ON THE ANATOMY OF *MARPHYSA GRAVELYI* SOUTHERN.

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Introduction.

The following investigation was mostly carried out at the Department of Oceanography, University of Liverpool, on material taken from India. Observations on the living worms were made at the University Zoological Laboratory, Madras, and were of invaluable help in elucidating points particularly in regard to the vascular system and the nephridia, a knowledge of which could not be easily gained from preserved material.

For killing and preserving Bouin's fluid, corrosive sublimate, corrosive acetic, 2 per cent. ammonium bichromate or 0·5 osmic acid was tried. Sublimate mixtures, followed by Mann's methyl-blue Eosin, or Heidenhain's iron-haematoxylin stain gave the most satisfactory results. For the brain and the sense organs ammonium bichromate and osmic acid were both found to be useful. Fixing in osmic vapour followed by maceration in 40 per cent. alcohol was employed for studying certain histological details. For nephridia, injection of carmine was tried, but though the worms survived the treatment for twelve hours, subsequent examination showed no carmine particles in the nephridia.

For peripheral nerves, vital staining with methylen blue and Bielschowsky's nerve staining with silver nitrate were tried, but several points could not be cleared up.

Marphysa Quatrefages.

Marphysa is a widely distributed genus; species of it have been recorded from all coasts, though so far only a few have been described from the Indian coasts; namely *M. mossambica* (Peters), *M. furcellata* (Crossland), *M. mcIntoshi* (Crossland), *M. gravelyi* (Southern) and *M. sanguinea* (Montagu). Of these *M. gravelyi* has taken to a brackish water life while the others are marine with a littoral habitat.

Marphysa gravelyi, which forms the subject of this memoir, occurs in large numbers near Madras, wherever brackish water conditions prevail. I have not found it to occur on the sea shore, but only in those low-lying parts of the Madras Coast which, while retaining their connection with the sea during the rainy months, are completely cut off from it during the rest of the year. The general physical conditions of

such areas are similar to those of the Chilka Lake described by Annandale and Kemp (1915). There is the same flooding and consequent decrease in salinity during the rainy months. During the hot weather a sand bar forms gradually and all connection with the sea is lost. The soil in these areas is partly clay and partly sand. These worms show a preference for the less sandy parts, and seem to thrive in places where there is admixture of sewage water. Like *Arenicola* of the European coasts, they live head downwards in burrows, which may be located by the worm castings. The burrows of two or three individuals often merge underground. The walls of the burrows are usually lined with sand grains, cemented together with mucus. Frequently the worms take up their abode in the empty tubes of *Diopatra variabilis*, another Eunicid which is of common occurrence in the brackish waters of these parts. Like *Marphysa sanguinea* in Europe this form is used as a bait for fish. With a strong flat piece of wood the local fishermen dig up large lumps of clay which are taken out of the water and then carefully examined for worms which are dislodged without injury from the clay and kept in water in earthenware vessels. The worms do not exhibit any rapid movements when caught. When a sufficient number has been collected, they are carefully washed several times, freed from all adhering sand-grains and left in pots of clean water. Care is taken to place only the entire worms together. Introduction of broken worms, as has been observed in *Arenicola* by Ashworth (1904), has a softening effect on healthy animals, probably due to the admixture of coelomic fluid with water. If kept cool in the open at night, they live for two to three days but after that they are useless as bait as they become flaccid and motionless and the skin also peels off. During day the men, while engaged in fishing, frequently change the water to keep the worms in a healthy condition as living worms only can be used as bait. On a low estimate about 150 fishermen are engaged daily throughout the year, in and around Madras, in digging up the worms for bait to catch such fishes as *Sillago sihama* (the Indian whiting), *Chrysophrys berda* (the black rock-cod), *Therapon jarbua*, *Therapon quadrilineatus*, species of *Mugil*, *Etroplus suratensis*, *Lates calcarifer* and species of *Ophicephalus* (the murrel), and *Sciaena*. All these take bait freely. Most of the species of fish mentioned live in the sea, but also enter brackish waters. McIntosh (1910) mentions that the closely related *M. sanguinea* is used as a bait by the fishermen of St. Peter Port and Channel Islands, generally under the term ' Varme,' being highly prized as a tempting bait for the capture of whiting, wrasses, and other ordinary fishes, as well as dog-fish. The men search for the worms with spades at low water. The fishermen of Marseilles also use *M. sanguinea* as bait.

The Madras worms lay their eggs in large cylindrical masses of jelly, about nine inches long and 1½ inches in diameter, narrowed at one end to a stalk, which is enclosed in the burrow of the worm. Though mature worms are not rare all the year round, there is a distinct reproductive period immediately after the onset of the rainy weather (October), when the egg masses are produced in very great abundance. The larvae pass their initial stages of development in the jelly, but later, when about half a dozen setigerous segments have been formed, the creeping mode of

life is commenced. It is interesting to note that there is no free swimming stage at all, and the adult characters are acquired very slowly. Other details of development, in so far as the external characters are concerned, have been published by me in a previous paper (1931).
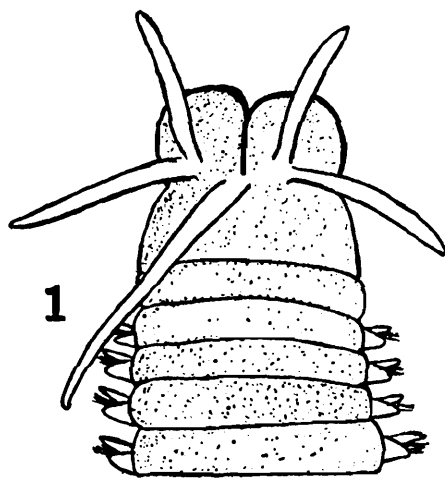

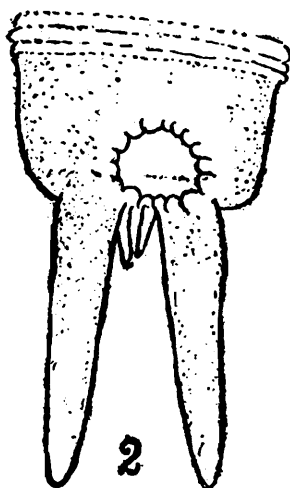Fig. 1.—Anterior end of worm, dorsal view.

Fig. 2.—Anal end of worm, dorsal view.

External characters.—Some of the largest worms are nearly 45 cm in length and contain more than 700 segments. The anterior end of the body up to the 5th segment is cylindrical, but behind this segment it is dorsoventrally flattened. The skin is iridescent, and the first few anterior segments are greenish. The posterior region is usually blood-red in colour but the intensity of colour in this region varies according to the state of contraction of the body. The gills vary from deep red to yellowish red. The tentacles are light yellow. The head has a deep notch (Fig. 1) which is continued back dorsally as a median groove to the base of the middle tentacle and ventrally to the mouth. The lobes of the prostomium are almost spherical, slightly broader in front than behind, and as long as, or a little longer than, the peristomium. Eyes, when present, are very small and are situated at the base of and external to the intermediate tentacles. They are, however, better developed in the young than in the full grown forms. There are five fleshy tentacles which are not ringed. The median tentacle, which is the longest, is twice as long as the prostomium and extends, when folded back, to the posterior edge of the second pedigerous segment. The anal segment (Fig. 2) is

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rounded and the anal opening is directed dorsally and has thick tumid lips. Two pairs of anal cirri are present, the ventrals being much the shorter.

Various terms have been employed by different authors to describe the pieces forming the dental armature. Those employed by Southern are used here and the corresponding terms used by other English workers are given within brackets. The mandibles (Fig. 4) are mostly jet black, the posterior ends being light in colour. The anterior end is truncate and ringed, and the inner edge is black while the outer is more lightly coloured. The maxillae (*mx.*) (forcipate jaws) are stout with supports which are fused together along their whole length and are shorter than the blades. The anterior end of the blade is black. The maxillary plates (*mx. p.*) (second pair of maxillae) have six teeth on the right side and only five on the left. The azygos plate (*az. p.*) (third pair of maxillae) is crescent shaped. Its rim is thickened and is very black and is provided with 12-13 teeth. The right anterior crescentic plate (*cr. p.*) (fourth pair of maxillae) has eight teeth. The left is smaller and has six teeth. Two rectangular horny pieces (*r. p.*) (fifth pair of maxillae) with thickened rims occur in front of the dental apparatus. There is usually an extra anterior crescentic plate, on one side.
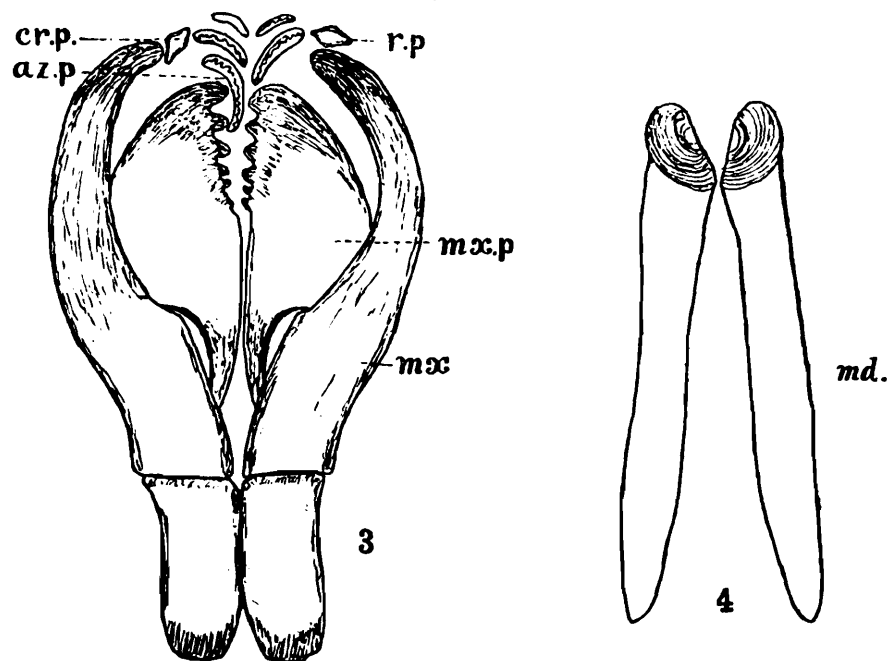

FIG. 3.—Dorsal view of dental armature; mandibles are not shown. *az.p.* Azygos plate; *cr.p.* Crescentic plate ; *mx.* Maxilla; *mx.p.* Maxillary plate; *r.p.* Rectangular piece.
FIG. 4.—*md.* Mandible.

The feet increase in size up to the 9th or 10th segment. The first foot (Fig. 5) has a dorsal cirrus, broad at the base and rapidly narrowing to a blunt point. It is highly vascular. The ventral cirrus is stouter and shorter. Between the two is a rounded lobe with a fillet in front. There are three black acicula. Above these there is a group of capillary setae of various lengths with flattened, very finely serrated blades. The ventral group consists of several compond setae with very minutely serrated terminal blades.

The 10th foot (Figs. 7 and 8) has 4 black acicula and two fillets. The acicula are more internally paced and the two groups of setae are enclosed between two fillets (Fig. 8). The acicula are black except at their tips where they are light yellow,

In the 40th foot (Fig. 9) the dorsal and ventral cirri are smaller. The median lobe is provided with two fillets and three acicula. The dorsal
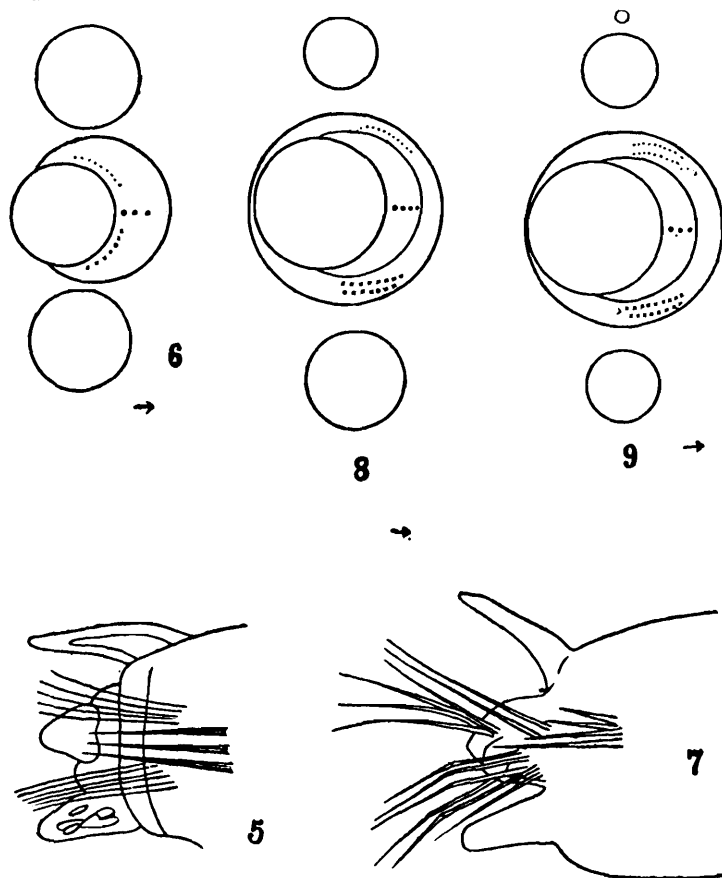

Fig. 5.—First parapodium.
Fig. 6.—Parapodial diagram of first foot, side view ; arrow points to the front.
Fig. 7.—10th parapodium.
Fig. 8.—Parapodial diagram of 10th foot, side view ; arrow points to front end.
Fig. 9.—Parapodial diagram of 40th foot ; arrow points anteriorly.

group of setae has very often, in addition, one comb seta. The comb seta projects only one third up the side of the other setae. The teeth of the comb are very fine and the two outer teeth are longer. The ventral group of setae consists of compound setae with uniformly serrated blades. Along with the ventral group of setae is a hook seta, the tip of which is protected by two minute wings.

Behind the 150th foot (Figs. 10 and 11), in moderately large specimens, the compound setae on the ventral side are gradually replaced by capillary setae and the replacement is complete before the 250th foot is reached. A single aciculum is present which has a powerful spine with a guarded tip on the ventral side. In addition to the capillary setae in the dorsal set, comb setae of two kinds are present (Fig. 12). There may be as many as 4-5 comb setae in a group. One kind is shorter than the other, is abruptly broadened at the distal end, and is provided with 14-15 coarse long teeth (Fig. 13). The second kind of comb seta is longer and projects more to the outside. The distal end is spatulate and has 23-26 fine short teeth of which the outermost on each side projects beyond the rest (Fig. 14).

Branchiae.—The gills are well developed and are found on the greater part of the body, commencing in full sized specimens from about the 30th segment. They attain their full development in the posterior two-thirds of the body. They are typically pectinate, and in big specimens,

as many as 12 filaments may be seen in some of the gills. The filaments are not ringed, and the branchiae do not meet over the back of the worm.
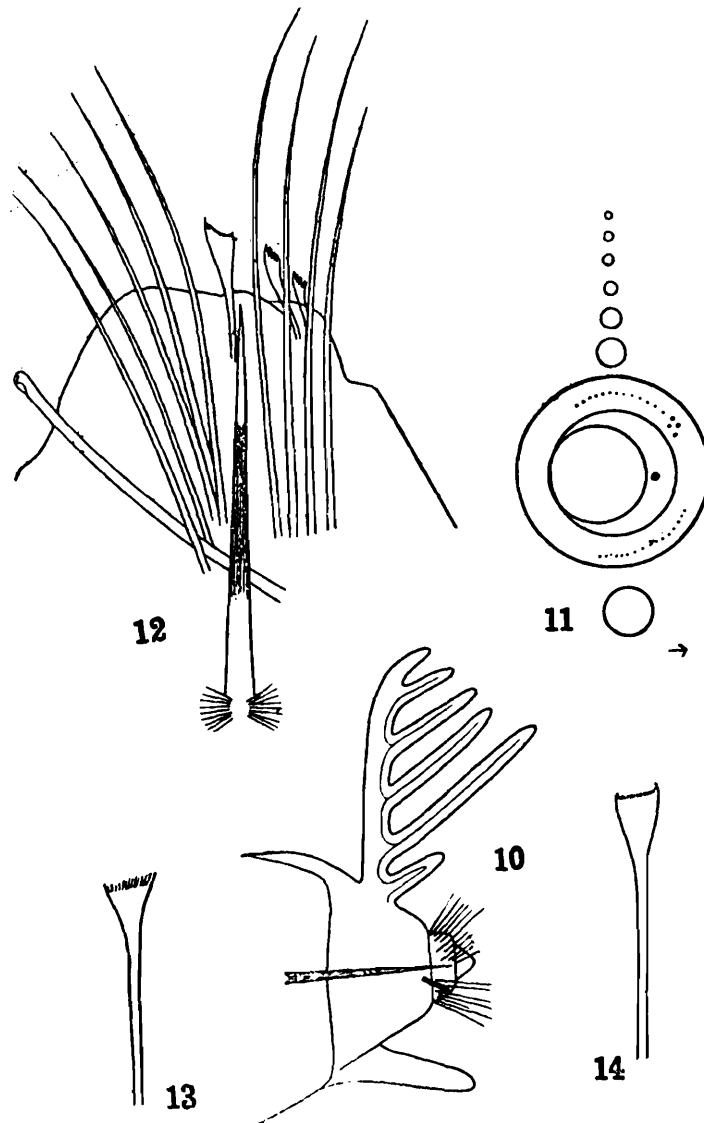

FIG. 10.—450th parapodium of a medium sized worm.
FIG. 11.—Parapodial diagram of 450th parapodium.
FIG. 12.—Parapodium from a posterior segment of a large worm to show the nature of setae. Cirri and gill are not shown.
FIG. 13 and FIG. 14.—Two forms of comb setae.

