The Anatomy of Pœcilochætus, Claparède.

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With Plates 7—12 and one Figure in the Text.

Contents.

Historical.

Claparède, in his 'Beobachtungen über Anatomie und Entwicklungsgeschichte wirbelloser Thiere an der Küste von Normandie Angestellt,' published in 1863, describes and figures (pp. 77—80, Taf. vi, figs. 1—11) several stages in the development of an annelid larva, which he was unable at the time to assign to any known genus. This larva was very common in the plankton at St. Vaast, and the same, or a very similar one, had previously been found (in 1855) by Claparède on the coast of Norway. He surmised that the larva must belong to some common worm at that time still undescribed.

No further advance seems to have been made in the knowledge of this form until the appearance in 1874 of a report by Claparède on the annelids collected by the "Lightning" Expedition. This report is contained in Ehler's paper, "Beiträge zur Kenntniss der Verticalverbreitung der Borstenwürmer in Meere" (Ehlers, 1874). Amongst the material collected by the "Lightning," Claparède found a number of fragments of a worm, which he considered must be the adult form of the larva he had previously described. He states that the species is represented in the "Lightning" material "par un fragment dans les préparations Nr. 15 et Nr. 24, et par tous les fragments inclus dans la préparation Nr. 22." The localities from which these specimens were obtained are not mentioned. In the same paper Ehlers refers to two fragments of the worm described by Claparède, which he found amongst the material dredged by the "Porcupine." According to the table given (loc. cit., p. 25), these were dredged on July 21st, 1869, at 48° 51′ N., 11° 7′ W. (11° 9′ W.) in 725 fathoms, on a bottom of muddy sand.

From the fragments at his disposal Claparède was able to give a fair account of the general external features of the worm, and to convince himself that it was the adult form of the larva which he had previously described, or at any rate closely allied to the adult of that larva. He gives to the worm the name Pœcilochætus fulgoris, both the generic and the specific name being new. He was still unable to include it in any known family, and thought it not improbable that a special family would have to be made to receive it. Figures are given (loc. cit., Taf. i, fig. 1, A, B, C, and D) of the head end from the dorsal and ventral surfaces, of several chætæ, of a parapodium, and of the external opening of one of the epithelial glands, the latter being described as "petits tubercules granuleux."

Levinsen (1883, p. 106) gives some further details of the structure of late larval stages of Pœcilochætus from observations upon specimens which had been taken by the "Hauch" Expedition in the Skager Rack. He also discusses the relations of Pœcilochætus with Disoma multisetosum, Oersted, and points out that the two genera are closely allied. He places both genera in the family Spionidæ.

McIntosh (1894) furnishes some notes, accompanied by four figures, on the larva described by Claparède. He considers that the first notice of this larva is due to Maximillian Müller (1852), but reference to Müller's paper has not convinced me that the tail end of a larva which he figures is really the same as Claparède's larva.

McIntosh makes no mention of Claparède's discovery of the adult Pœcilochætus, nor of Levinsen's discussion of the subject. He states that the larva occurs in considerable numbers in the bottom-nets at St. Andrews from July to October. McIntosh gives a figure of an advanced larval stage, showing the two palps well developed.

Mesnil (1897), in his monograph on the Spionidæ, discusses the position of Pœcilochætus in relation to that family. He proposes to place it with Disoma in a new family, the Disomidæ (see further, p. 140).

Occurrence at Plymouth.

The larva of Pœcilochætus has been constantly and regularly taken for many years in the plankton collected at Plymouth during the summer months, though I believe no record of the fact has ever been published. The larva is probably frequent in plankton taken all round our coasts, and its appearance will be well known to workers, as it renders itself conspicuous by its rapid, wriggling motion and by the row of pigment spots (large branching chromatophores) between the parapodial cirri along each side of the body.

On April 10th, 1902, the Laboratory fisherman brought in two specimens of a worm which he recognised as unfamiliar. These specimens he had obtained when digging on a patch of sand exposed at low spring tide immediately south of the coastguard station at Mount Batten, on the eastern side of Plymouth Sound. The worm has proved to be the adult Pœcilochætus, which forms the subject of the present paper.

Since that time I have always been able to obtain a few specimens whenever the tide has allowed of digging on this particular patch of sand. Unfortunately the sand is only uncovered at the lowest spring tides, and it is only on comparatively few days during the year that the worm can be obtained. During the hour, or hour and a half, that the sand may be uncovered at any tide from six to eight head ends of the worm have been collected. As the animals break very readily when disturbed, complete specimens are difficult to procure, and only two such have as yet been obtained. The local area of distribution of Pœcilochætus is very restricted. The portion of shore where it is known to live consists of patches of sand covered with zostera, with intermediate patches of a somewhat different texture on which no zostera grows. The worm appears to live only in these intermediate patches, and never in the zostera beds. It has never yet been obtained from any other locality in the Plymouth district.

I propose for the species of Pœcilochætus found at Plymouth and described in this paper, the name Pæcilochætus serpens, the specific name being selected to indicate the rapid, wriggling movement both of the larva and of the adult worm when swimming.

Habits.

Pœcilochætus serpens constructs U-shaped tubes in fine sand. These tubes are lined with a stiff layer of fine particles of mud or clay held together with mucus. The worm in its tube is shown in fig. 12 (Pl. 9). This drawing, of natural size, was made from a tube which had been constructed by a worm in a glass cell formed of two glass plates lying about $\frac{1}{16}$ inch apart and partially filled with sand. The process of burrowing was carefully watched, and the animal remained under observation in its tube for some hours. The burrowing was accomplished with the head end of the worm, more particularly with the forwardly directed parapodial cirri of the first segment and the long bristles belonging to it. During the process the anterior part of the body was constantly waved to and fro in a transverse direction. The burrowing movement was persisted in until the complete U-shaped tube had been formed.

When at rest the animal lies in its tube either with the two long palps extended in front, the ends being often protruded for some distance beyond the opening of the tube, or with the palps lying in a number of loose coils immediately in front of the head. A constant current of water, drawing small particles with it, is kept up through the tube by means of an undulatory movement of the body and of a fan-like movement of the parapodia and bristles. The movement of the numerous feather-like bristles in the posterior part of the body (Pl. 9, fig. 10) plays an important part in the production of the current that enters the tube at the end towards which the head of the worm is directed, and passes backwards over the body. If the animal reverses its position in the tube, which frequently happened in the specimen under observation, the direction of the current is immediately reversed.

As the worm possesses no jaws, it seems probable that its food consists entirely of fine organic particles and of small organisms carried in the current which it sets up. This is confirmed by the appearance presented by food-masses in the intestine, as seen in sections of preserved material, which generally show skeletons of diatoms, etc.

When removed from its tube and irritated, Pœcilochætus often swims with a rapid, serpentine motion, which recalls the motion of the larva.

Specimens were easily kept alive for some weeks in the Laboratory when provided with sand in which to construct their tubes, and worms which through injury had lost the posterior part of their bodies generally regenerated new tail ends of characteristic structure.

Pœcilochætus appears to breed practically the whole year round. Specimens were taken in February, April, May, June, August and December, and on all occasions some were found to contain almost or quite mature eggs or spermatozoa. The mode in which the eggs are laid has not been determined. The larva of Pœcilochætus is remarkable for the late stage of development to which it retains the pelagic habit.

Methods.

As careful a study as possible was made of the living worm. For further examination specimens were preserved by the methods to be described. The worms were anæsthetised by the gradual addition of alcohol to the sea-water in which they were living. They were then placed on a glass plate and killed by dropping on to them a small quantity of the preserving fluid to be employed, the worms being kept straight and extended with camel's-hair brushes until contraction had ceased. They were then transferred to a large quantity of the fixing fluid and allowed to harden.

The most successful fixation was obtained with Hermann's fluid, in which the specimens were allowed to remain from five to twelve or fourteen hours. The shorter time gave rather better results for the epithelial structures, especially the nuchal organ and lateral sense-organs, whilst the longer time was rather better for internal parts.

Good results were also obtained by the use of corrosive sublimate-acetic mixture (3 : 1) for three or four hours, the specimens being then rapidly rinsed in water and at once transferred to 70 per cent. alcohol, to which tincture of iodine was added.

Staining was for the most part done with Gustav Mann's methyl-blue-eosin mixture (Mann, 1902), sections being allowed to remain in the mixture overnight, rinsed with water, and differentiated in absolute alcohol. This method gave very excellent results with both Hermann and corrosive sublimate preservation. The formula for the stain is—

1 per cent. Methyl blue . . .	35 c.c.
1 „ „ Eosin	45 c.c.
Water	100 c.c.

Heidenhain's iron-hæmatoxylin was also employed, but, excepting for some few special points, I do not consider the resulting preparations nearly so good as those obtained by the simpler methyl-blue-eosin method.

