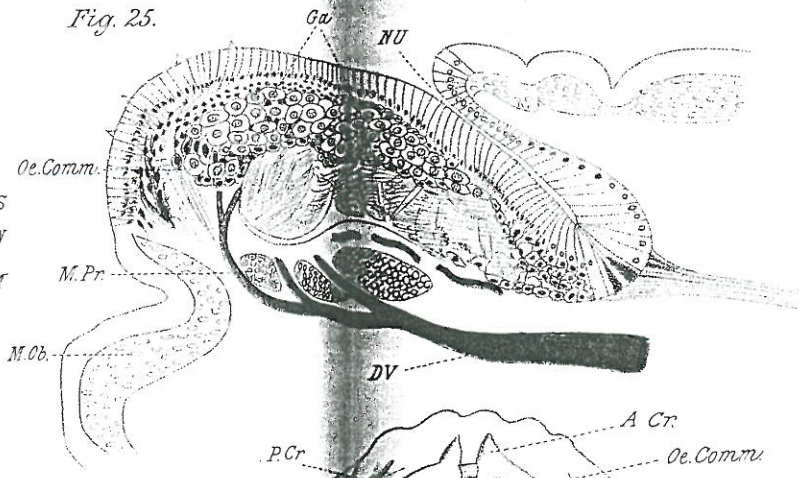


Fig. 26.

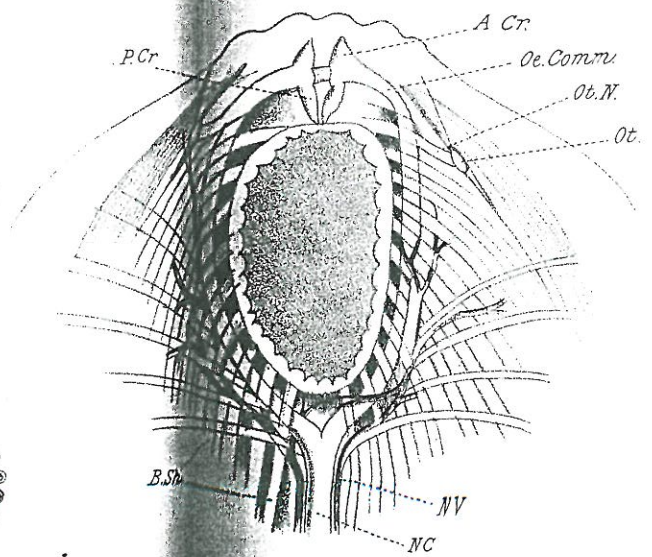


Fig. 32.



Fig. 33.

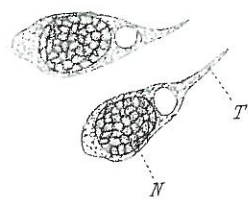


Fig. 36.

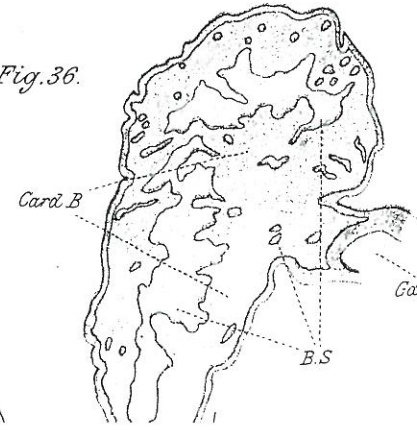


Fig. 27.

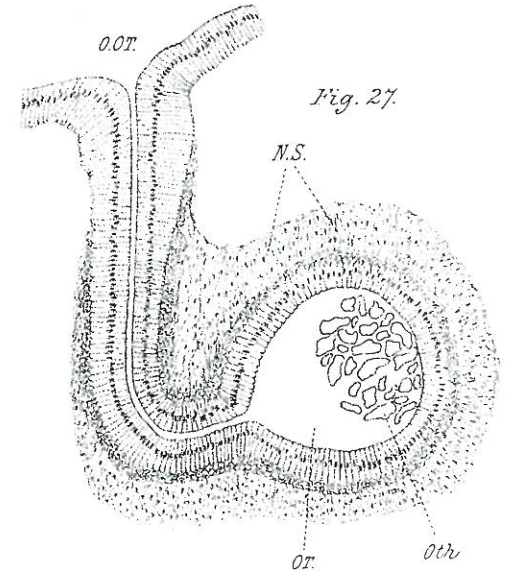


Fig. 37.

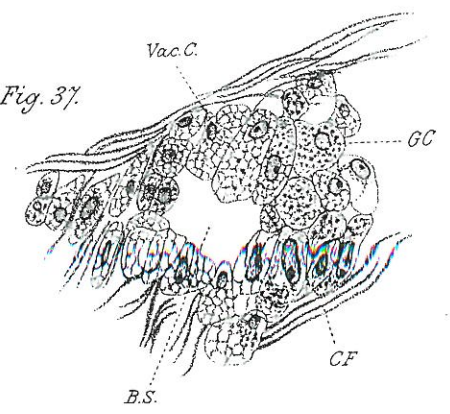


Fig. 38.