There is considerable variation in the distribution of the gills and in the number of filaments they carry. In some cases the first gill is present on one side only. The following table gives the variations for 4 specimens.

No. of Specimen.	1	2	3	4
Total No. of segments in each	168	200	215	250
Segments with gills of—				
1 filament	21-22	22-25 21-22	21-24	24-
2	23-39	26-48 23-43	25-37	26-38
3	40-49	49-66	38-52	38-47
4	50-78	67-131	52-90	48-75
5	79-124	80-112	90-170	75-140
Reduction of filaments in segments	125-168	113-200	171-215	141-250

In a big specimen with 650 segments, the first gill filament was on the 31st segment, and the maximum number of filaments was 12.

The present form is very peculiar in having capillary setae in the lower setigerous group of the feet in the middle and posterior segments. During the development of the worm, the posterior segments give rise to both compound and capillary setae until the growing worm has 120-150 segments. When about 150 segments have been formed only capillary setae are produced in the posterior segments.

The Madras worm differs from the typical specimens of *Marphysa gravelyi* in having two kinds of brush setae, one with a few coarse teeth and the other with a larger number of finer teeth. The published figures of the brush setae of *Marphysa gravelyi* do not resemble these. The Madras form differs also in having 12-13 teeth on the azygos plate, in having the compound setae slightly different and in the larger number of branchial filaments.* Eyes are present in young individuals only.

The present form shows some resemblance to *M. californica* but differs in :—

(1) The tentacles are not ringed,
(2) The median tentacles are the longest,
(3) The presence of fewer acicula in large specimens,
(4) The variability in the number of teeth in the dental apparatus, and
(5) The relative length of the segments.

The *cuticle*, which is a characteristic structure in the Annelida, forms the external covering of the body. It not only covers the body, gills and the parapodia but is also continued into the mouth forming an internal lining to the pharynx and the dental pouch.   It has a stratified appearence, consists of several layers, 8-12 of them being made out in some regions of the body. It stains blue with Mann's methyl-blue eosin after fixation in corrosive sublimate. The thickness of the culticle varies and, speaking generally, it is thicker on the ventral surface han on the dorsal. On the gills, parapodia, and the posterior segments it is very thin.

Below the cuticle there is the hypodermal layer, which by its activity gives rise to the cuticle. It is generally formed of a single layer of vertically elongated cells (Fig. 15). In some parts of the body, it is more than one cell in thickness. They are short, for instance, on the anterior and the posterior face of each parapodium, while below they are more elongated. The protoplasm of the cells is granular and the cell boundaries are well marked, when properly stained. The nuclei are spherical to oval and stain well with iron-haematoxylin and Mann's methyl-blue eosin. They lie generally near middle of the length of the cells. The chromatin in the nucleus is granular and forms a network. In the newly formed posterior segments the cells are for the most part very short,

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* For the reasons stated above it was my intention to describe the Madras *Marphysa* as a new species, and Southern to whom the specimens were sent also thought them to he different from *M. gravelyi.* Fauvel, however, to whom the specimens were sent by Dr. Gravely of the Madras museum refers them to *M. gravelyi,* and I have followed the identification of the French authority.

though considerably elongated ventro-laterally where the ventral sur-face of the body wall passes into the lower half of the parapodia. Pig-
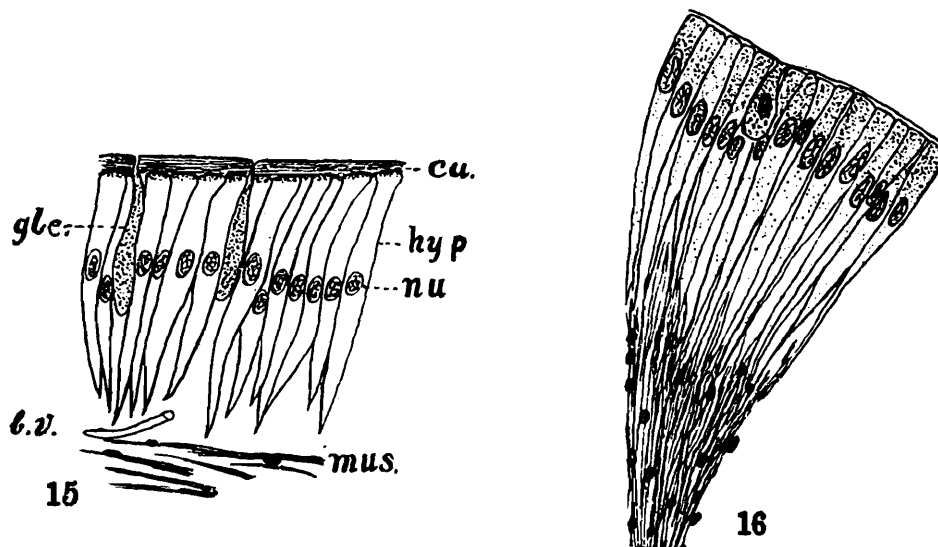

FIG. 15.—Hypodermal cells from the side of the body. *b.v.* Blood vessel; *cu.* Cuticle; *gl.c.* Gland cell; *hyp.* Hypodermis; *mus.* Muscles; *nu.* Nucleus.
FIG. 16.—Prostomial cells.

ment granules occur at the outer ends of the cells and are more numerous in the cells of the prostomium (Fig. 16) and peristomium than in the rest of the body, and in these regions the nuclei are situated in the outermost half of the cells.

In addition to the hypodermal cells there are gland cells which occur singly. These are (Fig. 15 gl. c.) elongated and have granular contents and oval nuclei. They open through pores in the cuticle.

Parapodial Glands.—In addition to the gland cells in the hypodermis there are other glandular structures which do not belong to that layer, but occupy definite positions in relation to the body wall. The more important of these glands are specially well developed in the parapodia of the middle and the posterior segments, and may be called parapodial glands. Each gland (Fig. 17) lies ventral to the setigerous tuft and consists of large protoplasmic cells which do not stain readily. The cells are slightly elongated and have their inner ends broader than the outer. They are all closely packed together and there is no internal cavity. Jourdan (1887) has suggested that in *Eunice harassii* the cells open by separate pores to the outside. No pores of the kind described could be made out in this form. The same author has suggested that the glands secrete mucus. There is no doubt that this is so. The eggs of this worm are known to be laid in a jelly which is formed by the action of water on mucus. Often, when the worm is irritated the glands secrete rapidly and the mucus swells up in water in the form of minute masses of jelly on either side.

Pigment glands.—Below the dorsal cirrus in each parapodium there is another gland about the nature and function of which there has been some confusion. These glands are easily seen in transverse and longitudinal sections and in the living worm appear as dark pigment spots. Such structures are of common occurrence in species of *Eunice* also, and were considered as segmental organs by Ehlers (1864-8). Later Claparede (1871) pointed out the misapprehension, but thought them to

be visual in function. Fig. 18 shows one of these glands. There is a rather eccentrically placed cavity filled with pigment. Projecting into
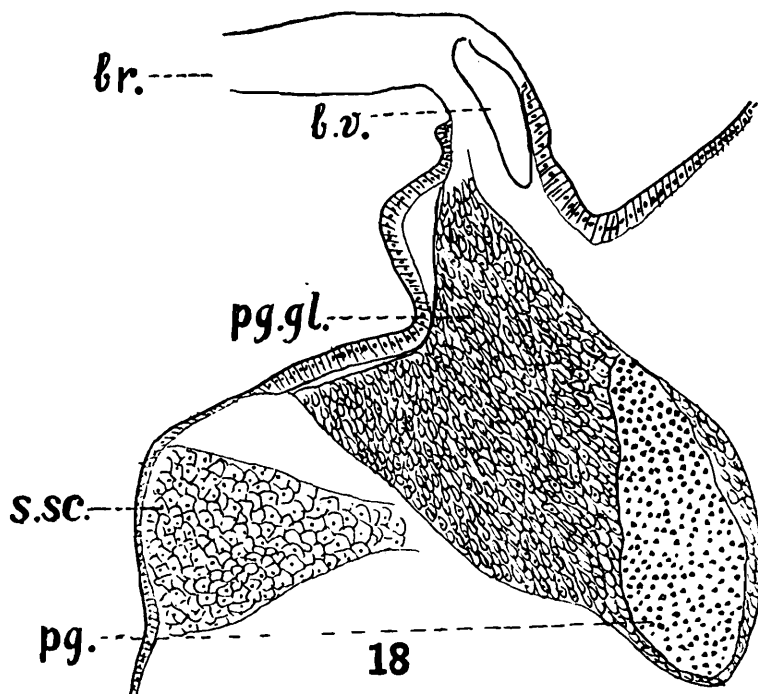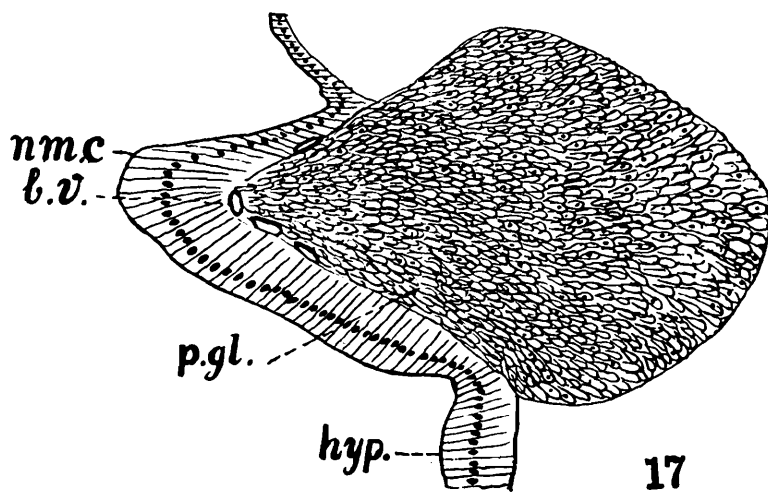

Fig. 17.—A parapodial gland. *b.v.* Blood vessel; *p.gl.* Parapodial gland; *hyp.* Hypodermis; *nm.c.* Neuropodial cirrus.

Fig. 18.—A pigment gland. *br.* Gill; *b.v.* Blood vessel; *pg.* Pigment; *pg.gl.* Pigment gland; *s.sc.* Setal sac.

the mass of pigment are sometimes seen two or three slender spines which are the only representatives of the absent notopodium. No duct of any kind could be seen. The cells constituting the walls of the pigment gland are very similar to those of the parapodial glands. Pruvot (1885) has suggested that the pigment granules are formed as the result of the katabolic activity (désassimilation) of the cells and are actually of the nature of an excretory product got rid of in a manner not clearly understood. Jourdan (1887) basing his conclusions on a histological study has supported Pruvot's suggestions.

It is interesting to note that in sections of newly formed segments the pigmental organs contain very little pigment. Further, pigment formation becomes very pronounced when the coelomic cavity is filled with reproductive elements. These facts seem to point to the conclusion

that the cells are homologous to those forming the parapodial glands and that the centrally placed cells undergo degeneration and that the rate of degeneration is greatest during the reproductive phase.
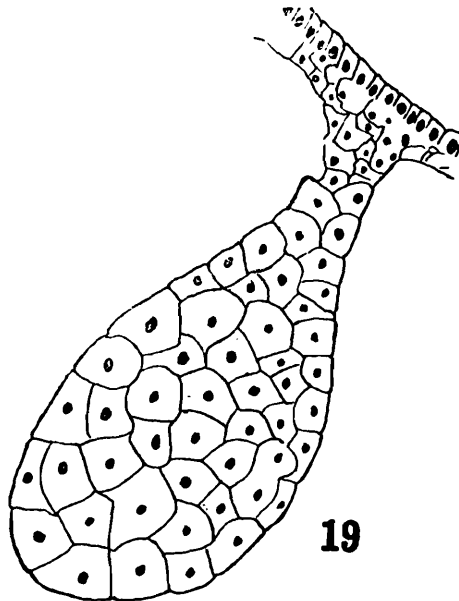

Fig. 19.—A solid gland from the peristomium.

Other glands.—Besides the glands mentioned there are others, which I believe are recorded here for the first time, and which are confined to the anterior end of the peristomium only. They are in the form of clusters (Fig. 19) and occur in grape-like bunches on the sides and on the ventral part of the peristomium bounding the entrance to the mouth. The cells composing the glands are highly protoplasmic and the nuclei are difficult to stain. Though the narrow end of the cell clusters are in relation with the hypodermis, no duct could be made out. The glands seem to belong to the category of solid glands and probably secrete mucus.

There is very little connective tissue between the hypodermis and the underlying circular muscle-sheath. The muscle-sheath is generally of uniform thickness throughout the body but is better developed behind the prostomium in the region of the pharynx, especially on the ventral side. Intersegmentally it is interrupted and laterally it is carried inwards along the ventral and dorsal bands of longitudinal muscle. In the newly formed posterior segments it is but little developed and is hardly recognizable. No intermuscular substance in the form of any connective tissue has been observed.

The layer of longitudinal muscles is internal to the circular muscles and consists of four large bands, two dorsal and two ventral (Fig. 32). The dorsal bands, unlike those of *Nereis,* are closely apposed and the blood vessels are therefore completely pushed into the body cavity, whereas in *Nereis* the two bands are separated by the single dorso-median blood vessel. The ventral bands are well developed, and are separated from each other by the median ventral nerve cord. The dorsal and the ventral bands are separated by a space on the sides occupied by septal muscles which work the setae. In the middle and the posterior segments the ventral bands are better developed, while in the pharyngeal region the dorsals are more powerfully developed.

In the anterior region the dorsal bands are attached to the base of the prostomium and the ventrals to the extreme anterior end of the peristomium. McIntosh (1910) has observed the strong development of the ventral bands in species of *Marphysa* generally. In a number of Eunicids studied by various workers the powerful development of the longitudinal bands has been observed. In *Eunice* and *Lysidice*, the dorsal bands are better developed than the ventral, while in *Marphysa* the reverse is the case in the greater part of the body. Under high magnification the longitudinal muscle fibres appear to be flattened and to have a wavy margin, and obliquely cut ends. Often an oval nucleus can be seen about the middle of the muscle fibre. The oblique muscles are uniformly developed and are characteristic of the Polychaetes. They are practically absent in the first few segments where the coelomic cavity is almost obliterated by the greatly developed dental pouch. Behind the dental pouch they occur in each segment. From the dorso-lateral border of the nerve sheath of the ventral nerve cord they pass obliquely outwards and upwards external to the outer side of the dorsal longitudinal muscle on each s de and are inserted into some of the circular muscles. By this arrangement, they divide each compartment into three parts, a central containing the two dorsal blood vessels and the alimentary canal, and the two lateral containing the nephridia and the vascular loops (Fig. 32).