Embedding was done in paraffin. Transverse, horizontal and sagittal sections, 4 μ and 5 μ in thickness, were cut with the Jung microtome, and fixed to the slide with distilled water to which a trace of albumen had been added.

I take this opportunity of acknowledging my very great indebtedness to Mrs. Sexton for the drawings which she has made, with remarkable skill and accuracy, of the external features of the animal, as well as of some of the sections.

External Characters.

The **body** of Pœcilochætus serpens is long and slender, narrowing posteriorly. A specimen about 55 mm. long, when alive and extended, was from 1·5 to 1·7 mm. broad (not including the parapodial cirri) in the anterior region, and consisted altogether of about 110 segments. The body is divided into a number of regions, which will be described in detail subsequently (see p. 138).

The **colour** of the anterior segments (1—15) varies from bright scarlet to deep purple-red according to the degree of aëration of the blood, which, showing through the transparent body-walls, gives its own colour to this region (see p. 126). The parapodia and their cirri are here almost colourless. The posterior part of the body is black or dark green and white, the dark colour being due to pigment in the cells of the intestine; the white, which is specially marked in ripe males, to the genital products.

The **head** is small and hemispherical, as can be seen from the dorsal view (Pl. 7, fig. 1, and Pl. 8, fig. 7) and from the ventral view (Pl. 8, fig. 8). It is provided with four eyes, two small dorsal and two larger ventral. A short **median tentacle** has its origin on the ventral side of the head, being placed so far back that when the proboscis is completely withdrawn into the body, the base of the tentacle also comes to lie actually within the mouth (Pl. 8, fig. 8). The tentacle, which is covered with minute papillæ (the external openings of epithelial glands), extends for a short distance beyond the anterior margin of the head (figs. 1 and 7). As will be shown later, the single median tentacle represents two lateral tentacles fused together, for it receives two nerves, one from either side of the brain.

The very large **palps** (*plp.*) arise between the head proper and the parapodia of the first segment. These palps are capable of great extension (cf. Pl. 9, fig. 12), and may attain a length equal to at least half the length of the body. Their general appearance can be seen from figs. 1 and 7. They are horse-shoe shaped in transverse section, are richly supplied with papillæ, and a crenated membrane runs along each margin of the flattened side. A single large blood-vessel, along which in the living worm a constant succession of strong pulsations is seen to pass, extends through nearly the whole length of each palp.

In describing the habits of the worm it was stated (p. 83) that when the worm is in its tube the palps may either lie straight in front of the head, being often protruded out of the mouth of the tube, or they may be formed into a number of oose coils lying immediately in front of the head. They clearly serve, amongst other functions, as important organs of respiration.

From the posterior dorsal region of the head three long tentacle-like processes arise, a long median process, which falls back on the dorsal surface of the body, and two lateral processes, the three being united into one broad base, which is attached to the head. These three processes constitute the **nuchal organ** (fig. 1 and fig. 7, *nuch.*), the very great development of which is one of the most striking features of the genus Pœcilochætus. Occasionally a specimen is seen in which one or other of the three processes has further divided, or rather given off a well-developed lateral branch. The nuchal organ is generally of a brownish colour in the living worm.

The **first segment**, or prostomium, is greatly developed, and its parapodia and chætæ are directed forwards. Each parapodium consists of a neuropodium and a notopodium completely united together, and carries a neuropodial and a notopodial cirrus, the former being large, flask-shaped and directed forwards, whilst the latter in this first segment is small and rudimentary, showing merely as a small projection on the dorsal surface of the parapodium (Pl. 8, fig. 7).

There are two bundles of simple, long, smooth chætæ, which extend for a considerable distance in front of the head. The notopodial chætæ are about twice the length of the neuropodial, and both sets curve inwards, the longest ones often crossing their fellows of the opposite side.

The parapodia and their cirri are covered with small papillæ, at the ends of which are the external openings of mucus glands. Between the neuropodial and notopodial cirrus lies a well-developed lateral sense-organ, similar in structure to those found on all the anterior segments of the body. These organs have the appearance of small, projecting, pear-shaped lobes, with the narrowest portion at the point of attachment to the parapodium. A number of sensory hairs can be seen projecting from a cup-like depression at the outer extremity of the lobe.

The **mouth** (fig. 8) lies on the ventral surface of the first segment. It is bordered posteriorly and laterally by large cushions or lips, which are distinctly ridged, whilst anteriorly it is limited by the base of the median tentacle, of which a portion may actually lie within the mouth, when the proboscis is completely retracted.

The **proboscis** is seldom protruded; indeed, I have only seen it thus on one occasion. It was then short and broad, almost spherical in shape, and appeared to carry the median tentacle on the base of its anterior wall.

The **second segment** is only a little less developed than the first, and the parapodia with their cirri still tend to be directed forwards. The neuropodial cirrus is similar in shape to that of the first segment, but is slightly smaller. The notopodial cirrus, unlike that of the first segment, is well developed, being of about the same size as the neuropodial. Between the two cirri is a well-developed lateral sense-organ, like that on the first segment.

The notopodial chætæ spring from a chætal sac situated immediately at the base and in front of the notopodial cirrus, which may itself be said to form the posterior lip of the sac. The anterior lip of the chætal sac is broad and short. The majority of the notopodial chætæ are long, slender, and unjointed, having the form of simple, smooth hairs. At least one bristle, however, on each side in this second segment belongs to another type, being provided with rows of short spines, the type being the same as that found in segments 7 to 16 (cf. Pl. 3, fig. 15). The neuropodial chætæ (fig. 9) consist of three (or sometimes four, the fourth being rudimentary) [1] short, stout, slightly curved hooks, which arise immediately in front of the neuropodial cirrus. In addition to these hooks a few very fine, hair-like bristles occur, which are best demonstrated in sections.

[1] In sections the rudimentary fourth hook can always be seen, though it seldom pierces the skin.

The **third segment** resembles the second, excepting that the cirri are slightly smaller and more conical in shape, and there is not quite such a tendency for them to be directed forwards. The neuropodial chætæ consist of three well-developed and one rudimentary stout hooks and a few fine hairs, all as in segment 2 (Pl. 7, fig. 2). The notopodial chætæ are all smooth hairs, no spiny bristles like those in segment 2 being present.

In the **fourth segment** the cirri are not quite so large as in the third, and are usually directed outwards or slightly backwards. The chætæ of the neuropodium are no longer stout hooks, but form a bundle of straight, smooth bristles, similar to those of the notopodium. There are no spiny bristles.

The **fifth segment** (figs. 1, 3, and 7) differs from its neighbours in the fact that the neuropodial cirri are short, whilst the notopodial cirri are long and slender, being the longest cirri, with the exception of those on the first segment, which are found on the whole body of the worm (fig. 3). These two long cirri are also often carried in a somewhat different position from those on other parts of the body, being arched over the back of the worm.

The **sixth segment** closely resembles the fourth (fig. 1), the cirri being generally directed backwards. The chætæ from the third to the sixth segment are all smooth hairs, amongst which no spiny bristles are found.

Segments 1 to 6 may be considered as constituting the first sub-division of the anterior region of the body. With segment 7 a change takes place, which is expressed both in the external and internal structure of the worm. Externally—that is to say, regarded from the point of view of the structure of the parapodia only—the second sub-division of the body would seem to comprise the **segments from the seventh to the thirteenth**, but, as will be shown later (p. 139), this does not quite agree with the division indicated by the internal anatomy, which points rather to segments 7 to 11 only being classed together.

The peculiarity of the parapodia of segments 7 to 13 (figs. 4 and 5) lies in the form and structure of the notopodial and neuropodial cirri. These cirri are flask shaped, but the basal part of each cirrus or body of the flask becomes swollen and almost spherical, whilst the neck is thin, elongated and nearly cylindrical, with a slight enlargement at the distal end. The whole cirrus, including the neck, is very rigid, being much less flexible than the cirri of the other segments, and only moves from its base at the point of attachment to the body of the worm. The stiff movement of the cirri gives a characteristic appearance to this region of the body in the living worm. The chætæ in these segments are of two kinds, smooth, slender hairs (Pl. 9, fig. 13), which show longitudinal striation under a high power, and spiny bristles (Pl. 7, figs. 4 and 5; Pl. 9, fig. 15), the number of the latter being few in each bundle.

Lateral sense-organs in the form of pear-shaped papillæ are still found between the cirri, but the bases of the papillæ, where they are attached to the parapodium, are broader than in the more anterior segments.

In **segments 14, 15 and 16** (Pl. 9, fig. 9) the parapodia have a structure more nearly resembling that found in the fourth and sixth segments. The cirri are shorter and stouter, nearly conical in shape, and are without the long stiff necks found in the segments immediately in front. The chætæ remain of two kinds, as in the latter segments, and the lateral sense-organ still protrudes from the surface of the parapodium.