The *alimentary canal* commences in the mouth, which in front, is in continuation with a deep groove on the ventral side of the prostomium. The front end of the peristomium does not project uniformly all round but the upper portion extends a little more forwards than the lower. Fig. 20 is a transverse section of the worm just in front of the lower lip of the peristomium. It will be seen that in this region the entrance to the mouth is formed by the overhanging lateral walls (*l. w. per.*) of the extreme anterior end of the peristomium. On the inner side of the lateral wall there are two deep grooves (v. gr. and d. gr.) on either side, which mark off the more centrally placed structures including the roof of the mouth. Between these lie two folds, the upper (c. f.) large and cushion-like, the lower (f. f.) small and frill like. The cuticle on the roof of the mouth is thick while the folds are covered by thin cuticle only. The hypodermal cells below the cuticle are normal, except on the folds mentioned where they are greatly elongated and some of them can be observed to have their bases produced into protoplasmic processes passing into the tissues below (Fig. 44). There can be no doubt, considering their position, shape and arrangement, that they are sensory cells.

The mouth leads into a buccal cavity which occupies the anterior half of the peristomium. The floor of the cavity is pierced by a median longitudinal slit—the pharyngo-oesophageal slit—leading into a ventrally placed pharynx or dental pouch. The slit extends up to the first setigerous segment. The dental pouch is highly muscular and is a sort of *cul-de-sac*, characteristic of the Eunicidae. It is lined throughout by cuticle, which, in certain regions, is thickened into the jaws, constituting the dental armature. The pouch extends up to the middle of he 6th setigerous s gment. It is highly interesting to note that while in forms like *Nereis* the muscular pharynx containing the
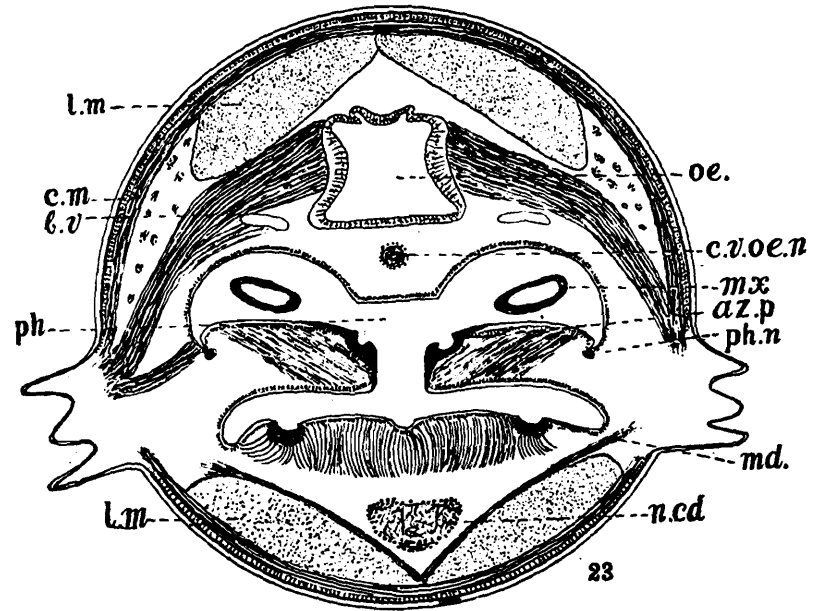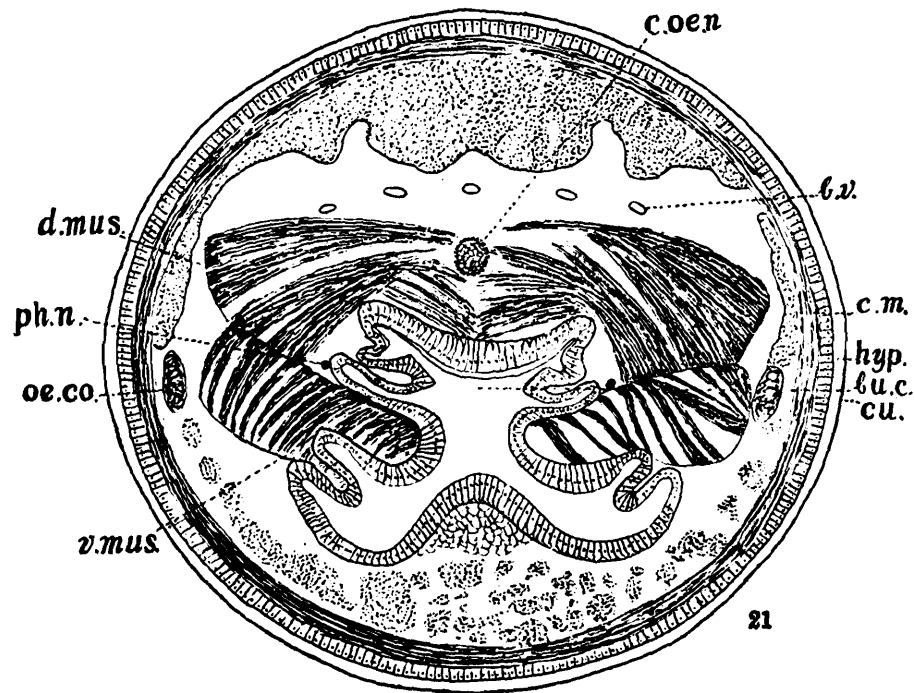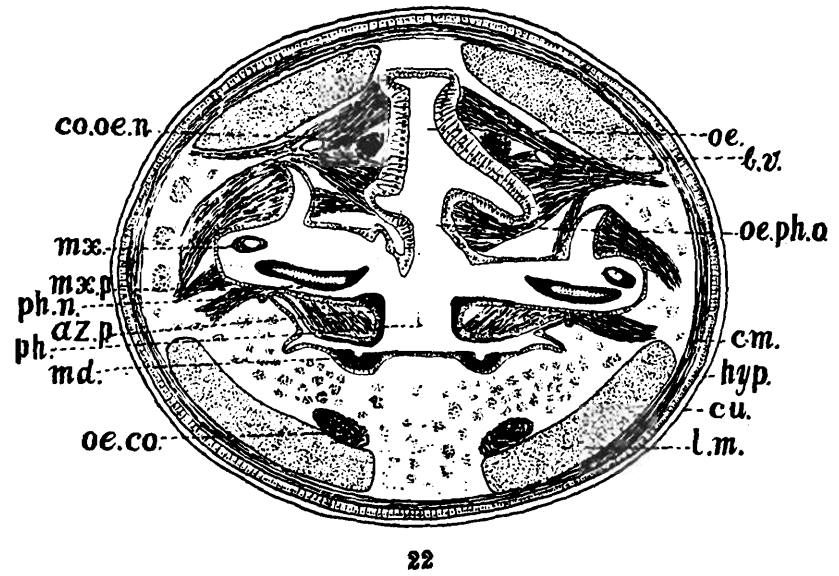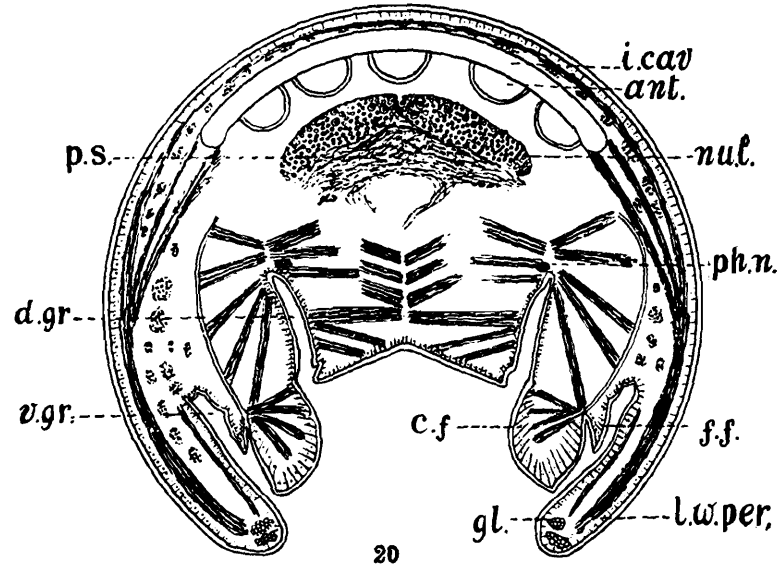
FIG. 20.—Transverse section of the worm through the part just in front of the lower lip of the peristomium. *anl.* Antenna ; *c.f.* Cushion like fold ; *d.gr.* Upper groove on the side of the roof of the mouth ; *f.f.* Frill like fold ; *gl.* Cland ; *i.cav.* Inter-space between peristomium and base of prostomium ; *l.w.per.* Lateral wall of peristomium ; *nu.l.* Nuclear layer ; *p.s.* Punctated substance ; *ph.n.* Pharyngeal nerve of the stomato-gastric nervous system ; *v.gr.* Lower groove.

FIG. 21.—Transverse section through the anterior part of the peristomium. *b.v.* Blood vessel ; *bu.c.* Buccal cavity ; *c.m.* Circular muscles; *c.oe.n.* Common dorsal oeso-phageal nerve of the stomato-gastric nervous system ; *cu.* Cuticle ; *d.mus.* Upper group of muscles of the dental pouch ; *hyp.* Hypodermis ; *oc.co.* Oesophageal commissure ; *ph.n.* Pharyngeal nerve of the stomato-gastric nervous system ; *v.mus.* Ventral group of muscles of the dental pouch.

FIG. 22.—Transverse section through the posterior part of the peristomium. *az.p.* Azygos plate ; *b.v.* Blood vessel ; *c.m.* Circular muscles ; *co.oe.n.* Commissural oesophageal nerve of the stomato-gastric nervous system ; *cu.* Cuticle ; *hyp.* Hypo-dermis ; *l.m.* Longitudinal muscles ; *md.* Mandible ; *mx.* Maxilla ; *mx.p.* Maxillary plate ; *oe.* Oesophagus ; *oe.co.* Oesophageal commissure ; *oe.ph.o.* Oesophageo pharyngeal opening ; *ph.* Pharynx ; *ph.n.* Pharyngeal nerve of the stomato-gastric nervous system.

FIG. 23.—Transverse section passing through the third setigerous segment. *az.p.* Azygos plate ; *b.v.* Blood vessel ; *c.m.* Circular muscles ; *c.v.oe.n.* Common ventral oesophageal nerve of the stomato-gastric nervous system ; *l.m.* Longitudinal muscles; *md.*Mandible ; *mx.* Maxilla *n.cd.* Nerve cord; *oe.* Oesophagus ; *ph.* Pharynx ; *ph.n.* .Pharyngeal nerve of the stomato-gastric nervous system.

jaws lies in a direct line with the gullet, in the Eunicids, the pouch occupies a position which is unique in the Polychaetes. Figs. 21-24 show the relationship of the dental pouch and the gullet in the seven anterior segments. It will be seen that the pouch occupies so much of the body space that the gullet is highly compressed and occupies a dorsal position. Anteriorly, the pouch and the gullet are encircled by muscles while posteriorly they are practically free. In segments 7 and 8 the gullet makes a sharp bend downwards and again turns upwards thus forming a distinct U-shaped loop from the anterior limb of which a few muscles pass to the posterior blind end of the dental pouch. These muscles probably aid the retractors of the pouch. At this point a bundle of muscles passing on each side from the posterior end of the dental pouch, runs outwards and backwards on either side of the U-shaped bend of the gullet and is inserted into the body-wall. These two bundles are the great retractors (*r. m.*) of the dental pouch (Fig. 26).

The dental pouch is circular in section and contains the complicated jaw apparatus. It is developed very early, being present even in the nectochaeta stage of development. The muscles which work the jaws are symmetrically disposed and they are so well developed that they project into the lumen of the pouch as thick cushions carrying the dental armature (Fig. 21). They may be said to fall roughly into two groups, the dorsal and ventral, and according as the jaws are attached to the dorsal or the ventral group they have been called "superior" and "inferior" by various workers. The mandibles (inferior jaws) are worked by the ventral group of muscles. The remaining pieces of the dental armature are carried by the dorsal group and hence the maxillae, the maxillary plates and the azygos plates are dorsal in posi-tion (Fig. 22), while the mandibles or the lower jaws are ventral in posi-tion, but the position of the dental pieces in a section varies very much according to the state of contraction of the muscles of the dental pouch at the time of fixation. In Fig. 25 which is an instance in point, the jaw

apparatus seems thrust forward and the various pieces have an unusually anterior position. The muscles carrying the mandibles, as shown in
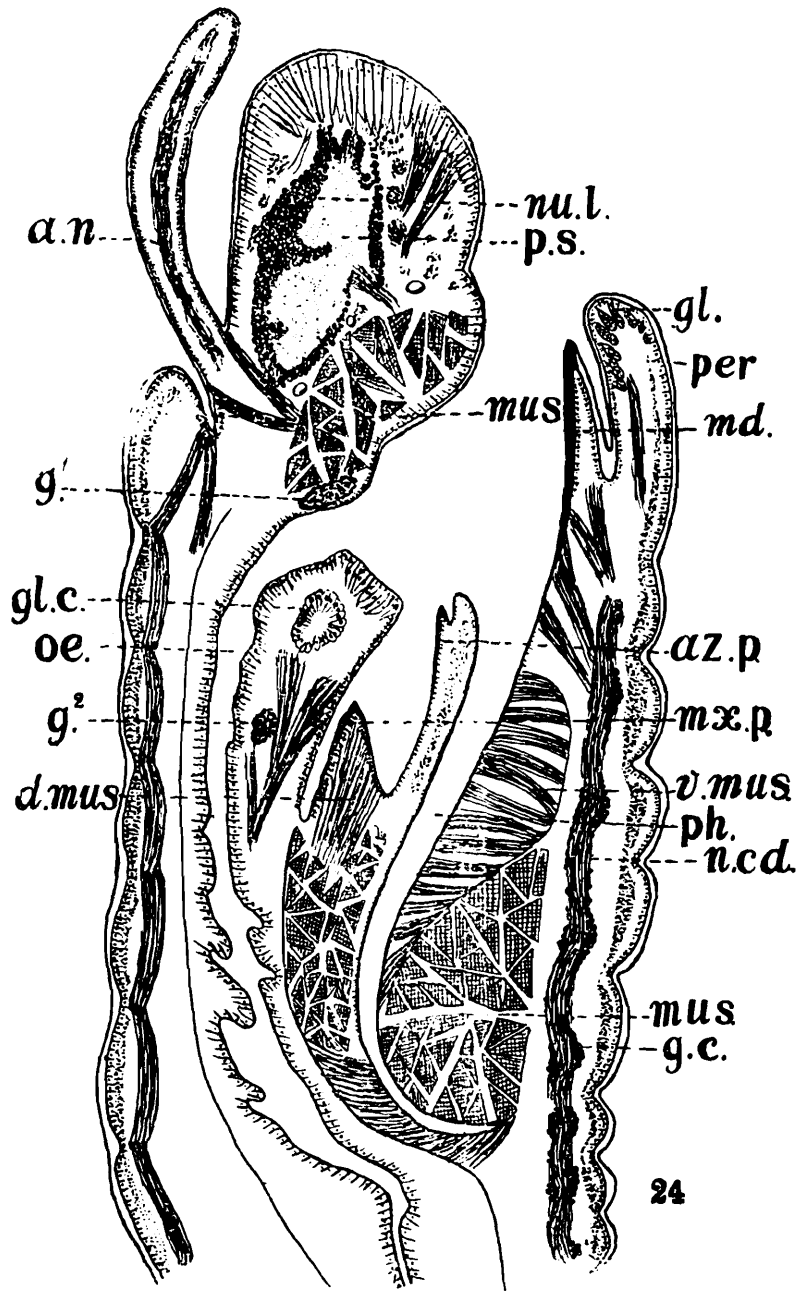

FIG. 24.—Vertical longitudinal section of the anterior end of worm. *a.n.* Antennal nerve; *az.p.* Azygos plate; *d.mus.* Upper group of muscles of the dental pouch; *g.c.* Ganglion cell; *g.¹* & *g.²* Ganglia of the stomato-gastric nervous system; *gl.* Gland; *gl.c.* Gland cells; *md.* Mandible; *mus.* Muscles; *mx.p.* Maxillary plate; *n.cd.* Nerve cord; *nu.l.* Nuclear layer; *oe.* Oesophagus; *per.* Peristomium; *ph.* Pharynx; *p.s.* Punctated substance; *v.mus.* Ventral group of muscles of the dental pouch.

the figure, project so much that the extremities of the mandibles meet along the midventral line dividing the central cavity into a narrow ventral lumen and a more spacious dorsal chamber containing the rest of the dental armature. Behind the posterior end of the mandibles the muscle ridges actually fuse and form a partition between the dorsal and ventral chambers. The posterior end of the dental pouch is firm and it is to this part that the great retractor muscles (Fig. 26. *r. m.*) are attached. In life, the dorsal pieces of the dental armature can be seen to protrude and have a large amount of play on one another, as well as against the lower jaw.