With **segment 17** there is again a change, but the structure then found continues in its essential features, with the exception of the addition of gill filaments commencing at segment 21, until about thirty segments from the end of the body.

Both the notopodial and neuropodial cirri, conical in shape, are now much smaller in size (figs. 1, 10, and 11), and vary considerably and somewhat irregularly in the extent to which they are developed from segment to segment.

There is, on the other hand, a very remarkable development of the chætæ. In both notopodium and neuropodium the smooth, slender chætæ of the anterior segments are replaced by large, hairy, feather-like bristles (Pl. 7, fig. 3; Pl. 9, figs. 10, 14, and 16), the most dorsal and most ventral in each segment having long, fairly stiff shafts, with lateral hairs of moderate length (fig. 14), whilst the inner ones (ventral bundle of notopodium and dorsal bundle of neuropodium) are more slender and flexible, but have very much longer hairs (fig. 16). These bristles give to the region of the body now under consideration a kind of woolly appearance.

The spiny bristles of the anterior segments also undergo a special modification in this region. The stoutness of their shafts becomes very greatly reduced, the spines themselves become much elongated, show a slight thickening near the tip, and are connected with the shaft along almost their entire length by a thin, transparent membrane, which is practically invisible in fresh material, but becomes quite obvious after staining (Pl. 9, fig. 17). By this arrangement the surface of the bristle becomes very greatly extended.

The hairy, feather-like bristles, together with the modified spiny bristles just described spread out in each parapodium into a large fan, the movements of which are mainly responsible for the current of water which the worm constantly draws through its U-shaped tube (see p. 83).

In this region the lateral sense-organ no longer has the form of a papilla protruding from the face of the parapodium, but is seen as a slight depression from the centre of which a bundle of sensory hairs arises. The depression is surrounded by a circular rim, which rises slightly above the general face of the parapodial surface.

Gills.—The gill filaments commence on segment 21, and are found on the succeeding segments to quite near the end of the body. They are at first short and small in size (Pl. 7, fig. 1), but soon become longer and larger. When fully developed they consist of long filaments, as long as or longer than the cirri of the parapodia (Pl. 9, fig. 11), which appear bright red in the living worm from the colour of the blood which is in them. Two pairs of such filaments occur upon each parapodium, one pair being attached to the posterior face of the neuropodium and one pair to the posterior face of the notopodium.

The **terminal segments** (Pl. 8, fig. 6) show certain special features. The general shape of the body is here flattened, and the dorsal surface is somewhat concave. The neuropodial and notopodial cirri are of about the normal shape, but the neuropodial is double the size of the notopodial, and the latter assumes a more dorsal position than usual. The more dorsal of the notopodial chætæ are transformed into strong hooks (figs. 6 and 19), which form a transverse row on either side of the dorsal surface of the segment. Five or six such hooks are generally found on each notopodium. The curve of the hook is directed backwards, and those nearest the middle line are the stoutest as well as the most strongly curved. These hooks are found on the last sixteen or seventeen segments (in full-grown specimens), and obviously serve the purpose of enabling the worm to hold itself firmly in the tube.

The remaining chætæ of the notopodium and those of the neuropodium in these segments are mostly either of the ordinary smooth or spiny kinds, the latter being often rudimentary. There is also found in the terminal region of the body a special kind of bristle not met with elsewhere (Pl. 9, fig. 18). This consists of a stout, smooth shaft, showing longitudinal striations, and ending in a blunt tooth directed slightly outwards. From the base of this tooth there arises a hairy terminal portion of the bristle, which forms a kind of flexible brush attached to the end of the stiff shaft. Bristles of this character are a modified form of the ordinary stout, hairy bristles, which, as the end of the body is approached, at first lose the hairs along the greater part of the length of the shaft, retaining them only at the ends. The type of bristle with the hairy flexible end (fig. 18) becomes established at about the thirtieth segment from the end of the body (in full-grown specimens), and occurs in the segments from this point to about the ninth or tenth from the end.

In the terminal segments the lateral sense-organs have again the form of pear-shaped papillæ protruding from the surfaces of the parapodia between the cirri.

The **pygidium** is well developed; the anus is somewhat dorsal, and is surrounded by five large lobes (Pl. 8, fig. 6). There are two pairs of anal cirri, both situated below the anus, the more dorsal pair being long and slender, the more ventral pair short.

The anus and the terminal portion of the intestine are strongly ciliated, and all the cirri in the hindermost region of the body, as well as the dorsal and ventral surfaces of the body itself, are very richly provided with papillæ, at the extremities of which lie the external openings of epithelial glands.

No description of the general aspect of the living Pœcilochætus is complete without reference to the remarkable system of blood-vessels, which is visible through the tranparent body-wall (Fig. 1). A detailed account of this vascular system will be found in the special section on p. 126.

Internal Anatomy and Histology.

Epithelium and Cuticle.

The character of the epithelium differs in different parts of the body. The cells composing it may be either almost cubical, with spherical nuclei (Pl. 9, fig. 20), or they may be elongated in a direction either perpendicular (Pl. 9, fig. 21) or parallel to the body surface (Pl. 10, fig. 23). The elongated cells have oval nuclei, the long axes of which are parallel to the long axes of the cells.

Over the greater part of the body the epithelial cells are arranged in a single layer, but in isolated places, more especially on the ventro-lateral surfaces to be presently described, two layers can be recognised. The cuticle, which lies external to the epithelial cells, varies in thickness in different parts of the body.

Cells nearly cubical in shape are found on the dorsal surface of the anterior segments (Pl. 9, fig. 20). In preparations stained with methyl-blue-eosin the cuticle is coloured blue, a thin outer layer being distinguishable by its very dark colour from the main body of cuticular substance, which is stained uniformly of a much lighter shade. The protoplasm of the epithelial cells is very distinctly granular in preparations preserved in Hermann's fluid, and the divisions between the individual cells are often strongly marked. Each cell contains a spherical nucleus with a well-marked nuclear membrane. Within the nucleus is one large mass of deeply staining chromatin and a few small, scattered particles of the same substance. The nucleus as a whole has an exceptionally clear and transparent appearance in preparations preserved in Hermann's fluid. The internal ends of the cells appear to be in immediate contact with the muscular layers of the body-wall. Towards the tail end of the animal the epithelium of the dorsal surface becomes more flattened, the individual cells are less clearly marked, and the nuclei are transversely oval (Pl. 10, fig. 23).

On the ventro-lateral surfaces of the body the epithelial cells are generally more elongated in a direction perpendicular to the body surface (Pl. 9, fig. 21 ; Pl. 10, fig. 22), and have oval nuclei in which the chromatin is present in the form of a number of deeply staining particles connected by a network, no one particle standing out so prominently as the large single mass of chromatin in the nuclei of the cubical cells of the dorsal surface. In certain spots the elongation of the cells is very great, and some of the cells have migrated inwards, so that an internal layer of nuclei can be recognised (fig. 21). In this way a pad or cushion of cells is produced, and this cushion forms the point of insertion of certain muscle-bands.

Epithelial Gland-cells.

Gland-cells opening externally by means of short, chitinous tubes which project beyond the general surface of the body are abundant in places. In their simplest form these consist of individual cells lying amongst the cells of the epithelium. One such cell is illustrated in fig. 22 (Pl. 10). It is pear shaped, with granular protoplasm staining much more deeply than that of the surrounding cells, and with an oval nucleus, the long axis of which lies parallel to the body surface. The protoplasm at the mouth of the cell is inserted in a depression on the internal face of the chitin. The chitinous tube, which places the interior of the cell in communication with the external water, forms a conical projection on the body surface, and can also be seen to project internally for a short distance into the protoplasm of the neck of the cell.

Such simple gland-cells are not, however, very numerous. The more usual arrangement is for several cells to be associated together and to open externally through one tube. Glands of this type are especially numerous in the epithelium towards the tail end of the animal, where the tubes are situated upon raised chitinous papillæ, which form a characteristic feature in external views of the animal. These papillæ and tubes are figured by Claparède (in Ehlers, 1874), and their great abundance on the dorsal surface of the anterior segments in the specimens examined by him constitutes one marked difference between his Pœcilochætus fulgoris, obtained from deep water, and the specimens found at Plymouth near low-tide mark on the shore.

A section through such a gland opening on the dorsal surface near the tail end of one of the Plymouth specimens is shown in fig. 23 (Pl. 10). The epithelium here consists of flattened cells, with large, oval nuclei. The cuticle is comparatively thin, except in the neighbourhood of the opening of the gland. It is there greatly thickened and pushed outwards, forming a tubercle with a stout chitinous covering hollowed out internally, the internal hollow being filled with the protoplasm of the ends of the gland-cells. Through the centre of the tubercle runs the chitinous tube, which places the gland-cells in communication with the exterior, the tube projecting to an equal extent externally beyond the surface of the papilla and internally into the protoplasm of the gland-cells.

On account of the flattened nature of the epithelium, the gland-cells, which are easily distinguished by their more deeply staining protoplasm, do not lie immediately beneath the tubercle, but are drawn considerably to one side. The nucleus of each gland-cell lies near its proximal end. It is much smaller than the nuclei of the ordinary epithelial cells surrounding it, spherical rather than oval in shape, contains a large quantity of chromatin in the form of a considerable number of large, deeply staining granules of about equal size, and is thus very readily distinguished from the nuclei of the epithelium. Usually three or four such nuclei can be distinguished lying close together in the neighbourhood of the base of each of the chitinous tubercles. In the figure (fig. 23) only one such nucleus is shown; but three were distinguished in the sections, two lying one over the other, in the section from which the figure was made, and one in the following section.

Scattered over the ventral surface of the cuticle, especially in the anterior segments of the body, a number of rounded tubercles or callosities are found. A section through two of these is shown in fig. 21 (Pl. 9). They are almost entirely cuticular structures (*cal.*), the epithelial cells only protruding for a very short distance into them. The internal, lightly staining layer of the cuticle found in this region of the body, though curved slightly outwards, is little if at all thickened. The tubercle is chiefly formed, therefore, by a great thickening of the outer or deeply staining layer of the cuticle. The character of this layer seems also to be slightly altered, for in methyl-blue-eosin preparations it takes on a deep reddish or purple tint rather than blue, and often exhibits a characteristic radial structure due to a number of deeply staining, radiating bars (fig. 21).

The appearance of these tubercles at once brings to mind those upon which stand the tubes of the gland-cells already described. In the present case, however, no external openings can be demonstrated, unless the radial lines already mentioned really represent pores. Nevertheless an examination of a large number both of the gland papillæ and of the callosities produces a conviction that the latter are in reality essentially the same structures as the former, either in a more highly developed or in a regenerate state.

The cells lying immediately beneath the tubercle on the right-hand side of the section figured (fig. 21) are somewhat difficult of interpretation. It is possible that the long process (*p*) immediately beneath the cuticle is homologous with the internal portion of the tube of the gland-cells (figs. 22 and 23), and that the nucleus (*n'*) is the nucleus of a gland-cell with which this tube communicates. I have not, however, found other sections which appear to confirm this view.

Although gland-cells are by no means uncommon in the general body epithelium, by far the largest development of such cells takes place in the dorsal and ventral cirri of the parapodia. Fig. 25 (Pl. 10), was drawn from one of the cirri from the regenerated tail end of a living worm, where the transparency of the tissue allowed the gland-cells to be seen. Fig. 24 (Pl. 10) represents a section through a cirrus from about the eighteenth segment of the body. From the latter figure it will be seen that a cirrus is crowded with a number of flask-shaped cells, the long necks of which open to the exterior through papillæ elevated above the surface of the cirrus. (In fig. 25 the long necks of the cells are not shown, the fact that they were not visible in the fresh tissue being probably due to their great transparency. In fig. 24 the actual continuity between any one cell and the external opening does not appear, but this is quite easily demonstrated in a series of sections.)

The gland-cells in the cirri appear under at least three forms, which are illustrated in figs. 26, 27, 28, and 29 (Pl. 10). The figures have been drawn from transverse sections of cirri preserved in Hermann's fluid and stained with methyl-blue-eosin. Cells of each of the three types possess long necks opening at the exterior as above described.

Type A.—Fig. 26 represents a section of a type of gland-cell which occurs in cirri from all parts of the body. In those on the anterior segments, from 1 to 13, it is the only kind found. In the cirri of the segments behind the thirteenth cells of this character are not numerous and general, but sometimes occur towards the distal end of the cirrus (cf. fig. 24, the very dark cells). These cells stain very deeply, the protoplasm being crowded with granules, which take on an intense blue colour. There are also present a number of short rods and particles of different shapes, which are even more deeply stained than the granules. The nucleus stains red with the eosin. It contains one large mass of deeply staining chromatin (nucleolus) surrounded by a clear space. This space is bounded by a membrane, and attached to this membrane is a hemispherical cap of deeply staining substance half enclosing the nucleus. A section through this cap gives the crescent-shaped figure shown in fig. 26 (Pl. 10). The relation of the cap to the nucleolus reminds one of the relation of the yolk nucleus of the ovum to the germinal vesicle (cf. fig. 61). The remainder of the nucleus—that is to say, the space between the nuclear membrane and the nucleolar membrane and cap—is filled with a large number of small granules, stained red with the eosin, but not taking on by any means such an intense colour as the nucleolus and the nucleolar cap.

Type B.—Figs. 27 and 28 represent sections through the type of gland-cells which occupy the greater part of the bodies of the cirri on all the segments from the fourteenth backwards. The change from cirri packed with cells of Type A in segment 13 to those containing almost entirely cells of Type B in segment 14 is very marked.

Cells of this type have a ground-substance with a homogeneous appearance—or showing in preserved material at most a faint indication of a network—which stains pale blue. In this ground substance are a number of rods (sections of the rods appear circular) which stain a deeper blue than the ground substance of their cell, but do not take on by any means the intense blue colour of the granules in cells of Type A. The nuclei of cells of Type B resemble those of Type A in general structure. The nucleolus is, however, somewhat smaller, and all the structures take on a much less intense stain. A noteworthy feature in the sections of these cells is that the cell-substance outside the nucleus contains patches of fine red granules exactly resembling the red granules seen in the nucleus itself. These patches occur more especially in immediate contact with the nucleus, and their whole appearance seems to suggest very strongly that the granules are being manufactured in the nucleus and passed out into the surrounding substance.

For a valuable summary of our knowledge of the part played by the nucleus in secretion, and a very extensive list of the papers dealing with this subject, reference may be made to a recent paper by Launoy (1903).

Type C.—In cells of the third type (fig. 29), which also occur in the cirri of segments from 14 backwards, the ground substance stains pale blue, shows a reticular structure in preparations preserved in Hermann's fluid, and contains a few deeply staining rods. The nucleus stains deeply and diffusely, but is shrunken and irregular in shape. Cells of this type are apparently those in which the process of the formation of the secretory product is complete and the nucleus no longer active. If this be so they are in reality a later stage in the condition of cells of Type B.

If fragments of the living worm are strongly irritated, a large mass of clear, transparent mucus is secreted, which is in all probability discharged from the gland-cells of the cirri above described.

For a summarised account of epithelial gland-cells of various kinds found in other Polychætes reference may be made to Eisig's monograph on the Capitellidæ (Eisig, 1887).

Palps.

The external appearance of the palps (Pl. 7, fig. 1) has already been described (p. 86). A section of the palp shows it to be a hollow tube having a large central cavity, through which the blood-vessel of the palp runs (Pl. 10, fig. 30, *p. bv.*). The walls of the tube are composed of two layers of cells, a thick outer layer of large epithelial cells (*ep.*) lined internally by a thin sheet of mesoderm cells. The nuclei of both the epidermic and mesodermic cells have a very characteristic appearance, since each possesses a single, large, deeply staining nucleolus. Occasionally a nucleus is seen with two such nucleoli of equal size, which may indicate division. The walls of the blood-vessel which runs along the length of the palp are thick, and contain nuclei similar to those of the mesodermic cells. From the pulsation of the vessel in the living worm these walls are known to be muscular.

The cavity of the palp communicates with the general body-cavity of the first segment of the worm by means of a tube formed by a continuation into the body-cavity of the meso-derm-cells lining the cavity of the palp (fig. 30, *plp. v.*). This tube, just after it leaves the palp, is surrounded by a strong band of annular muscle-fibres, by the contraction of which the cavity of the palp can be completely cut off from the body-cavity of the first segment. It is clear that the palps, which are capable of very great extension, are elongated by the pressure of fluid from the body-cavity into their cavity. When once the palps are filled, the contraction of the annular muscle-fibres just described will enable them to continue extended without the necessity of the body pressure being maintained. (For an account of the muscular septa which come into play when the fluid is pressed forward see p. 123.)

At the outer side of the palp, between the base of the palp and the palp-ganglion, lies a small diverticle (*plp. div.*) of the palp cavity, which appears to run forwards and then end blindly. The meaning of this structure I have not fully understood.

Chætæ.

An account has already been given, in describing the external features, of the different types of bristles which Pœcilochætus possesses (see Pl. 9, figs. 13—19). The shafts of these bristles almost all show longitudinal striation, together with transverse markings at irregular intervals. The longitudinal striations are shown in sections to be due to the fact that the bristle is built up of a large number of longitudinal tubes lying side by side. This is especially marked in the stout hooks of the neuropodium, which occur in segments 2 and 3, and in the hooks of the notopodium in the terminal segments. All chætæ with stout shafts also show the structure well.