The colour, strength, and number of teeth on the dental pieces vary according to the age of the animals. Ehlers (1864-68) based his classification of the Eunicids into ' Eunicia labidognatha ' and ' Eunicia priognatha ' on certain differences in the dental characters. Bonnier (1893) subsequently pointed out the highly artificial nature of this classification and showed how *Ophryotrocha* would belong to the former group when young and to the latter when adult.
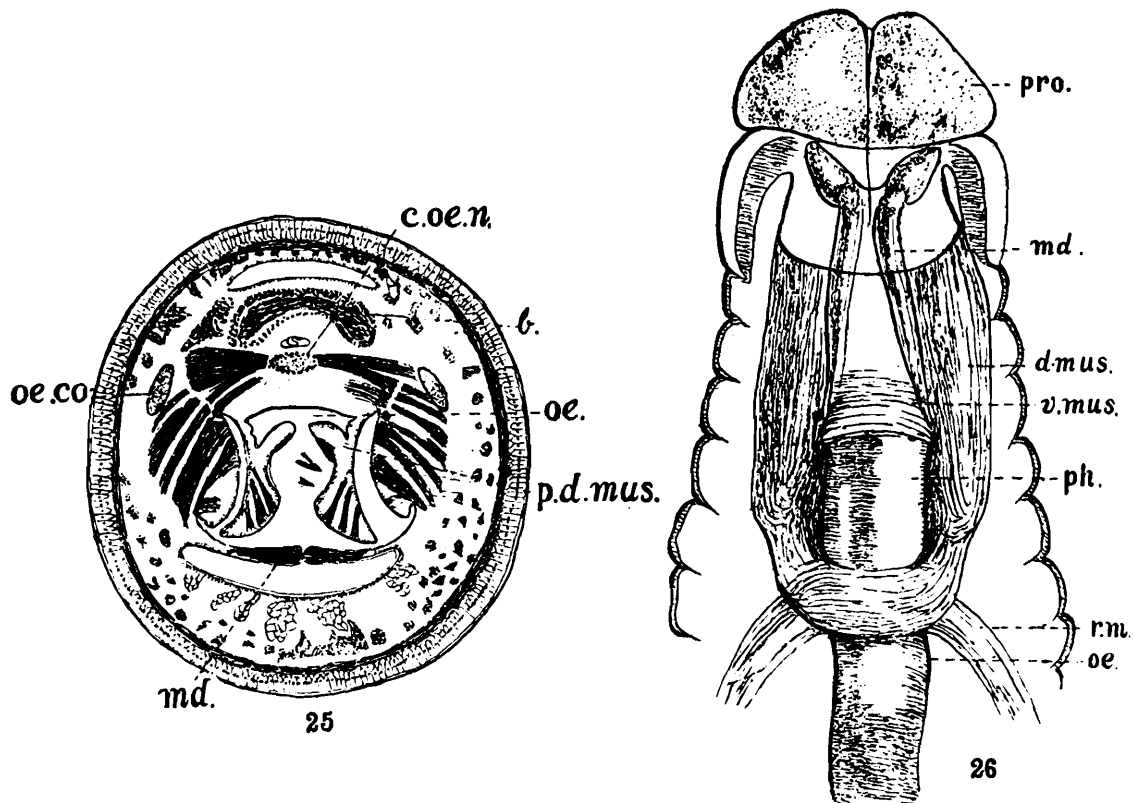

Fig. 25.—Transverse section through peristomium with the dental armature in a forward position. *b.* Brain ; *c.oe.n.* Common dorsal oesophageal nerve of the stomatogastric nervous system ; *md.* Mandible ; *oe.* Oesophagus ; *oe.co.* Oesophageal commissure.

Fig. 26.—Diagram of dental pouch dissected from the ventral side to show the retractor muscles. *d.mus.* Upper group of muscles of the dental pouch ; *md.* Mandible ; *oe.* Oesophagus ; *ph.* Pharynx ; *pro.* Prostomium ; *r.m.* Retractor muscle ; *v.mus.* Ventral group of muscles of the dental pouch.

The gullet at its commencement is cylindrical and has very thick walls (Fig. 27). Projecting into its lumen are four or five longitudinal ridges which almost occlude the internal space. These ridges are made up of a large number of protoplasmic cells of a glandular nature. The cells are very granular and are not arranged in clusters or groups but have a compact arrangement all round the walls of the gullet. The gullet may be said to pass into the intestine in the 7th and the 8th segments. About the 40th segment in full grown worms the intestine has lateral diverticula (Fig. 28). The lumen of the intestine also becomes very spacious and several folds project inwards (Fig. 29) thus greatly increasing the inner surface of the intestine. There may be as many as six to eight folds on each side. Two of these lie close to each other near the median ventral line giving rise to a median groove (Fig. 29, *c. gr.*), which is ciliated in the posterior segments. Such a groove is by no means peculiar to this form but has been described in other Polychaetes also. Eisig figures it for Capittellids under the name of ' nebendarm ' (1887).

The wall of the intestine (Fig. 30) consists, from within outwards, of an epithelial layer, a layer of longitudinal muscles, a layer of circular
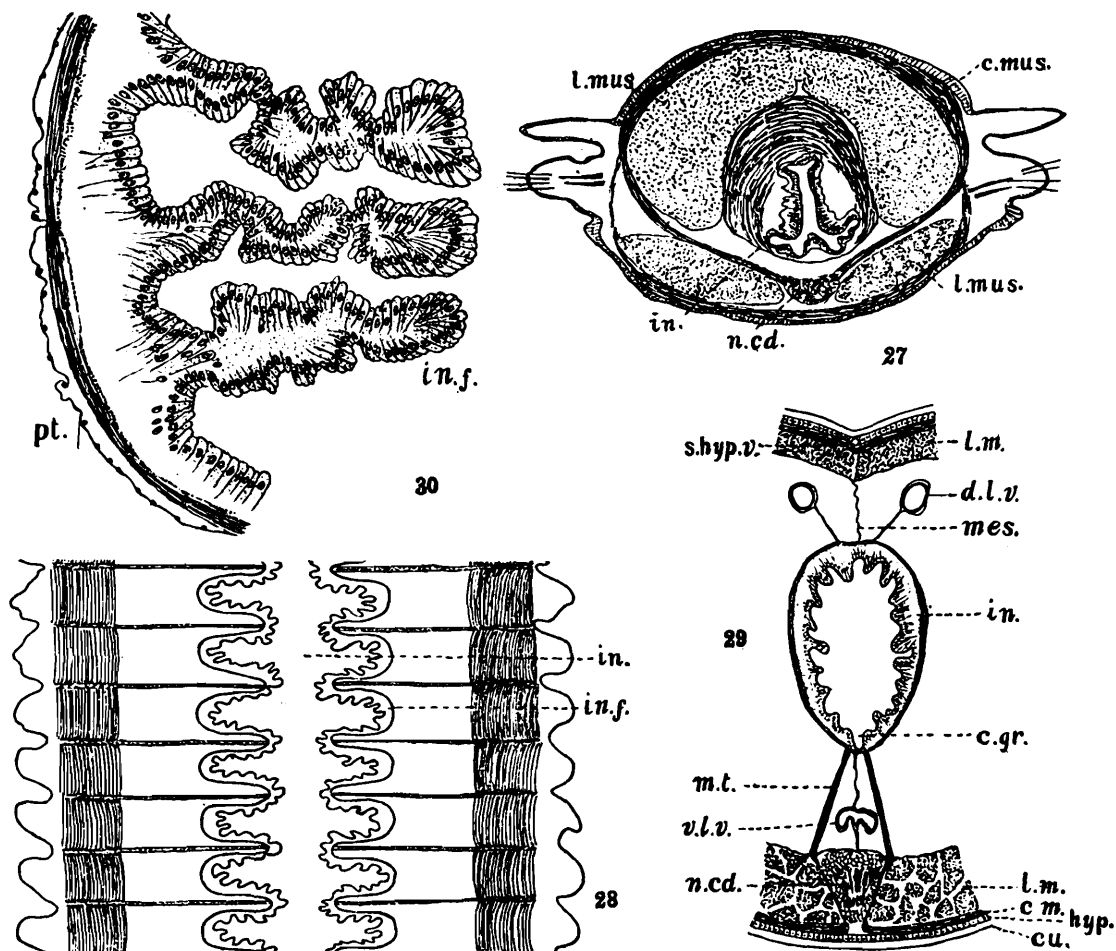

Fig. 27.—Transverse section through the body behind dental pouch to show great development of the dorsal longitudinal muscles. *c.mus.* Circular muscles ; *l.mus.* Longitudinal muscles ; *in.* Intestine ; *n.cd.* Nerve cord.

Fig. 28.—Horizontal section of a big worm behind 50th segment showing diverticula of the alimentary canal. *in.* Intestine ; *in.f.* Folds of intestine.

Fig. 29.—Diagram showing the relation between the alimentary canal, main blood vessels and the body wall. *c.gr.* Ciliated groove ; *c.m.* Circular muscles ; *cu.* Cuticle ; *d.l.v.* Dorsal longitudinal vessel ; *hyp.* Hypodermis ; *in.* Intestine ; *l.m.* Longitudinal muscles ; *mes.* Mesentery ; *m.t.* Muscle tunnel ; *n.cd.* Nerve cord ; *s.hyp.v.* Sub-epidermal blood vessel ; *v.l.v.* Ventral longitudinal blood vessel.

Fig. 30.—Diagram of intestinal folds (Highly magnified). *in.f.* Folds of intestine ; *pt.* Peritoneum.

muscles and externally the coelomic epithelium. The inner intestinal epithelial membrane consists mainly of a large number of elongated cells. These are very granular and the nuclei are placed almost in the middle of the cells. Most of these cells have probably a digestive function while a few secret mucus. The longitudinal and circular layers of muscles are best developed in the first 40-50 segments, while in the following segments these layers are thin, particularly the longitudinal. The coelomic epithelial covering consists of rather flat cells in which large nuclei could be seen in places.

The intestine of a freshly captured worm contains a quantity of mud mixed with fragments of animal and vegetable matter. Pieces of *Enteromorpha*, a common form of alga in the brackish water, have been noticed. Remains of molluscan shells have also been observed. There is no doubt that these worms take in large quantities of mud with a

considerable amount of organic matter and as this passes down, it is probably well mixed with mucus secreted from the mucus cells of the gullet.   Once in the intestine, the food is subjected to the action of the digestive juices from the cells of the intestinal fold and the faecal matter is gradually moulded into cylindrical pellets which are voided at the anus.
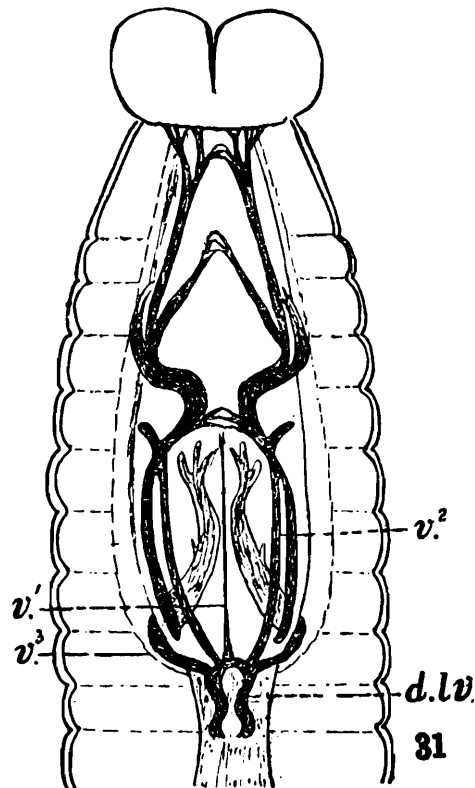

Fig. 31.—General diagram of blood vessels in the anterior region.   Dorsal view.   Capillaries are not shown.   *d.l.v.* Dorsal longitudinal vessel ; v^1, v^2 and v^3. Anterior branches of dorsal vessels.

The *Vascular system* consists of a closed system of tubes.   It is very well developed in this worm.   Running above the alimentary canal are two dorsal longitudinal blood-vessels in which the blood travels forwards (Fig. 29).   Below the intestine there is a single blood-vessel, running above the nerve cord.   These three vessels constitute the essential part of the vascular system.   The two dorsal vessels are held in position by folds of peritoneum.   They are peculiar in that, instead of occupying a position internal to the circular layer of muscles and between the right and the left longitudinal bands of muscles, as in *Nereis* for instance, they lie entirely in the body cavity in the greater part of their course.   In front, the two vessels unite and from the loop thus formed spring five vessels one of which is small and median and the rest large and paired (Fig. 31).   The median vessel is continued forwards (v^1).   The inner paired vessel (v^2) runs forward, becomes enlarged and gives rise to two or three blind branches, and on reaching the anterior end breaks up into small vessels.   The outer paired vessel (v^3) turns downwards after its origin and enlarges into a sinus before entering the space between the gullet and the pharynx, and finally divides into a number of branches.   Capillary connections exist between the vessels on one side and also between the corresponding vessels of the opposite sides.

H

Each dorsal vessel gives off anteriorly in each segment a lateral branch (*l. v.*) which runs outwards along the anterior septum of the
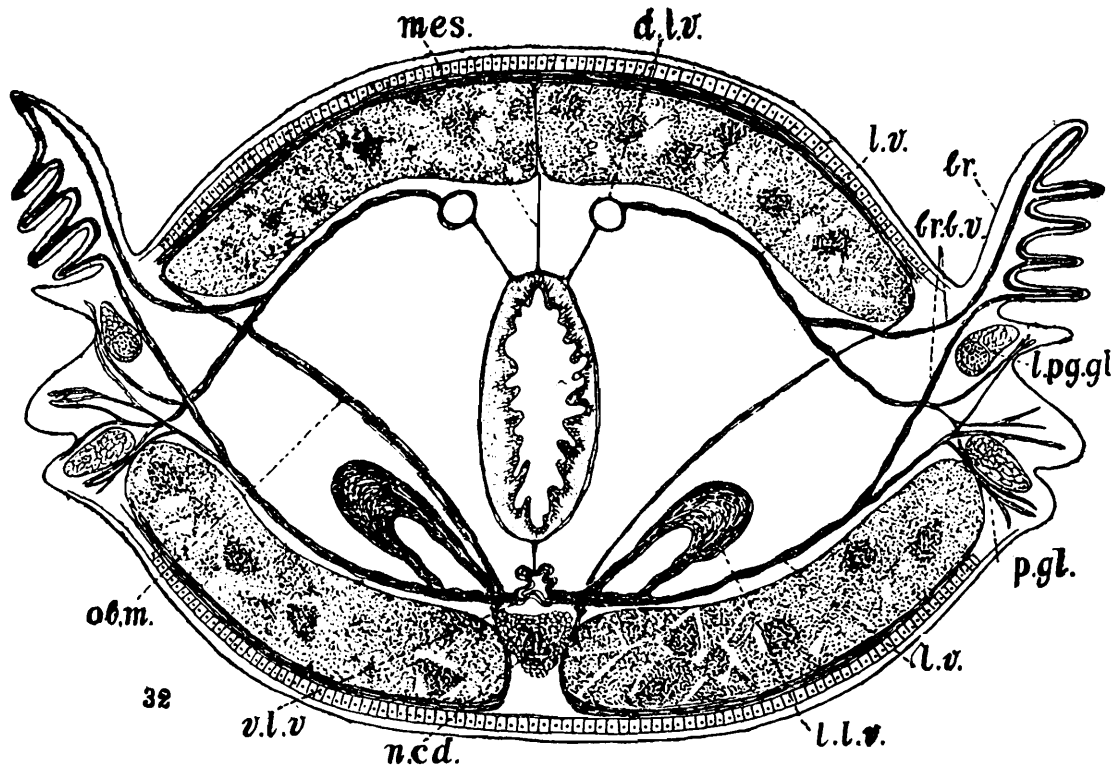

FIG. 32.—Diagram showing the general arrangement of the blood vessels in a segment. *br.* Gill; *br.b.v.* Blood vessel to the gill; *d.l.v.* Dorsal longitudinal vessel; *l.l.v.* Loop of lateral vessel; *l.pg.gl.* Lateral pigment gland; *l.v.* Lateral vessel; *mes.* Mesentery; *n.cd.* Nerve cord; *ob.m.* Oblique muscles; *p.gl.* Parapodial gland; *v.l.v.* Ventral longitudinal blood vessel.

segment just internal to the longitudinal layer of muscles and divides into two branches (Fig. 32). The dorsal branch (*br. b. v.*) runs upwards and is soon accompanied by a branch from the ventral lateral blood vessel about to be mentioned. The two lie close together near the base of the gill, when one is present in the segment, and supply that organ. The other branch runs downwards and backwards and is soon in close proximity to a branch of the ventral lateral blood vessel. They break up into capillaries which supply the parapodium and also the body wall.

The two median dorsal vessels are not simple straight tubes. They are dilated segmentally and constricted intersegmentally, the dilated portions being filled with blood. The narrow parts are free from blood. It is also seen that the dilated portions in which the blood collects, when the animal is killed, have very thin walls in which muscle fibres are poorly developed (Fig. 33). The alternating intersegmental narrow parts have several layers of circular muscle fibres.

The single ventral vessel lies in a distinct tunnel (*m. t.*) formed by a number of muscle fibres, rather loosely arranged. Like the dorsal vessels, the ventral vessel is segmentally dilated and intersegmentally constricted (Fig. 34). The dilated parts, which are much more conspicuous here than in the dorsal vessels, are extremely thin walled, while the intersegmental portions are well provided with several layers of circular muscles. In the hind region of each segment the median ventral vessel gives off on each side a lateral vessel. Each such vessel, near its origin, forms a U-shaped loop with a dilatation at the bend which

projects freely into the body cavity. The U-shaped structure with its limbs arising close together appears to be a bag with a single stalk and was called ampulla by Delle Chiaje. A careful examination however
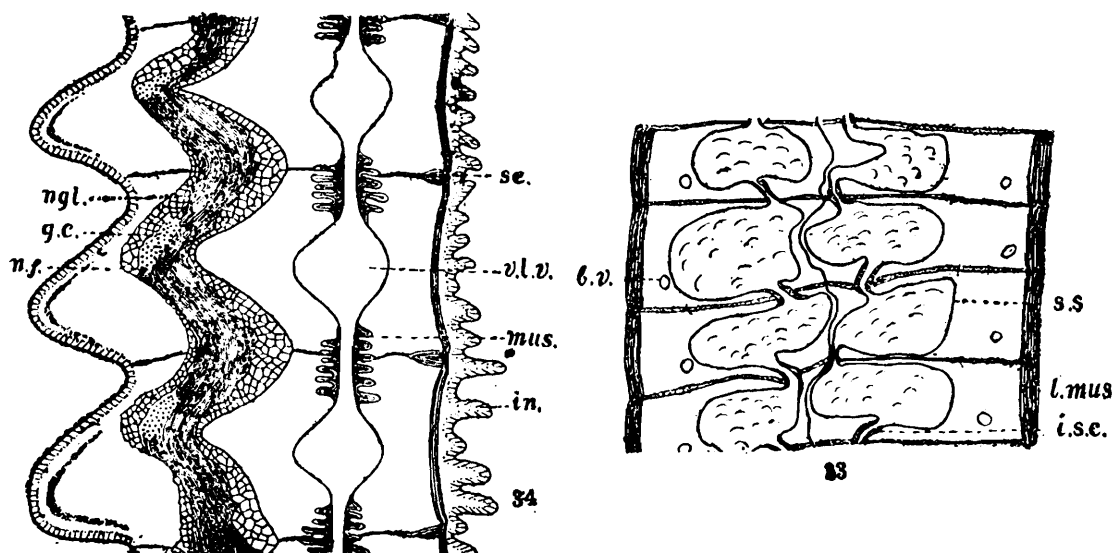

FIG. 33.—Diagram of a horizontal section showing the constricted nature of the dorsal blood vessels. *b.v.* Blood vessel ; *i.s.c.* Intersegmental constriction of dorsal longitudinal blood vessel ; *l.mus.* Longitudinal muscles ; *s.s.* segmental dilatations of dorsal vessels.

FIG. 34.—A longitudinal section of the nerve cord and the median ventral blood vessels showing the segmental dilatations and the intersegmental constrictions of the blood vessel. *g.c.* Ganglion cell ; *mus.* Muscles ; *in.* Intestine ; *n.f.* Nerve fibrillae ; *ngl.* Neuroglia ; *se.* Septum ; *v.l.v.* Ventral longitudinal blood vessel.

shows the two arms of the loop. These vascular loops are contractile and are of approximately uniform size throughout, except at the anterior end, where behind the dental pouch, in segments 7-10, they are considerably larger. In the living worm 5 or 6 loops belonging to consecutive segments, as well as the swollen portions of the dorsal and ventral vessels can be seen to contract together. Each lateral vessel, after giving off the loop, runs to the inner border of the longitudinal muscle band and on reaching the base of the parapodium divides into two branches One of them runs forwards and upwards and arriving by the side of the corresponding branch from the longitudinal dorsal blood vessel
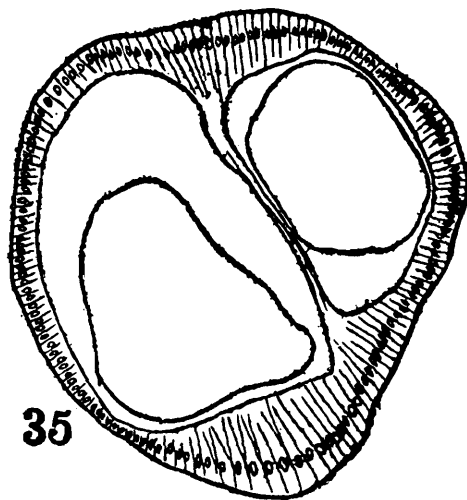

FIG. 35.—Section through the base of gill.

reaches the base of the gill. The two vessels then run up to the tip of the gill and there unite thus forming the ascending and descending

vessels of the gill (Fig. 35). They are connected by minute transverse branches during their course.

The ventral median vessel divides into two branches at the hind end of the dental pouch. Each branch runs outwards and divides again into three branches (Fig. 36), one of which ($b.$ $v.^{1}$) runs along the outer side of the muscles of the dental pouch, the second ($b.$ $v.^{2}$) runs forward along the body wall giving off some branches in its course ; the third ($b.$ $v.^{3}$) sharply turns backwards and divides into small branches in the body wall. All the vessels give off numerous small branches which anastomose into a network on the walls of the dental pouch. At the point where the three vessels branch on each side there is a bag-like swelling (*am.*) which is seen to be filled with blood.
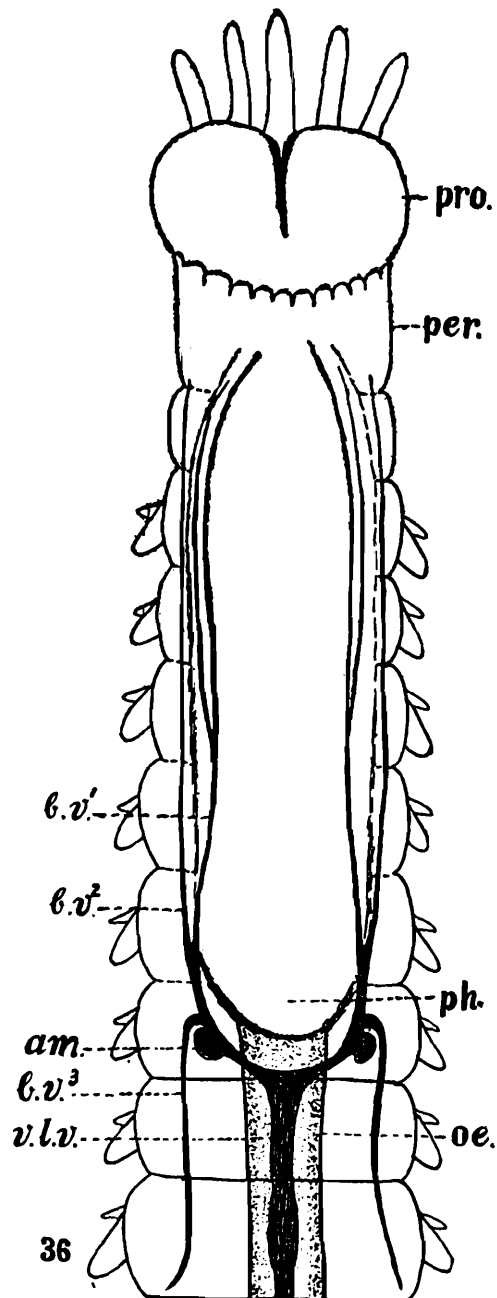
Fig. 36.—Diagram showing the main blood vessels on the ventral side of the dental pouch. Capillaries are not shown. *am.* Ampulla ; $b.v.^{1}$, $b.v.^{2}$ and $b.v.^{3}$ Branches of main blood vessel ; *oe.* Oesophagus ; *per.* Peristomium ; *ph.* Pharynx ; *pro.* Prostomium ; *v.l.v.* Ventral longitudinal blood vessel.

In addition to the connection which exists between the dorsal and the ventral vessels by means of lateral branches and capillaries there is

another connection which, though not quite so pronounced, is none the less important. This consists of minute vessels which are given off from the two dorsal vessels and the single ventral vessel. These vessels are not of very regular occurrence. They break up into capillaries in the walls of the intestine and freely unite together thus bringing about a very close connection between the dorsal and the ventral median blood vessels. The vessels which supply the parapodia form the capillaries, some of which pass up the sides of the body wall just below the hypodermis and divide into a very fine richly branched network of capillaries ramifying immediately below the skin.

Ultimately they open into a small dorso-median longitudinal subdermal vessel which sends down in each segment minute vessels which running between the two bands of dorsal longitudinal muscles reach the body cavity and open into the right or left dorsal longitudinal vessel.

It will thus be seen that the vascular system is very well developed. All the parts are well provided with capillaries. The blood is deep red and is without corpuscles. The presence of the segmental contractile loops of the ventral lateral blood-vessels, however, introduces a factor which greatly alters the nature of the circulatory processes. The loops not only enable an independent segmental circulation to be kept up in each segment, but also by sending a branch to the gill, which, after oxygenation returns the blood to the upper lateral vessel, make the blood in the dorsal vessels arterial, while it is venous in the ventral. The walls of the smaller blood-vessels are very thin and membranous, and as far as can be made out have no definite structure. No nuclei have been made out in their walls and the vessels are always filled with blood of a deep red colour.

The vascular system of *Eunice sanguinea* (*Marphysa sanguinea*) was worked out in a general way by Milne Edwards (1838). He noticed the two dorsal blood vessels and the single ventral blood-vessel, as also the loops of the ventral lateral blood vessels which he figures as mere bends in the lateral vessel. His figure shows the two dorsal vessels uniting in front about the 15th segment into a single vessel which is continued forwards in the form of a single dorsal vessel to the terminal portion of the body. He describes the vessel as being contractile. In regard to the median ventral vessel he does not go into details with reference to its fate at the anterior end. He makes a comparison between the circulatory system in *Terebella* and that in *Eunice* and points out that the branchiae in *Terebella* are both contractile and respiratory, while in *Eunice* the circulation is brought about by the contraction of the vascular loops to which also he attributes the capacity that mutilated portions of *Eunice* have of remaining alive some time after separation from the worm.

The central nervous system comprises the brain, the oesophageal commissures, the stomato-gastric system and the median ventral nerve cord (Fig. 37).

The brain has been studied in species of the allied genus *Eunice* by Grube (1838), Quatrefages (1844), Ehlers (1864-68), Pruvot (1885), Jourdan (1887), Racovitza (1896), and Heider (1925). Racovitza in his classical work on the Polychaete brain (encéphalon) distinguishes three regions—Cerveau antérieur, Cerveau moyen, Cerveau postérieur.

The terms may be rendered into the fore-brain, the mid-brain, and the hind-brain. Often these three parts are distinguished according to
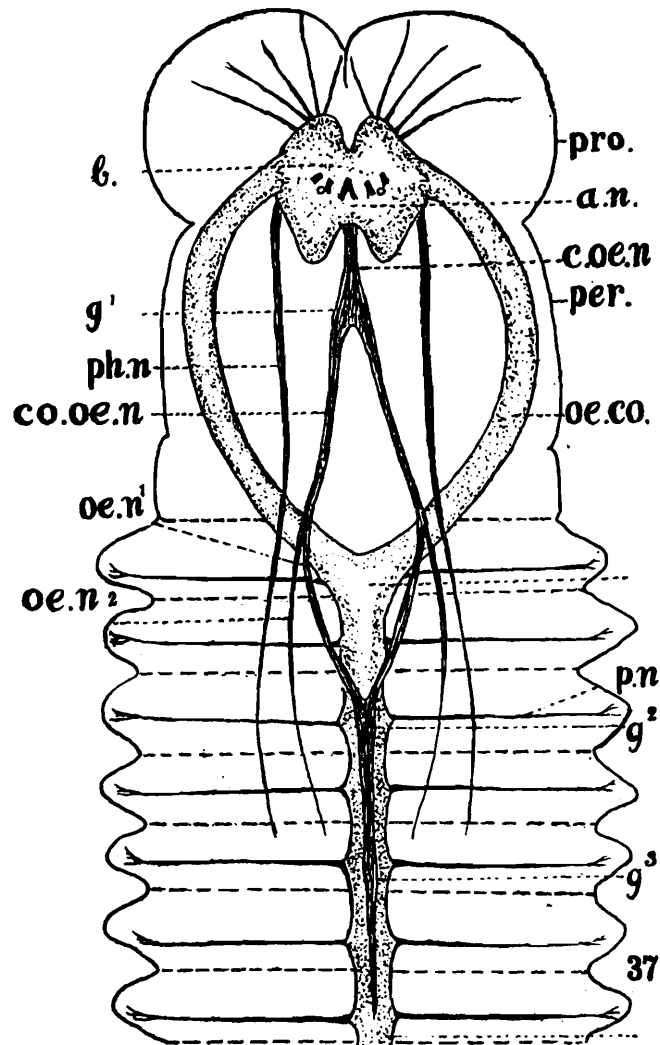

FIG. 37.—A diagram of the nervous system. *a. n.* Antennalnerve ; *b.* Brain ; *c.oe.n.* Common dorsal oesophageal nerve of the stomato-gastric nervous system ; *co.oe.n.* Commissural oesophageal nerve of the stomato-gastric nervous system ; $g.^1$ $g.^2$ and $g.^3$ Ganglia of the stomato-gastric nervous system ; *oe.co.* Oesophageal commissure ; *ce.n.[1]* Ventral oesophageal nerve branch of the stomato-gastric nervous system ; *oe.n.[2]* Dorsal nerve branch of the stomato-gastric nervous system ; *per.* Peristomium ; *ph.n.* Pharyngeal nerve of the stomato-gastric nervous system ; *p.n.* Podial nerve ; *pro.* Prostomium.
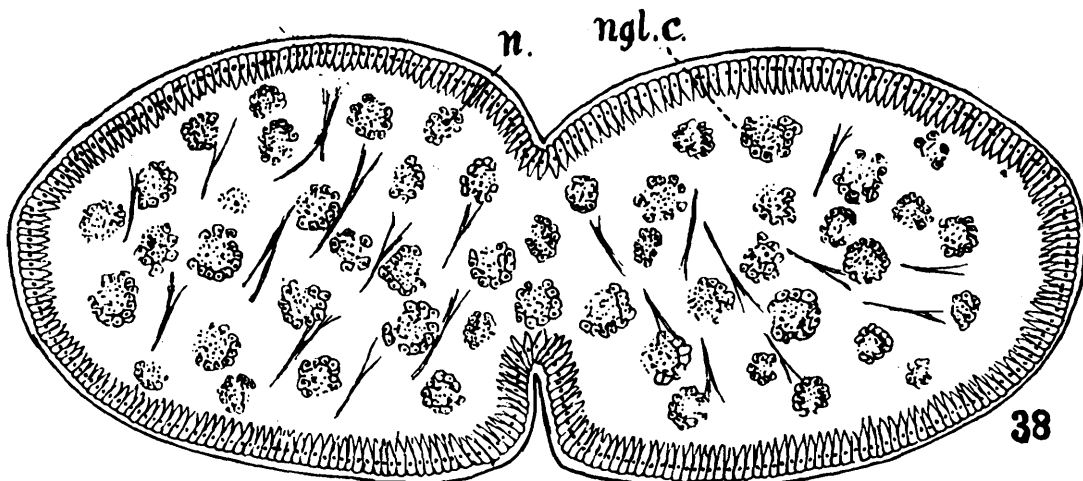