This type of minute structure in the bristles of Chætopods has recently been described in detail by Schepotieff (1903), to whose paper reference should be made for further details.

Nervous System.

Brain.—Practically the whole of the head of the worm is occupied by the substance of the brain. This substance consists of a ventral[1] mass of nervous felt-work (punctated substance) covered externally by a mass of ganglion-cells.

The arrangement of the parts can be best explained by reference to the diagrammatic figure of a section of the brain given in the text (Fig. 1).

This figure represents a thick sagittal (longitudinal-vertical) section through the brain cut a little on one side of the middle line, and has been constructed from an examination of several series of thin sections. The large circumœsophageal commissures, which put the brain in communication with the ventral nerve-cord of the worm, can be traced from the particular mass of punctated substance which occupies the centre of the brain

[1] In the description of the brain the terms anterior, posterior, dorsal and ventral are used on the assumption that the worm has the proboscis slightly everted as in the sagittal section fig. 42 (Pl. 11). In the position of repose, what is here called the anterior surface, becomes more ventral in position.

(*m. b.*), it being probably here that the fibres of the commissures from the two sides cross each other. From this region the fibres pass first forwards and downwards and then turn outwards, after which, in sagittal sections, they form a circular patch of transversly cut fibres (*comm.*), which can be easily followed through the brain substance. Arising from the same central mass of punctated substance (*m. b.*), but at a level external to that at which the fibres of the commissures leave it, a bundle of fibres can be traced, which passes forwards and downwards into the epithelium in front of the brain, from whence it can be easily followed as a well-marked

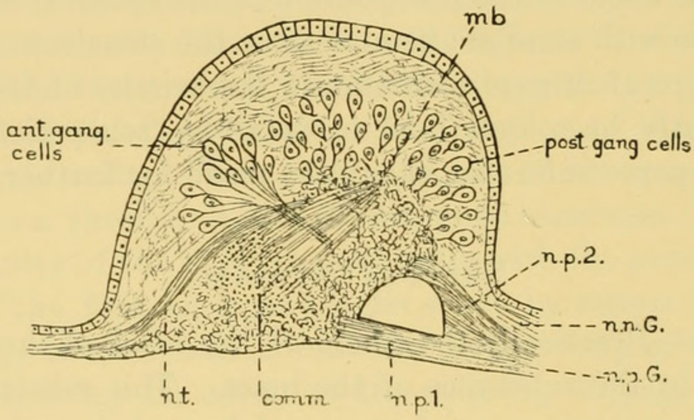

Fig. 1.—Diagrammatic sagittal section through one side of the brain of *Pœcilochætus*. *ant. gang. cells*, anterior ganglion cells; *n. t.*, nerve to median tentacle; *comm.*, œsophageal commissure; *n. p. 1*, anterior root of nerve to palp-ganglion; *n. p. 2*, posterior ditto; *n. p. G.*, nerve to palp-ganglion; *post. gang. cells*, posterior ganglion-cells; *m. b.*, central mass of fibres from which œsophageal commissures and tentacle nerve arise; *n. n. g.*, nerve to nuchal ganglion.

nerve (*n. t.*) to the median tentacle, which lies just in front of the mouth (cf. Pl. 11, fig. 42). The bundle of fibres just described exists on each side of the brain, and two nerves, one from each side, can be followed with perfect certainty from the centre of the brain to the single median tentacle.

From about the middle of the ventral surface of the brain on each side a bundle of fibres arises (*n. p.* 1) which passes backwards. This bundle of fibres is subsequently joined by a second bundle (*n. p.* 2), which leaves the brain at its posterior end. The two bundles unite to form a stout nerve, which runs outwards to a large ganglion, situated at the base of the palp, the palp-ganglion (cf. Pl. 10, fig. 30). The nerve of the palp-ganglion thus has a double origin in the brain.

From the posterior end of the brain, fibres also pass backwards and enter the nuchal organ, where they mingle with the felt-work of fibres of a large ganglion which lies in the base of that organ—the nuchal ganglion (fig. 42). The fibres passing from the brain to the nuchal organ are not easy to demonstrate, as they do not form definite nerve-bundles, but rather two thin sheets, one from each half of the brain, the individual fibres of which pass between or below the epithelial cells lying at the junction of the nuchal organ and brain.

The ganglion-cells of the brain form an almost continuous cap covering the punctated substance. It is, however, possible to distinguish in each half of the brain an anterior group of cells (Text-fig. 1, *ant. gang. cells*), the fibres from which unite in a bundle, which is directed downwards and backwards into the mass of punctated substance lying below that region (*m. b.*), where the œsophageal commissures take origin. The further fate of this bundle of fibres could not be ascertained, but a comparison with transverse sections appears to suggest that it may cross with its fellow and then give rise to the anterior root of the palp-ganglion nerve (*n. p.* 1) of the opposite side.

A number of very large ganglion-cells (*post gang. cells*), situated at the posterior end of the brain, which send their processes into the general mass of the central felt-work, are also conspicuous. These cells, however, do not appear to constitute a definite group, but grade off into the general mass of ganglion-cells.

The Palp-ganglia.—The two palp-ganglia are situated at some distance from the brain. They are ganglia of considerable size, and contain large ganglion-cells, as well as a nervous felt-work. They lie one on each side of the body at the base of the palp and external to that structure (Pl. 10, fig. 30). Each ganglion receives the fibres of the palp-ganglion nerve (the origin of which in the brain has already been described), and gives off a bundle of nerve-fibres, which immediately enters the palp.

The Nuchal Ganglion.—The nuchal ganglion lies in the base of the nuchal organ, and consists of a considerable mass of nervous felt-work surrounded by a number of ganglion-cells, some of them of large size. Bundles of nerve-fibres pass from it into the different branches of the organ, and these doubtless supply the external ciliated grooves which run along those branches (cf. p. 112), though individual fibres have not actually been traced so far.

The Relation of the Different Parts of the Brain to one another.—The arrangement of the brain and the ganglia connected with it in Pœcilochætus is of some theoretical interest when considered in connection with that of other Polychætes. Our recent knowledge of the structure of the Polychæte enchaphalon is largely based on the careful work of Racovitza (1896). This author distinguishes three regions, to which he gives equal morphological importance—the fore-brain (Cerveau antérieur), with which the palp-ganglia are connected; the mid-brain (Cerveau moyen) with the antennary and optic ganglia; and the hind brain (Cerveau postérieur) with the nuchal ganglia. The relations of the parts in Pœcilochætus are noteworthy in that the palp-ganglia and the nuchal ganglion are not fused in the mass of the brain, as in the forms described by Racovitza, but are separated distinctly from it. The eyes being simple, there is no development of optic ganglia, and the antennary ganglia are also not obvious. With regard to the divisions of the brain itself, the facts point to the presence of the first two at any rate of Racovitza's three regions, though the matter is by no means clear. The anterior ganglion-cells (Text-fig. 1, *ant. gang. cells*), with their bundle of fibres, which, as has been stated, very possibly form the first root of the palp-ganglion nerve, would represent the fore-brain of Racovitza, whilst the fact that the nerves to the tentacle (*n. t.*) and the œsophageal commissures all spring from the same point in the centre of the brain (*m. b.*) would seem to point to this region as the mid-brain of that author. With regard to the hind brain, there is more difficulty. Judging from Racovitza's figures of Eurythœ borealis and Euphrosyne Audonini, it would seem that what I have termed the nuchal ganglion of Pœcilochætus is homologous with what he calls the hind brain in those species. But in Pœcilochætus this structure is separated sharply from the brain itself, being only connected with it by nerve-fibres. These fibres leave the brain at its posterior end, but there is no region in the brain itself which can be clearly marked off as a hind brain. The large posterior ganglion-cells to which reference has been made (Text-fig. 1, *post. gang. cells*) might at first sight be regarded as an indication of such a structure, but against this view it can be urged that they give off their processes to the region of the mid-brain, from which the commissures and tentacle nerves take origin.

The relations found in Pœcilochætus seem to indicate that it would be more correct to term what Racovitza calls the hind brain in Eurythœ and Euprosyne the nuchal ganglia. The nuchal ganglion of Pœcilochætus is clearly comparable to the palp-gaglion, and not to any division of the brain itself.

Ventral Nerve Cord—The ventral nerve-cord lies entirely in the epidermis (Pl. 10, fig. 32). The ganglia of the different segments are not very sharply marked off from each other, ganglion-cells being scattered somewhat irregularly along the whole length of the cord. Definite ganglia are, however, indicated in each segment by a considerable increase in the number of ganglion-cells, by the presence of masses of nervous felt-work (punctated substance) as well as by the roots of the lateral nerves.