FIG. 38.—Transverse section through the prostomial lobes. *n.* Nerve ; *ngl.c.* Neuroglia cells.

their supposed functions as the taste ganglia, the tactile and optic ganglia and the olfactory ganglia. According to the polychaete plan

of brain the palp ganglia are associated with the anterior brain, the antennary and optic ganglia with the mid-brain and the nuchal ganglia with the posterior brain. In some polychaetes the ganglia mentioned
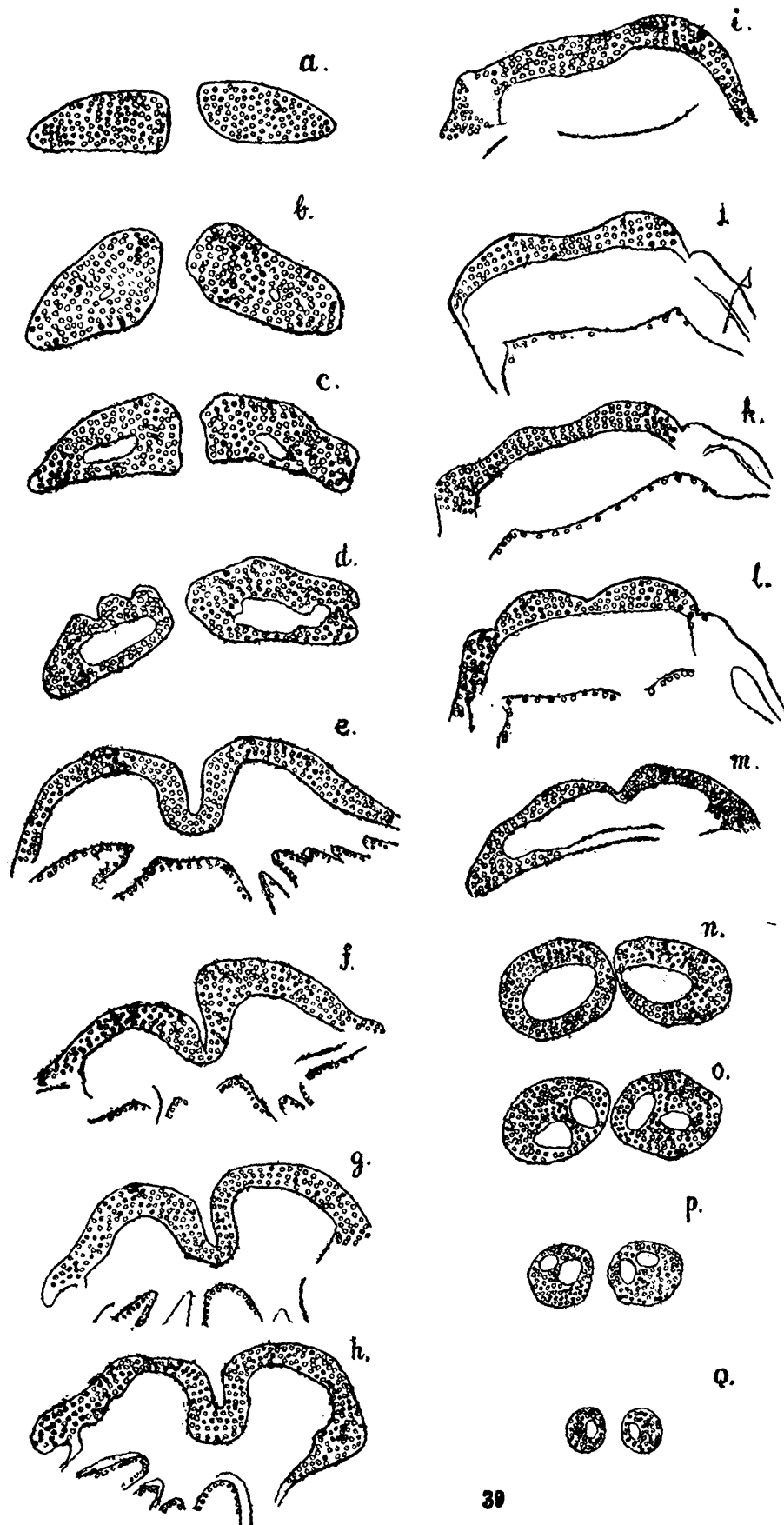

FIG. 39.—Diagram of a series of sections showing the relationship of the two halves of the brain and the arrangement of the ganglion cells of the brain. (Sections showing the origin of antennae are not included.)

are not fused but stand in close proximity, though more or less distinct.

In the present form the anterior and the middle moieties are distinct and well developed. The posterior part, however, is much less distinct and has undergone almost complete absorption into the middle part.

The brain measures but little more than half a millimetre in length even in large specimens and occupies the posterior part of the prosto-mium immediately below the hypodermis. Anteriorly the right and left portions of the front brain are quite separate and, in the space bet-ween the two portions, the fibrous and other non-nerve elements pass to become connected with the hypodermis. A little behind, the two halves unite, but are separated by a deep dorso-median groove. Further behind the groove gradually disappears until the mid-brain is reached. Posteriorly, there is again a separation of the right and left sides but it is not quite so pronounced as in the front region (Fig. 39).

The dorsal surface of the brain is more or less arched throughout, and lies close to the superficial skin. Ventrally the brain is flat and is limited by a membrane below which are the muscles. Heider (1925) describes the mid-brain of *Eunice punctata* (Risso) as being formed of two parts—an anterior mid-brain and a posterior mid-brain. I have not been able to observe this distinction externally in *Marphysa* but judging from the arrangement of the ganglion cells, it seems that such demarcation exists (Fig. 24).

Anterior brain.—The two horns of the anterior brain fill up the basal part of the prostomium. Numerous nerves are given off from the front of the brain. These consist of several very fine nerve fibrils having a wavy course. The bundles of fibrils composing the nerves are separated from one another by fibrous tracts and neuroglial tissue (Fig. 38, *ngl. c.*). The anterior brain also gives from its ventral side two pairs of nerves constituting the stomato-gastric system. The latter will be described under a special section.

The *mid-brain* constitutes the best developed and the broadest part of the brain. The front part is marked into right and left halves by a groove but in the posterior part the surface appears to be level.

The antennal nerves take their origin from the core of the brain substance and occupy the axis of the antennae in their course to the tips (Fig. 46). The lateral antennal nerves have their origin in the front part of the middle brain while the intermediate and median antennae have theirs in a more posterior position. Pruvot (1885) showed the origin of the median antennal nerve by means of two roots and suggest-ed that the median antenna has really been formed by the fusion of two antennae. Heider (1925) has recently observed that the nerves to all the antennae in *Eunice torquata* and *E. fasciata* arise by means of two roots. In the present form the nerves to the lateral and the intermediate antennae seem to arise by a single root only. The nerve supplying the middle antenna (Fig. 47) is composed of two bundles of nerve fibrillae at the base of the antenna but in the antenna itself they unite completely.

The eyes, when present, have a position just external to the origin of the nerves passing to the intermediate antennae. They are sub-

epidermal and are pressed against the brain mass. No special optic nerves or lobes are observed to be present.

The oesophageal commissures have their origin from the inner core of the broadest part of the mid-brain. They curve outwards and downwards to the first setigerous segment, and unite together to form the first pair of ganglia of the ventral chain. They have a covering of ganglion cells at the base but as the commissures reach the ventral side very few ganglion cells are noticed.

Pruvot (1885) and Heider (1925) state that each one of the commissures in *Eunice torquata* arises by two roots. Heider further states that one of these roots arises from the anterior brain and the other from the mid-brain. In the present form also the commissures arise by two roots (Fig. 40) which are very short and unite into a single nerve before they are well out of the rind of the ganglionic cells of the brain. There are no indications of branches being given off from the commissures. Quatrefages does not describe any in *Eunice sanguinea.*

. *Histology of the brain.*—The brain is covered dorsally by the hypodermis and the cells forming it are of three kinds (Fig. 16). Ordinary columnar cells, gland cells with moderately elongated nuclei and granular contents, and thirdly slender sensory cells whose bases seem to be embedded in the substance of the brain. There are no cells of any kind between the lower surface of the hypodermis and the brain. On the dorsal surface the association between the brain and the hypodermis seems to be intimate but on the ventral side it seems to be less so.

Below the brain there is a strong membrane, and still further below there are masses of muscle tissue richly supplied with blood vessels lying between the membrane and the hypodermis.

The outer portion of the brain (Fig. 47 *nu. l.*) is formed by a complete layer of ganglion cells. This layer is best developed on the dorsal surface and at the sides. Ventrally the layer is thin and in some parts even absent. The nuclei are round and fill up almost completely the entire cell area, there being only a thin pellicle of protoplasm. There is a distinct nuclear membrane. They are best stained with iron haematoxylin or Mann's methyl-blue eosin.

A transverse section of the brain through the anterior region shows these ganglion cells crowded together in the dorso median line, less so on the sides and still less on the ventral side. A section passing through the posterior part of the anterior brain shows a different state of things. The right and the left halves of the brain, as has been stated above, are separated by a deep median groove. The ganglion cells are well developed dorsally. The two halves are connected by a bridge of feltlike substance to be described presently. In between the ganglion cells minute fibrils could be seen to run into the internal substance of the brain. What relationship these fibrils bear to the ganglion cells on the one hand and to the felt like substance on the other is a problem which has not been satisfactorily solved. Jourdan (1887) says that in *Eunice* these ganglion cells are provided with 2 fibrils Unfortunately my preparations do not show the existence of these fibrils There is a certain amount of uncertainty in regard to the nature of the cells constituting the so-called nuclear layer. The most important

characteristic of the ganglion cells is the greatly reduced protoplasmic covering and for this reason they have been regarded by Jourdan as primitive ectodermal cells which have had an arrested development.

In addition to these cells, there are other ganglion cells which, by reason of their size, should be called giant ganglion cells. They are less numerous and have a restricted distribution. They are entirely confined to certain parts of the dorsal surface of the brain, and are absent in sections passing through the anterior part of the brain. These cells are 4-6 times the size of ordinary ganglion cells of the nuclear layer. They are spherical or pear shaped (Fig. 47 *g.g.c.*) with a large nucleus and a distinct nuclear membrane. The cytoplasm is massive and seems to be produced on one side into a blunt protoplasmic process. It is difficult to trace the ultimate fate of these protoplasmic processes : probably they get inextricably lost in the middle of the fibrils amongst which the ordinary ganglion cells lie.

The punctated substance (*p. s.*) forms the inner core of the brain. It does not stain readily. In transverse sections it appears to be finely granular and interspaced with minute fibrils. In longitudinal sections of the brain it is seen to be composed of extremely fine fibrils forming a felt work. These fibrils have a wavy course and are of uniform thickness throughout. Nuclei have not been noticed. All the nerves arise from this inner core of the brain.
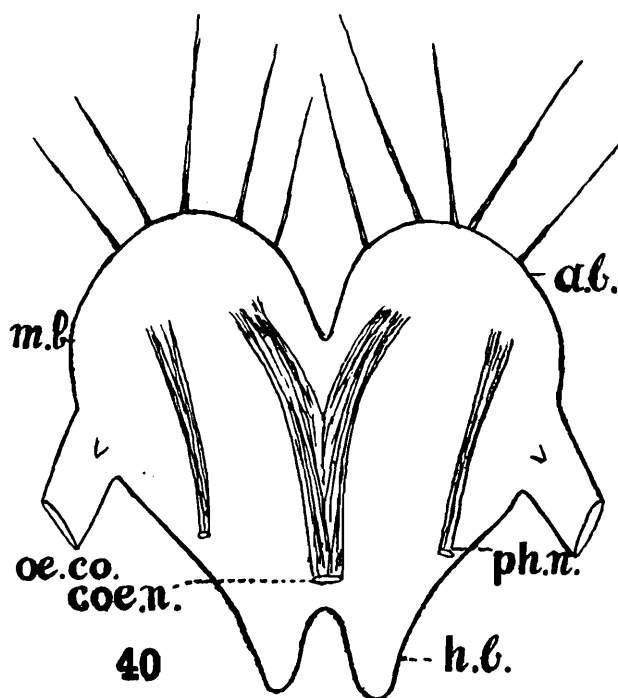

Fig. 40.—Diagram of the ventral view of the brain. *ab.* Anterior brain ; *c.oe.n.* Common dorsal oesophageal nerve of the stomato-gastric nervous system ; *h.b.* Hind brain ; *m.b.* Middle brain ; *oe.co.* Oesophageal commissure ; *ph.n.* Pharyngeal nerve of the stomato-gastric nervous system.

The stomato-gastric system.—Grube (1838) was probably the first to point out the existence of a stomatogastric system in *Eunice*. Ehlers (1864-68), Quatrefages (1844), Pruvot (1885) and Heider (1925) have described it in certain genera of Eunicidae. The description given by the last mentioned author for *Eunice fasciata* and *E. punctata* seems to be the most complete.

The following is based on dissections under the binocular and on serial sections. There are four nerve strands constituting this system (Figs. 37 and 40). All of them arise from the punctated substance of the brain and emerge at the same level from the ventral side of the anterior brain. Quatrefages distinguishes the inner two as the supra-oesophageal and the outer as the sub-oesophageal strands. They have also been referred to simply as the oesophageal and pharyngeal strands of the stomato-gastric system. The oesophageal strands, at their origin and throughout their course, are stouter than the pharyngeal nerves. They arise slightly apart, turn sharply backwards converging towards each other, and fuse into a stout median cord running a little below the brain (Figs. 21, 37 and 40, *c.oe.n.*). Some distance behind, this cord swells out into a ganglion with a covering of ganglion cells very similar to those of the nuclear layer of the brain (Figs. 25, 37, g^1). From this ganglion, the supra-oesophageal ganglion of the stomato-gastric nervous system, two strong nerves invested by ganglion cells are given off behind (Fig. 37, *co.oe.n.*). They run on either side of the dorso median line of the gullet (Fig. 22, *co.oe.n.*). In the posterior part of the peristomial segment they lie just external to the dorsolateral cushion like thickenings of the gullet. Gradually the two nerves pass to the ventral side, and on reaching a point just above the level of the sub-oesophageal ganglia of the ventral chain (1st setigerous segment) each gives off a slender branch (Fig. 37, $oe.n^2$) which is continued backwards, gradually taking up a position dorsal to the gullet. The two main strands, however, continue their downward course until they meet below the gullet in the third setigerous segment and fuse together into a ganglion (g^2), the infra oesophageal ganglion of the stomato-gastric system. This ganglion is continued as a median strand between the gullet and the dentral pouch until the 5th setigerous segment is reached where the ganglion (g^3) is formed. In the following few segments the ganglion is continued as a mere strand of nerve.

The pharyngeal strands already mentioned, also take their origin from the ventral surface of the anterior brain (Figs. 37 and 40, *ph.n.*). At first they run on the inner side of the dorsal groove on the side of the roof of the mouth (Fig, 20, *ph.n.*). Later on they pass external to the grooves and after a short course are completely lost in the muscles of the dental pouch. No branches are seen to be given off. No ganglion cells have been noticed in relation to them and they are probably motor in function.

The *ventral nerve cord* is formed, as in all Polychaetes, by the oeso-phageal commissures meeting below the gullet to form a ganglionated nerve chain. The two nerve strands are completely fused together and distinction between them has been lost. The nerve cord thus formed is slightly swollen to form a ganglion in each segment. Unlike the brain which has the epidermis in close relation to its dorsal side, the nerve cord in the present form has totally lost its connection with the ectoderm, and lies internal to the circular layer of muscles and between the two ventral bands of longitudinal muscles. In cross section it appears to be almost rectangular in the extreme anterior end, and triangular in the middle and the posterior parts of the body.

The ventral nerve cord consists of an outer sheath the neuril-
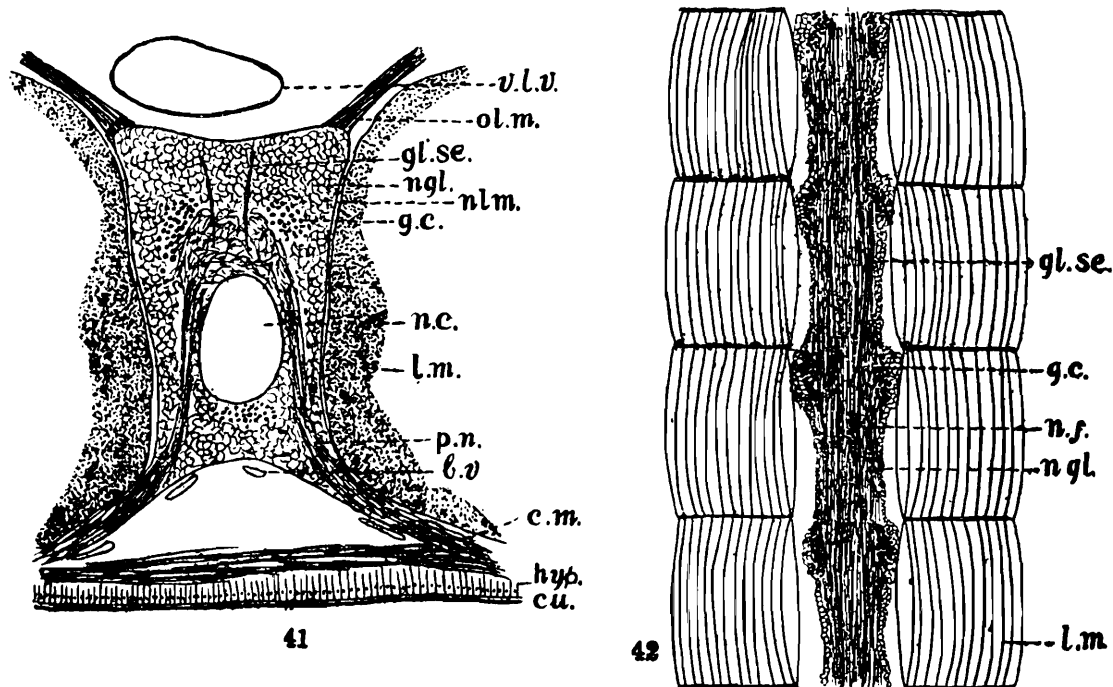emma (nlm.) and an inner layer of translucent cells, the neuroglial layer

FIG. 4J.—A transverse section of the ventral nerve cord. *b.v.* Blood vessel; *c.m.*
Circular muscles; *cu.* Cuticle; *g.c.* Ganglion cell; *gl.se.* Glia septum; *hyp.* Hypo-
dermis; *l.m.* Longitudinal muscles; *n.c.* Neural canal; *ngl.* Neuroglia; *nlm.* Neu-
rilemma; *ob.m.* Oblique muscles; *p.n.* Podial nerve; *v.l.v.* Ventral longitudinal
blood vessel.

FIG. 42.—A horizontal section of the nerve cord. *g.c.* Ganglion cell; *gl.se.* Glia septum;
l.m. Longitudinal muscles; *n.f.* Nerve fibrillae; *ngl.* Neuroglia.

(*ngl.* Fig. 41). Below this there are small distinctly nucleated cells
with very little of protoplasm. These cells are the ordinary ganglion
cells and are similar to those of the nuclear layer of the brain.
Forming the inner core of the cord, there is the punctated substance
formed of very minute wavy fibrils, as in the brain. The inner core is
split vertically by two septa (*gl. se*) —the glia septa—so that it appears
to be composed of three strands. In the posterior segments, sometimes
three glia septa could be seen so that there then appears to be four strands
in all; but this is unusual. Pruvot (1885) mentions the occurrence of
a pigment sheath for the nerve cord in *Eunice torquata* and Ehlers (1864-
68) describes a similar sheath in *E. harassii*. No pigment sheath is
present in *M. gravelyi*. The ganglion cells of the nerve cord lie in
three groups in the ganglionic enlargements and are practically absent
in the interganglionic portions. Two of these groups are dorso-lateral
and the third ventro-median (Fig. 41). Giant ganglion cells are not
present in any part of the nerve cord. Below the central axis formed
by the punctated substance is a median canal. *In Eunice fasciata* and
E. torquata (Heider 1925) a similar canal has been described as a
colossal nerve fibre; but Jourdan (1887) did not consider it as such.
Similar so-called nerve fibres have been described in other Polychaetes
also, but in some they have been referred to as a mere canal. From
the fact that in *Marphysa gravelyi* it exhibits no structure, and does
not take stain, it seems to be of the same category. It varies slightly
in position in different parts of the nerve cord. It may be central or

more ventral, may be round or triangular in vertical cross section, or altogether absent as in the extreme posterior end of the body. Probably in the living animal the canal is filled with a semifluid substance of a colloidal nature which after fixation and subsequent treatment is found to form an irregular strand connected at some points with the wall of the canal by delicate threads of the same substance.

A pair of podial nerves (*p.n.*) arise from the lateral strands of each ganglionic enlargement of the punctated substance. Ehlers (1864-68) describes three pairs of podial nerves in *E. harassii.* Quatrefages (1844) describes and figures five pairs in *Marphysa sanguinea.* Pruvot (1885) and Heider (1925) mention the occurrence of a single nerve only in *Eunice torquata.* In *M. gravelyi* there is only a single pair of podial nerves in each segment. Each nerve runs downwards and outwards to the space between the longitudinal and circular muscles and at the base of the parapodium branches into two or three minute nerves supplying the parapodium. It has not been possible to make out the 'ganglion de renforcement' of French authors—from which nerves are supposed to be given off. Preparations of the nerve by Bielchowsky's methods show that the branches run externally to the longitudinal muscles giving off numerous fine branches in their course.
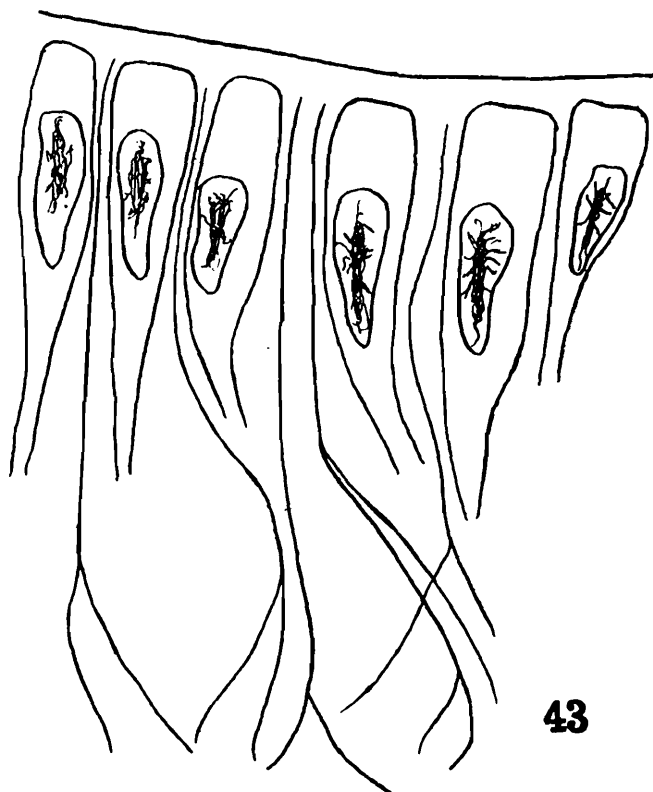

Fɪɢ. 43.—Hypodermal cells ; the nerve endings are shown as emanating from a network.

There seems to be a network of very minute nerve fibrils just below the epidermis (Fig. 43). Smallwood (1926-27) in his paper on the peripheral nervous system of *Lumbricus terrestris* describes the existence of a network of fibrils below the hypodermis. He has demonstrated in that form the occurrence of a connection between the basal ends of the sensory cells of the hypodermis and the subepithelial network. I have been able to observe what appears to correspond to the network mentioned by him, but not the connection with the sensory cells or the two kinds of nerve fibrils which he describes.

The sense organs are the prostomium, the antennae, the frill like folds already mentioned as occurring on the undersurface of the prostomium, the eyes, the dorsal and the ventral cirri, and the anal cirri.

As stated above some of the hypodermal cells on the prostomial lobes, especially on the dorsal side are elongated and have their slender inner ends continued, in some parts, as far as the ganglion cells of the nuclear layer of the brain. In front, where the cells are separated from the brain by a greater space, the inner ends of the cells are connected with fine nerve fibrils which emanate from the brain The greatly elongated cells covering portions of the lateral folds at the entrance into the mouth have their bases also extended. These cells are all no doubt sensory in function.

Eyes are formed in the early stages of development of the worm: In the metatrochal stage there is a pair of larval eyes of darkish brown colour on the prostomium. They undergo gradual reduction as the larva grows and additional segments are added. When the tiny worms are provided with 13-14 pairs of parapodia the larval eyes almost disappear, and the adult pair of eyes commence to form just external to the point at which the intermediate tentacles appear some time later.
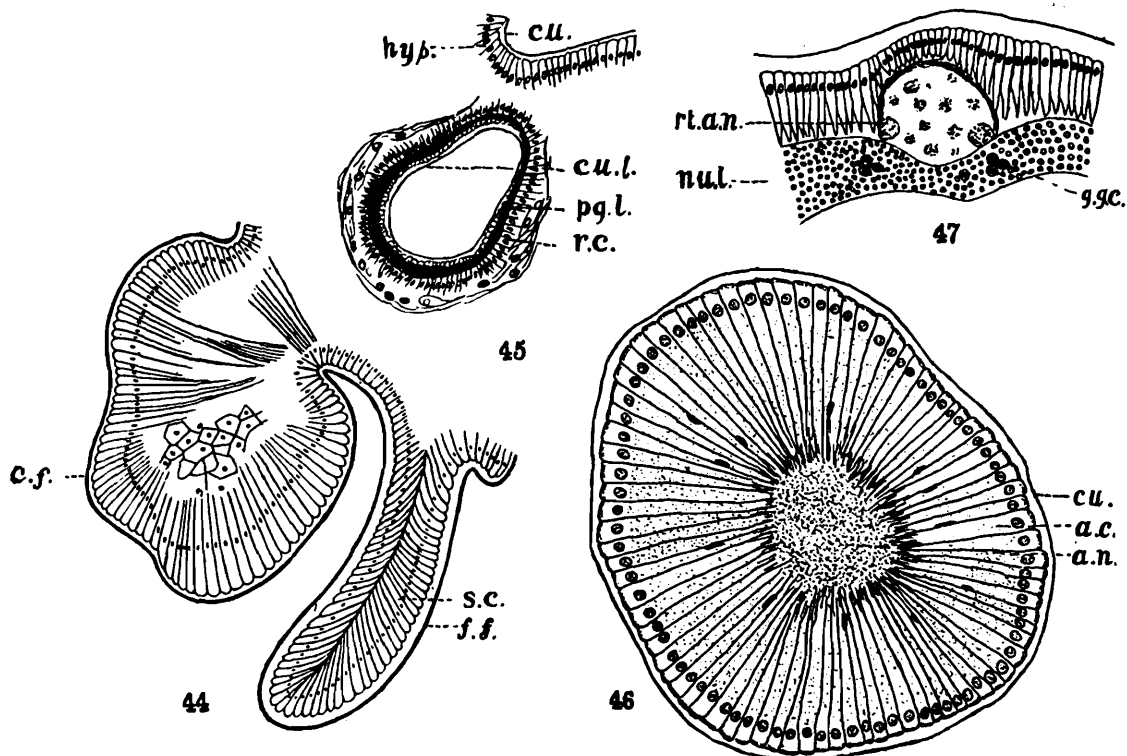

FIG. 44.—Section through the cushion and the frill like folds on either side of the roof of the mouth, showing the highly elongated cells. *c.f.* Cushion like fold; *f.f.* Frill like fold; *s.c.* Sense cell.

FIG. 45.—Section of the eye. *cu.* Cuticle; *cu.l.* Cuticular lens; *hyp.* Hypodermis; *pg.l.* Pigment layer; *r.c.* Retinal cells.

FIG. 46.—Transverse section of an antenna showing the axial position of the antennal nerve cord and the greatly elongated antenna cells. *a.c.* Antennal cells; *a.n.* Antennal nerve; *cu.* Cuticle.

FIG. 47.—Section showing the double origin of the median antennal nerve, at its very commencement. *g.g.c.* Giant ganglion cell; *nu.l.* Nuclear layer; *rt.a.n.* Root of nerve to antenna.

At this stage the worm is provided with two pairs of eyes, the anterior pair being very greatly reduced prior to their final disappearance, and

the posterior pair developing quickly and remaining functional longer. As the worm develops its cryptic habits these also degenerate and become subepidermal lying pressed against the ganglion cells of the mid-brain. The eye is almost spherical in shape with a cavity filled by a cuticular lens (Fig. 45). The wall of the eye has a single layer of elongated cells with oval nuclei occupying their inner half. There is a layer of intense black pigment near the base of the cells. Degeneration may even proceed further, and in very large worms the eyes seem to be completely absent.

There are five antennae which arise directly from the brain. It may be inferred from this fact that they are sensory organs of primary importance. In transverse and longitudinal sections of material fixed by 0-5 osmic or 2 per cent. ammonium bichromate the structure of the antenna can be made out easily. The antennal nerve which runs along the axis consists of a large number of fibrils of a wavy nature and does not fill the entire inside of the antenna (Fig. 24. *a.n.*). The cells of the antennal wall are greatly elongated with their inner ends so slender that they seem to be in close connection with the nerve fibrils. Except at the base of the antenna there are no muscle fibres in the wall.
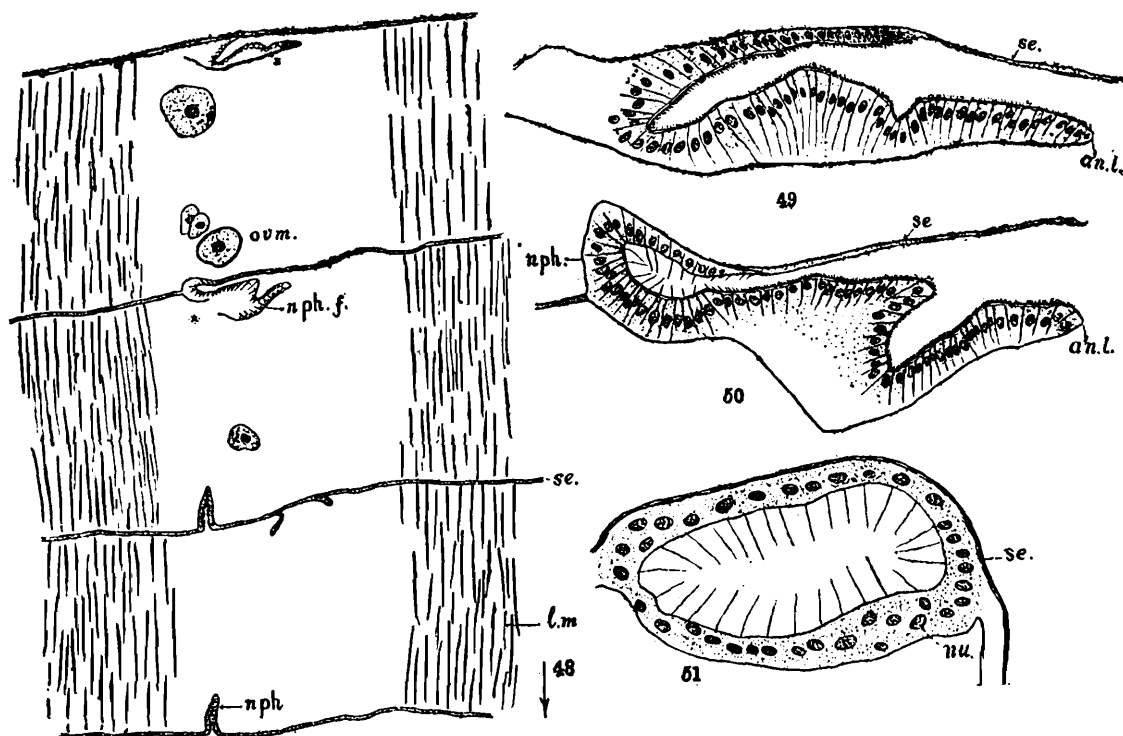

Fig. 48.—Longitudinal vertical section of segments from the middle region of a female worm to show position and origin of nephridia ; *l.m.* Longitudinal muscles ; *nph.* Nephridium ; *nph.l.* Nephridial funnel ; *ovm.* Ovum ; *se.* Septum.