Two giant fibres (fig. 32 *g. f.*) run along the cord. In preserved specimens these fibres vary in diameter in different regions, but are generally of very large size. The connection of these fibres with ganglion-cells has not been traced.

Stomatogastric System—What seems to be a well-developed stomatogastric nervous system, comprising a ganglion and a large bundle of nerve-fibres on the pharynx, is found in Pœcilochætus, but my preparations have not sufficed to discover the complete details of its arrangement.

Lateral Sense-organs.

The position and external appearance of the lateral sense-organs are described on pp. 87—92 (figs. 1, 2, 7, etc.). In segments 1—6, as well as in the segments at the tail end of the body, it will be remembered that these organs have the form of pear-shaped papillæ protruding beyond the surface of the parapodium between the cirri, whilst in the remaining segments they lie in the parapodium with only a slightly raised rim protruding beyond the general body surface.

The histological structure is best studied in detail in organs of the latter type, as, for example, in those at about segment 20, and the most instructive general view is seen in horizontal sections of the body. Such a section is shown in fig. 34 (Pl. 10), which passes through the middle of a lateral organ. Externally the organ appears as a cup-shaped depression or crater surrounded by a raised circular rim. From the floor of the depression there springs a mass of stiff hairs, which, when the organ is not much contracted, extend far beyond the raised margin of the rim.

The external rim itself is composed of clear, transparent, epithelial cells, often showing vacuoles of some size (Pl. 10, fig. 34, *ep. r.*) These cells, as well as the face of the depression (hair-bearing area) are covered externally by a continuation of the ordinary body cuticle (*cu.*), which, excepting at the points of attachment of the muscle-fibres to be described in the next paragraph, shows no marked variation in thickness in the region of the lateral organs.

Internal Muscular System.—Immediately within the epithelial ridge the hair-bearing area is surrounded on its dorsal, its anterior and its posterior sides by bands of muscle-fibre (*m.f.*), which extend from the cuticle to the internal apex of the organ, where they pass into the large muscles attached to that apex (fig. 34, *musc.*) The arrangement of these muscle-bands will be seen on comparing the three figures representing respectively a horizontal section (fig. 34), a section in the longitudinal-vertical plane of the animal, and therefore parallel to the hair-bearing surface of the organ (fig. 38), and a transverse section through the anterior row of muscle-bands (fig. 35). From figs. 34 and 38 especially it will be seen that along the anterior margin of the hair-bearing area a single row only of muscle-bands exists, that along the dorsal margin there are several rows, whilst on the posterior side there are two rows with a narrow strip of the hair-bearing area between them. On the ventral border there are no muscle-bands at all. The ends of the muscle-bands in contact with the cuticle broaden considerably, so that the surface of contact between the bands and the cuticle is greatly enlarged (figs. 34 and 35), the cuticle itself being at the same time very much thickened (fig. 35). The course of the fibres from the margin of the hair-bearing area to the apex of the organ is easily demonstrated in a series of horizontal sections such as fig. 34.

In fig. 35, which represents a transverse section through the anterior line of muscle-bands, it will be noticed that between the bands a row of rather large, oval nuclei exists. It is not clear to exactly what cells these nuclei belong. They may be the nuclei of the muscle-bands, in which case each band would be morphologically a single cell, or they may belong to a series of ganglion-cells of a similar type to the large ganglion-cells shown in figs. 36 and 37 (see below).

Fig. 37 is drawn from a transverse section at the level of the posterior rows of muscle-bands.

In addition to the bands already described a number of single muscle-fibres pass from the apex of the organ to the cuticle in the region posterior to the raised rim of the hair-bearing area; these are also indicated in fig. 34. All these muscle-bands and fibres stain deeply in sections.

By means of the muscular system just described, assisted by the larger muscles (*musc.*) attached to the apex of the organ, not only can the whole organ be withdrawn to a certain extent within the body, but the hair-bearing area and its rim can be at the same time still further withdrawn, until the external appearance of the organ is little more than that of a pore with a number of hairs protruding through it.

The hair-bearing cells are represented in figs. 34 and 36. The exact outlines of the individual cells are not marked out in any of the preparations, and the meaning of the appearances shown is therefore not quite clear. The great resemblance between these appearances and those shown by the ciliated cells of the nuchal groove (Pl. 11, figs. 40 and 41) and of the intestinal epithelium (Pl. 11, fig. 44) gives, however, an important clue to their interpretation.

Immediately under the external layer of cuticle is an unstained space or layer of unstained protoplasm,[1] through which the inner ends of the sensory hairs can be seen to pass just as in the ciliated cells of the nuchal organ (cf. p. 114) and of the œsophagus (p. 117).

Then follows a layer of deeply staining short rods (figs. 34 and 36 *s. r.*), which is succeeded by a layer of faintly staining long rods (*l. r.*), just as in the ciliated cells. The only difference exhibited in the two cases up to this point is that the hairs, in their course through the clear space between the cuticle and the line of short rods, stain somewhat deeply immediately below the cuticle, red in methyl-blue-eosin preparations like the short rods themselves, producing the appearance of a secondary layer of short rods (fig. 36, *s. r.* 2), which, however, is very much less marked than the main layer. This layer occupies a similar position to the layer of "bulbi" of ciliated cells, which are further referred to on p. 118.

The short rods, as in the ciliated cells, stain bright red in

[1] It is possible that the size of this space may be exaggerated by contraction of the protoplasm of the cells caused by the reagents employed. In that case the layer of short rods would lie closer to the cuticle.

methyl-blue-eosin preparations, the long rods blue. The diameter of the latter appears to be somewhat greater than the diameter of the hairs where these pass through the cuticle.

In the horizontal section shown in fig. 34, at a level immediately inside the ends of the long rods, three large oval nuclei (*n. h.*) are seen, and in neighbouring sections other nuclei appear in a corresponding position. These I take to be the nuclei of the hair-bearing cells, the interpretation being based on their similarity in situation to those of the ciliated cells of the œsophagus and nuchal organ already referred to (cf. p. 114 and p. 117). The possibility must, however, be borne in mind that these nuclei may really belong to the posterior row of muscle-bands, and their position in fig. 34 lends some support to this view. In this case they would resemble the nuclei shown in fig. 35 lying between the anterior muscle-bands. Should further investigation show this to be the case, the nuclei of the hair-bearing cells must be sought elsewhere.

Ganglion.—The remaining structure to be described in connection with the lateral sense-organ is the ganglion. The ganglion-cells may be conveniently divided into two groups—a group of large cells, which occupy the anterior dorsal portion of the organ, in front of and above the hair-bearing cells, and a group composed of a large number of small cells, which constitute the posterior portion of the organ.

The large ganglion-cells are represented in figs. 36 and 37 (transverse sections). They are large, uni-polar cells, with their processes generally directed towards the cuticle. Whether these processes eventually reach the cuticle or whether they come into contact with the hair-bearing cells I have been unable to determine with certainty. The nuclei of these ganglion-cells are very large, and either spherical or oval in shape. The contents of the cell-bodies stain deeply.

The small ganglion-cells (fig. 34, *g. l. o.*) do not for the most part show definite cell-outlines in the preparations, but appear rather as a mass of more or less closely packed nuclei, with an intermediate substance, much of which is clearly made up of a feltwork of fine fibres. The whole structure exactly esembles what is found in parts of the brain and the ventral nerve-cord. In many sections fine fibres can be clearly seen passing from this ganglionic mass to the hair-bearing cells (fig. 34). The exact relations of these fibres to the latter cells could not be determined.

The Protruding Lateral Organs of the Anterior Segments.—Fig. 39 (Pl. 10) shows a section through one of the protruding organs of the anterior segments, the external views of which are seen in figs. 2, 3, 4, and 5 (Pl. 7). The structure is essentially the same as that of the organs already described, but the various parts are packed more closely together, so that the details are less easily made out. No further description is, however, necessary.

Connection with the Central Nervous System.—The ganglion of each lateral organ receives a bundle of fibres from a nerve which passes up the body-wall from the ganglion of the ventral nerve-cord. The course of this nerve can be easily followed in sections, its fibres lying immediately beneath the cells of the epidermis, between these cells and the muscular layers of the body-wall. After giving off the branch to the ganglion of the lateral organ the nerve continues its course in a dorsal direction, and has been definitely traced as far as the notopodial cirrus.

Muscles.—The muscles attached to the apex of the lateral organs are described on p. 125.

Historical.—The first detailed description of the structure of the lateral sense-organs of Polychætes was given by Eisig (1879 and 1887), who studied them in the Capitellids. There are some differences of importance between Eisig's account of the minute structure of the organs in Capitellids and the description of what is found in Pœcilochætus set forth in the present paper. In Capitellids Eisig describes a layer of rods immediately under the chitin, and this is followed by an irregularly arranged layer of spindle-shaped bodies. The layer of rods would seem to correspond with the long rods in the organs of Pœcilochætus, whilst the deeply staining layer of short rods either does not exist in the Capitellids or was not rendered evident by the methods employed. The spindles of Eisig I am inclined to regard as the nuclei of the hair-bearing cells, being led to this view by a comparison of the structure of the hair-bearing cells with the ciliated cells of the nuchal grooves and of the œsophagus in Pœcilochætus. On the other hand, they may represent bipolar ganglion-cells.

Ashworth (1902) has recently written on the structure of the lateral sense-organs in Scalibregma inflatum. He describes and figures the sensory hairs, the layer of short, deeply staining rods, and the long rods, all of which have apparently the same relations as in Pœcilochætus. Ashworth, however, interprets the long rods as hair-bearing cells and the deeply staining short rods as their nuclei. With this interpretation I am unable to agree, both from the appearance of the structures themselves in my preparations as well as from a comparison with the known structure of ciliated cells (cf. p. 118).

Ashworth also describes and figures large unipolar and bipolar ganglion-cells similar to those found in Pœcilochætus, and states that the processes of these cells can be traced into continuity with the internal ends of the rods which carry the sense-hairs. I have been unable to make out with certainty such a connection in Pœcilochætus, though the appearances presented are in no way opposed to its existence.

Further studies on the lateral sense-organs in the different groups of Polychætes, made with the aid of more special methods for determining the course of the nervous fibres, are necessary before their structure can be fully understood.

Nuchal Organ.

One of the most characteristic features of the genus Pœcilochætus is the great development of the nuchal organ, which, as already stated, consists of a broad, basal portion springing from the dorsal surface of the posterior end of the head, and of three long, tentacle-like processes extending backwards from it (fig. 7, *nuch.*). Of these three processes, the middle one is the longest, and may run at least as far backwards as segment 6, the lateral ones ending about segment 4 (fig. 1). The lateral processes have occasionally been observed with a secondary branch. The whole organ is covered with a number of sensory hairs, and each process possesses two lateral ciliated grooves, which run along the whole of its length and extend on to the basal portion (Pl. 11, figs. 42 and 47, *nuch.*).

Claparède (in Ehlers, 1874) and Levinsen (1883) have both described the three processes, but have failed to recognise their true nature as nuchal organs. These two authors have, however, shown clearly that the organ in question develops as an outgrowth from the posterior cephalic region. Such enlarged nuchal organs are by no means unknown amongst Polychætes, though none have yet been described having dimensions comparable with those of Pœcilochætus. The nuchal organs of Virchowia clavata figured by Viguier (1886) may be referred to, as well as those of Amblyosyllis spectabilis and Autolytus longiferiens, figured by Malaquin (1893). Gravier (1896) describes the nuchal organ of Notophyllum, which takes the form of two lappets extending from the posterior end of the prostomium to the middle of the third segment. Racovitza (1896) shows that the caruncle of the Amphinomidæ is an enlarged nuchal organ.

In the living Pœcilochætus the nuchal organ has a brown or brownish-green colour. Sections show that this colour is due to granules deposited in the epidermic cells, and also to a number of spherical bodies scattered through the tissue, which possess a single, deeply staining nucleus, and are filled with dark granules (Pl. 11, fig. 40).

The base of the nuchal organ is occupied by the nuchal ganglion (fig. 42, *nuch. gang.*), which has already been described (p. 104). The central axis of each of the processes of the organ is formed by a tube lined with mesoderm-cells, the tube being in direct communication with the general body-cavity of the first segment of the worm. The space between this central canal and the epidermis is filled with an irregular mass of cells, forming a loose tissue, in which may be seen many of the spherical bodies filled with granules mentioned in the last paragraph. Figs. 40 and 41 (Pl. 11), representing respectively a transverse section through one of the ciliated grooves and an enlarged section of a portion of the epithelium of a groove, show the minute structure of the tissue of the nuchal organ. The epidermis, excepting in the ciliated grooves themselves, consists of low epithelial cells crowded with dark-coloured granules, the granules being in many places congregated into masses of considerable size. The epithelial cells are covered externally by a layer of cuticle resembling the general body cuticle. No gland-cells, such as have been described in other parts of the body, have been observed in the nuchal organ.

The ciliated epithelial cells of the grooves are very large and much elongated, the protoplasm of the bodies of the cells is filled with dark granules similar to those found elsewhere in the organ, and the large oval nuclei lie near the bases of the cells, their long axes being parallel to the long axes of the cells. The structure of the external or ciliated ends of the cells presents features of interest, and can be seen from figs. 40 and 41. The cuticle (*cu. g.*) covering the cells undergoes a very considerable external thickening. In sections stained with methyl-blue-eosin the basal portion only of this cuticle stains a deep blue, carrying on the line of the general cuticle of the nuchal organ; the external thickened portion remains clear and unstained (*cu. g.*), and in favourable places is seen to be traversed by a series of faint lines running at right angles to its surface. Since these lines are much more widely separated than the cilia, they would seem not to be due to the cilia passing through the cuticle. Racovitza (1896) has described a very similar thickening of the cuticle in the caruncle of Euphrosyne Audouini. In the case of that worm, however, the thickening does not extend over the areas of cuticle lying just above the ciliated cells.

Immediately inside the cuticle is a narrow zone, which in sections appears clear, but across which the cilia can be seen to pass. This zone may, to some extent at least, be due to shrinkage of the bodies of the cells during preservation and their consequent withdrawal from the cuticle. It is followed by what, in transverse sections, appears as a deeply staining line (stained red in methyl-blue-eosin preparations). This line, on examination with high powers, resolves itself into a layer of deeply staining short rods (fig. 41, *sr.*), one rod apparently corresponding with each cilium. Within this layer of deeply staining rods the internal ends of the cilia can be followed for a considerable distance as faintly staining rods (blue in methyl-blue-eosin preparations), the diameters of which appear somewhat greater than the diameters of the cilia outside the body (fig. 41, *l. r.*). In the portion of the cell occupied by these rods the protoplasm of the cell appears clear, and not granular as it does throughout the general body of the cell. These relations will be seen to correspond with those found in the ciliated cells of the wall of the œsophagus (p. 117, *et seq.*, where the work of previous authors is discussed, Pl. 11, fig. 44) and in the hair-bearing cells of the lateral organs (p. 108, Pl. 10, figs. 34, 36, 39).

In the nuchal organ of Pœcilochætus, I have failed to identify nerve-cells, other than the ganglion-cells already described in the basal portion of the organ. It is quite possible, however, that some of the cells of the intermediate tissue are really such nerve-cells.

For a full historical account of the nuchal organ in Polychæta, as well as for an excellent description of the detailed histological structure of that organ in a number of different types, reference should be made to the paper by Racovitza (1896) already several times mentioned.

Eyes.

As previously stated, Pœcilochætus possesses four eyes, one pair on the dorsal surface of the prostomium, and a larger pair on the ventral surface. All four eyes have practically the same structure, and are of a very simple type. Fig. 33 (Pl. 10) represents a section through one of the ventral eyes cut in the longitudinal vertical plane. The eye consists of a single large optic cell with one nucleus. The protoplasm of the swollen, rounded end of the cell is slightly modified, being more transparent than that found in the rest of the cell, and showing indications of a radial structure. This end of the cell is surrounded by a large cup-shaped mass of black pigment, made up of numerous spherical drops of black substance. A nucleus can often be detected at the outer margin of this mass of pigment, but I have been unable to satisfy myself as to whether more than one nucleus belongs to each; that is to say, whether the pigment cup is unicellular, or whether it consists of several cells.

Such simple eyes are now well known amongst the Platyhelminths, for instance, in Planaria torva, and also in certain Polychætes, as, for example, Spio fuliginosus and Polyophthalmus pictus. A full account of the literature of the subject, together with a wealth of new observations, will be found in the series of papers "Untersuchungen über die Organe der Lichtempfindung bei niederen Thieren," by Richard Hesse (see especially Hesse, 1897 and 1899).

Alimentary Canal.

The Divisions of the Alimentary Canal.—The external features of the mouth are seen in fig. 8 (Pl. 8), and have already been described (see p. 88). The animal possesses a short proboscis with thick walls, which in preserved specimens is always almost if not entirely withdrawn into the mouth. Fig. 42 (Pl. 11) represents a section through these parts. The external folds surrounding the mouth are seen, as well as the median tentacle (*m. tent.*), which has its point of insertion close to the anterior edge of the mouth, into which its basal portion can be withdrawn.