Fig. 49.—Section through the nephridial funnel. *an.l.* Anterior lip ; *se.* Septum.

Fig. 50.—Section through the funnel and the commencement of the nephridium at the mark* in fig. 48. *an.l.* Anterior lip. *nph.* Nephridium ; *se.* Septum.

Fig. 51.—Transverse section passing through the conducting part of the nephridium. *nu.* Nucleus ; *se.* Septum.

Quatrefages (1865) mentions the occurrence of an otocyst in *Marphysa sanguinea.* This was shown to be a misapprehension by Fauvel (1907), who observed that the otocyst was generally absent in the Eunicidae. There is no trace of an otocyst in *M. gravelyi.*

Nephridia.—Goodrich (1900) states that nephridia with large coelo·
mic funnels occur in the Eunicids. In *M. gravelyi* they occur in all
segments except a few of the anterior segments and lie close to the
posterior face of the anterior septum in each segment. They do not
project into the coelomic space but have a more or less straight course
to the base of the parapodium. Each nephridium is wide at its inner
end and pierces the septum in front at a level with the pigment gland
of its side, but does not project very much into the next segment.
The funnel is ciliated, and is close to the anterior side of the septum.
One side of the funnel is closely pressed against the septum while the
opposite is free with its lip projecting well beyond the level of the
posterior lip (Figs. 48, 49, and 50).

The walls of the nephrodium are formed of delicate, rather ill defined
cells, full of minute granules and with moderately large nuclei (Fig. 51).
The conducting part of the nephridium is a well defined but narrow ciliat-
ed tube which passes along the inner margin of the ventral longitudinal
muscles, and turning round its outer border, pierces the circular
muscles, which are but slightly developed in this part (Fig. 52). It
finally opens on the lower side of the ventral cirrus, slightly in front.

Cosmovice (1879) observed the funnel of the nephridium of *Marphysa
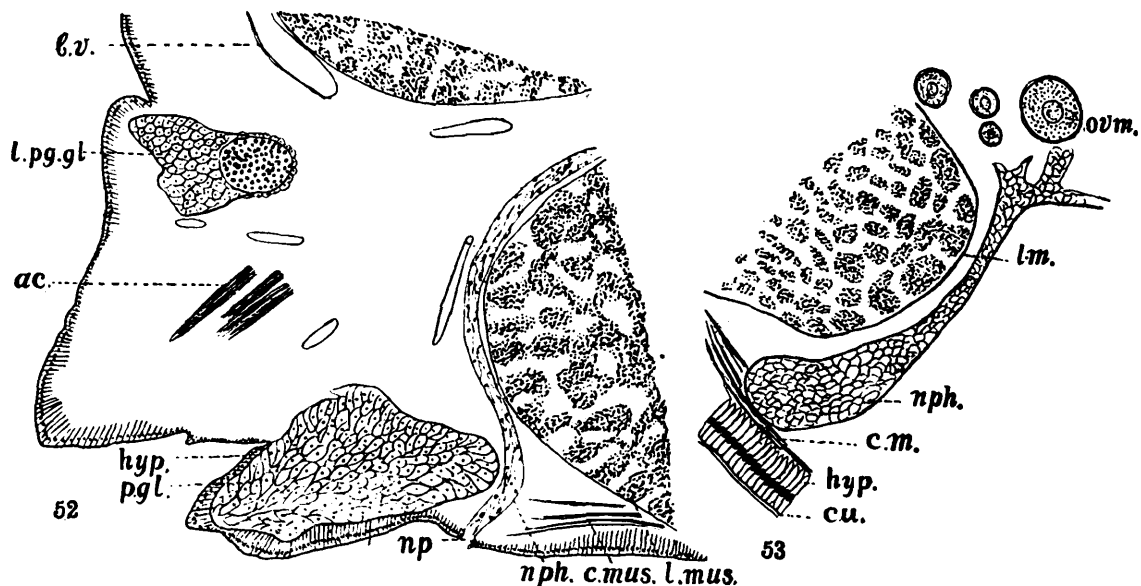sanguinea* but the external opening escaped his notice.

Fig. 52.—Section of the outer part of the parapodium showing position of pigment
gland, parapodial gland and nephridium. *Ac.* Acioulum; *b.v.* Blood vessel;
hyp. Hypodermis; *l.pg.gl.* Lateral pigment gland; *n.p.* Nephridiopore; *nph.*
Nephridium; *p.gl.* Parapodial gland.

Fig. 53.—The outer half of an enlarged nephridium of a fully mature female worm.
c.m. Circular muscles; *cu.* Cuticle; *hyp.* Hypodermis; *l.m.* Longitudinal muscles;
nph. Nephridium; *ovm.* Ovum.

The reproductive organs take the form of proliferations of the coelo-
mic epithelium covering the blood vessels and the septa. The sexual
elements are absent in the anterior one-third part of the body and in
several segments at the posterior end. Ripe sexual elements have not
been observed in worms of less than 150 segments. In fully ripe indivi-
duals with 400-750 segments the sexual products are confined roughly
to the middle one-third of the body. This localisation of sexual ele
ments is known to occur in other Eunicids also (Fage, 1927). In *Eunic*

harassii about thirty of the anterior and thirty of the posterior segments are stated to be devoid of sexual elements. A similar condition is said to prevail in *E. vittata*. In *Lysidice ninetta* sexual elements have been noticed after the 25th segment, in *Nematonereis unicornis* after the 62nd, and in *Lumbriconereis latreillei* the first 80 and the last 34 segments in the female have been found without sexual products. It seems therefore that the restriction of genital cells to the middle region of the worm is a characteristic of Eunicids in general.
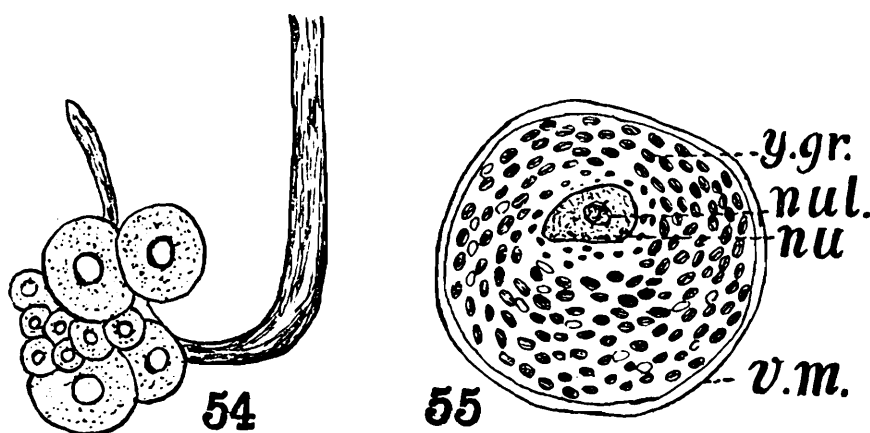

Fig. 54.—A blood vessel carrying eggs.

Fig. 55.—A ripe ovum.   *nu.* Nucleus ; *nul.* Nucleolus ; *v.m.* Vitelline   membrane;   *y.gr.* Yolk granules.

In the present form the sexual region is recognised by its tense inflated appearance, and in the ripe females the eggs can be seen shining through the body wall. Difference in colouration between the sexes has been observed in a few forms as in the Atlantic Palolo, *Eunice viridis*. In sexually ripe individuals of *M. gravelyi* the gills have a markedly vivid scarlet colour, but are otherwise of no value in differentiating the sexes. The body of the ripe male is whitish in colour while that of the female is pinkish owing to the colour of the eggs inside.

The ova are developed from the coelomic epithelium covering the finer blood vessels on the posterior face of the anterior septa of the middle segments. When shed they float freely in the coelomic cavity. Roughly speaking the young ova are found attached to the blood vessels in the course of the nephridia. They have fairly clear protoplasm of homogeneous appearance. As they grow, they are filled with yolk granules of varying size. The nucleus of the fully ripe ovum is vesicular and a distinct nucleolus is present. There is a moderately thick but smooth vitelline membrane. The larger yolk granules are situated in the outer portions of the cytoplasmic area. The granules in the immature ova stain more deeply than in the fully mature eggs.

In the male the minute blood vessels of the dorsal lateral vessel in each segment give rise to nodulor proliferations (Fig. 56). These give rise to the spermatogonia which at a very early stage are detached from the coelomic epithelium and undergo the rest of the development while floating in the coelomic fluid. No acrosome could be made out in the

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ripe sperm (Fig. 58). The wedge shaped piece which stains very deeply>
is the head. At its hind are two minute swellings with a notch
between from which a long extraordinarily fine flagellum has its
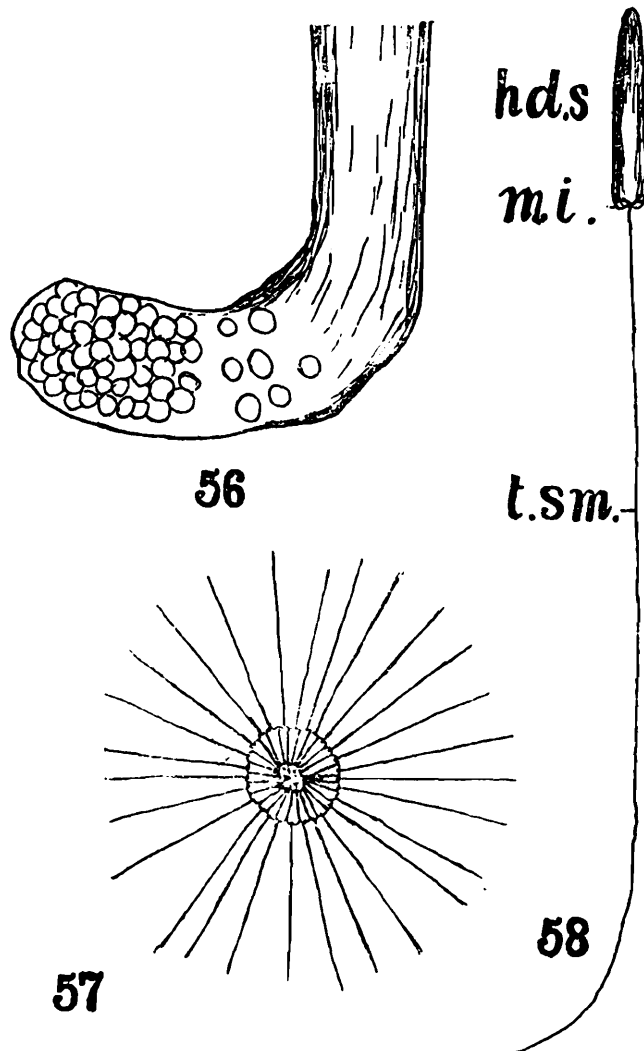origin. The swellings probably constitute the middle piece.

Fig. 56.—A blood vessel from a male worm showing origin of spermatogonia.
Fig. 57.—A cluster of almost ripe sperms.
Fig. 58.—A fully ripe sperm. *hd.s.* Head of sperm ; *m.i.* Middle piece ; *t.sm.* Tail
of sperm.

The ripe sperms are found to pass even in between the muscles to
the space between the muscles and the richly vascular skin. They often
fill up the bases of the parapodia penetrating to the base of the dorsal
cirrus. In fact, they are found so near the dorsal surface in fully ripe
individuals that the smallest puncture of the skin lets the male product
ooze out in a thin milky stream. Often they are found in regular aggre-
gations along the course of the dorsal blood vessels.

The fully mature condition of the sexes is accompanied by certain
structural changes which are highly interesting. With the reduction
in thickness of the longitudinal bands of muscles, the coelomic space
increases and this is in marked contrast to the muscles of the anterior
segments in which no such reduction takes place (Fig. 60). Fage
(1927) mentions the occurrence in certain Eunicids of degeneration of
longitudinal muscles accompanied by deposition of pigment. The
dorsal blood vessels in the region of the longitudinal muscles (Fig. 59.

d.l.v.) are very much swollen. The sexual elements pass to the out-
side by the nephridia. This is no doubt easy in the case of sperms, but
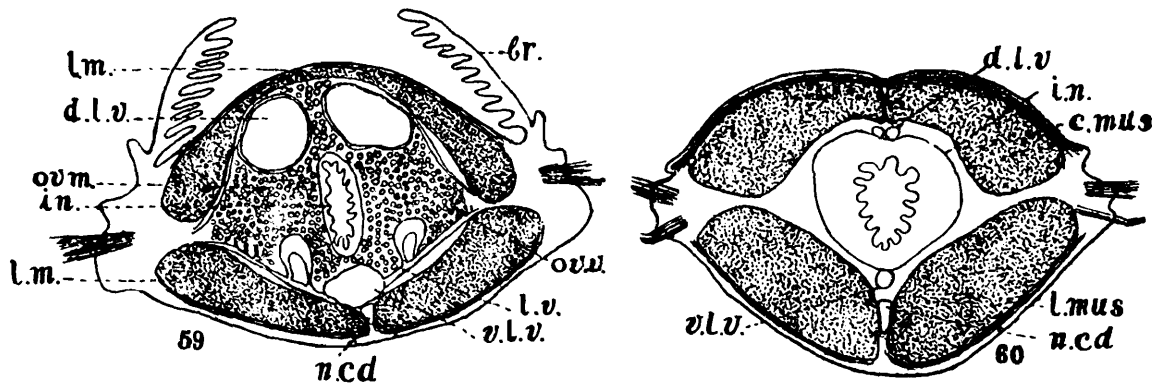

Fig. 59.—Transverse section through the sexual region of a female worm showing en-
largement of blood vessels and reduction of longitudinal muscles. *br.* Gill ; *d.l.v.*
Dorsal longitudinal vessels ; *in.* Intestine ; *l.m.* Longitudinal muscles ; *l.v.* Lateral
vessel ; *n.cd.* Nerve cord ; *ovm.* Ovum ; *ov.v.* Egg bearing blood vessel ; *v.l.v.*
Ventral longitudinal blood vessel.

Fig. 60.—Transverse section passing through the anterior non-sexual part of the same
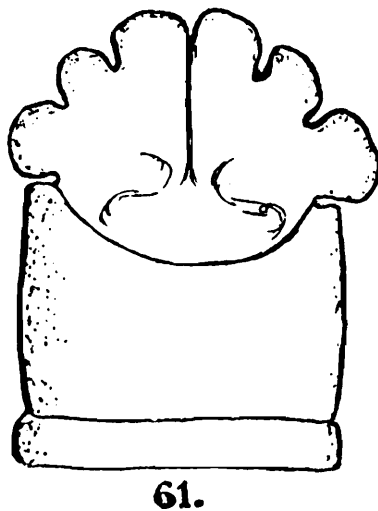worm where no enlargement of blood vessel and reduction of muscles take place.

61.

Fig. 61.—Diagram of worm with regenerated prostomial lobes.

the ova which are comparatively large cannot find their way out through
the nephridia, unless the diameter of the nephridial canal increases.
A comparison of nephridia of unripe individuals with the nephridia of
mature animals from the sexual segments reveals the fact that the
nephridial passage actually increases in diameter as the individuals
mature, enabling the eggs to pass through them to the outside (Fig.
53). Ova have been often noticed half way down the nephridial passage.
Even then it is not easy to explain why the fully developed ova always
accumulate in small groups along the course of the dorsal blood vessels
in the sexual region of the worm. Liberation of eggs has been known
to occur by rupture of the body wall in several Polychaetes but it is
not certain whether a similar phenomenon occurs in *M. gravelyi.*

Regeneration has been observed in *M. gravelyi.* The gills, anal
cirri, and the tail region are the parts of the body which are most easily
damaged. All these structures are soon regenerated. The regenerated

parts often differ from the lost ones in size as in the case of the gills, in the branching as in the case of the anal cirri, and in the largèr number of segments as in the hind part of the body. In one specimen the prostomial lobes had evidently been regenerated but these were found to be abnormal in that each lobe was found to be subdivided (Fig. 61).

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