The portion of the alimentary canal extending from the mouth to the posterior septum of the eighth segment may be conveniently divided into two parts corresponding to what are known in other Polychætes as œsophagus and pharynx (or gizzard). There is, however, no definite line of demarcation between these two parts. The œsophagus is lined by elongated, ciliated epithelial cells, outside which is a thin layer of annular muscles followed by a thin layer of longitudinal ones. Proceeding further backwards the epithelial layer becomes narrower, the cells being considerably less elongated, whilst, on the other hand, the muscular layers, especially the layer of annular muscles, become much more strongly developed (cf. figs. 42 and 48 with fig. 43). It is this muscular portion which may be termed the pharynx (*ph.*) In its hinder part the epithelium is thrown into folds or villi, and at the point where the septum of segment 8 is attached to the alimentary canal one large fold, forming a kind of valve (fig. 43, *v.*) seems to constitute a definite line of demarcation between the pharynx and the intestine. As is explained on p. 123, the septa in this region of the body are pushed very much backwards; the junction of the pharynx and intestine, although really at the posterior end of the eighth segment, may lie as far back as the level of the twelfth parapodia. From the posterior septum of segment 8 to the posterior septum of segment 13, the intestine continues as a comparatively straight tube, not differing much in structure from the pharynx, excepting that the muscular layers are rapidly reduced until they almost entirely disappear (figs. 43 and 50). In segments 14 and 15 the intestine is considerably dilated, but narrows again as it passes through each septum. In the segments from 16 backwards, this enlargement of the intestine in each segment becomes very great, so that the dilated intestine occupies a large part of the body-cavity (figs. 1 and 58). In the living worm these intestinal pouches are constantly expanding and contracting, the movements of the intestine constituting, in the posterior region of the body, the principal mode of circulation of the blood.

Ciliated Groove of the Alimentary Canal.—Transverse sections show the existence of a deep, longitudinal ciliated groove running along the mid-ventral line of the alimentary canal throughout its entire length. A similar groove has been described in many Polychætes, and is homologous with the secondary intestine ("nebendarm") of the Capitellids (Eisig, 1887).

The Epithelium of the Alimentary Canal.—The epithelium of the alimentary canal, though differing much in appearance in its different parts, consists essentially of cells of two kinds, (1) columnar epithelial cells, and (2) goblet-shaped gland-cells lying between the columnar cells and opening by more or less narrow necks into the lumen of the canal.

The columnar epithelial cells of the œsophagus (Pl. 11, fig. 44) are narrow and elongated, with large, oval nuclei, the long axes of which lie parallel to the long axes of the cells. The cells themselves are strongly ciliated and show a characteristic structure, similar to that which exists in other ciliated cells of the worm (compare the groove of the nuchal organ, p. 114, the lateral sense-organs, p. 108, and the epithelium of the genital funnels, p. 135). The appearance presented by the ciliated borders is seen in fig. 44. The surface of each cell is covered by a thin cuticle (*cu.*) continuous with the cuticle of the external body surface. Immediately within this cuticle is a clear space through which the inner ends of the cilia are seen to pass. This clear space, which may in part at any rate be due to contraction of the contents of the cells during the preservation of the tissue, is bounded internally by a layer of deeply staining short rods (*s. r.*), which appear to be in reality slightly thickened, deeply staining portions of the individual cilia. In sections these rods lie in a straight line which runs parallel to the cuticle. Beyond this deeply staining layer of rods the ends of the cilia (*l. r.*) can still be traced for some little distance into the protoplasm of the cell-body, which is at first clear excepting for the striation due to these inner ends of the cilia, and subsequently becomes granular, many of the granules being of a characteristic yellowish-brown colour. The cilia cannot be traced as far as the nuclei of the cells. In sections of material fixed in Hermann's fluid and stained with a mixture of methyl-blue-eosin (fig. 44), the cuticle stains deep blue, the cilia faintly blue, the layer of short rods bright red, the cell protoplasm bluish, whilst the nuclei are clear, with chromatin granules and network stained deep red.

The structure of the ciliated cells above described, as well as those of the nuchal groove (p. 114) and the hair-bearing cells of the lateral sense-organs (p. 108), agrees with that found by Engelmann (1880) in the ciliated cells from the intestine and gills of Cyclas cornea and Anodonta, and in the ciliated cells from the nose of the frog. Engelmann clearly describes the short rods under the name of "Fussstücke," and also the internal prolongations of the cilia within the cells, which he was, however, able to trace much further into the body of the cell than I have succeeded in doing. He also found between the short rods and the cilia proper a certain differentiation of the substance of the bases of the cilia, which he calls the "bulbus." These "bulbi" would appear to correspond to the secondary layer of short rods described in the present paper at the bases of the sensory hairs of the lateral sense-organs (p. 108, Pl. 10, figs. 34, 36, 39).

Englemann states that Eimer was the first to describe correctly the relations of the short rods (Fussstücke) to the cilia, and he gives several other references to previous papers dealing with the subject.

More recently Greenwood (1892) has shown a very similar structure in the ciliated cells of the intestine of Lumbricus, though in the latter worm, to judge by the figures, the layer of short, deeply staining rods is less marked. Greenwood, however, states (p. 245) "the cilia occasionally bear tiny varicosities before they pass into the body of the cell. Under a sufficiently high power these are distinguishable as belonging each to a ciliary thread, and they recall Heidenhain's description of similar thickenings, which may be seen under suitable conditions at the base of the intestinal rods of the dog."

The similarity in structure of the ciliated cells of, say, the œsophagus and nuchal organ of Pœcilochætus to that of the cells of the intestinal mucous membrane of vertebrates furnished with a "striated border," as described by Heidenhain (1888), is very striking, especially if his fig. vi is compared with my figs. 44 or 41, and seems strongly to support the suggestion contained in Greenwood's paper, that the cells of the vertebrate intestine may be modified ciliated cells.

Galvagni (1903) has just published a description with figures showing a similar structure in the ciliated cells of the alimentary canal of Ctenodrilus to that found in Pœcilochætus.[1]

In concluding the discussion on these ciliated cells it seems worth while to draw attention to the possibility that the "short rods" described in this paper ("Fussstücke" of Engelmann) are homologous with the middle-piece ("Mittelstück") so well known in spermatozoa. The staining reactions of the two structures are similar, and they occupy similar positions in relation to the cilium and flagellum respectively.

The goblet-shaped gland-cells in the epithelium of the œsophagus present themselves in at least three forms. In preparations preserved and stained by my usual method these cells show the following features (see Pl. 11, fig. 44) :—(1) Goblet-shaped cells crowded with granules which stain bright red, the bright red granules filling both the body of the cell and the long neck to where it opens into the lumen of the œsophagus; the intermediate substance of the cell remains unstained; the chromatin of the nucleus stains red; the nuclear membrane and the body of the nucleus are clear and unstained (fig. 44, *gl.* 1).

(2) Goblet-shaped cells containing granules, which are less

[1] Since the above was written an important paper on the epithelium of the intestine of Polychætes has been published by Brasil (1904) in which the structures here described are fully dealt with.

numerous than those in cells of the previous type and stain blue instead of red (fig. 44, *gl.* 2).

(3) Cells still of the same general shape, but less swollen, without granules, but filled with a homogeneous substance staining faintly blue and showing at most slight indications of a network such as is usually produced by the action of preserving fluids; the nuclei of these cells stain more deeply and more diffusely than those of the previous types, their ground substance taking on a faint blue tint, whilst the chromatin is red or purple (fig. 44, *gl.* 3).

Cells of the first and second kinds are clearly actively secreting cells, whilst those of the third kind seem to be cells of the second which have completely discharged their secretion and are in a resting condition, in all probability waiting to commence the secretory process upon suitable stimulation. In some specimens nearly all the gland-cells in the œsophagus are in the condition last described.

As will be seen by comparing the two sets of figures and the two descriptions, the gland-cells of the œsophagus show many points of resemblance with the gland-cells of the skin and of the parapodial cirri.

The structure of the epithelium of the pharynx and of the anterior portion of the intestine is essentially the same as that which has been described for the œsophagus; the cells, however, become gradually less elongated in shape, and the number of gland-cells diminishes.

At about segment 16 or 17 the type of intestinal epithelium which persists through the greater part of the body of the worm is established. This epithelium is found in two markedly different conditions, which appear to depend upon whether the intestine is filled with food and digestion is actively going on, or whether food is absent from it. These two conditions are illustrated in figs. 45 and 46 (Pl. 11).

Fig. 45 shows the state of things which is found when food is present and digestion is actively proceeding. The epithelial cells (*ep.*) are large and swollen, whilst the gland-cells have shrivelled till little more than the nucleus is visible (*gl.*).

The shape of the epithelial cells may differ considerably from that of those found in the anterior part of the alimentary canal already described. In those shown in fig. 45 the cell-body is short and broad, but more elongated cells are also common. The cells are filled with large granules, which have a dark brown colour in preparations preserved with osmic acid mixtures. The granules are crowded together at that surface of the cell which immediately borders the lumen of the intestine, and are more scattered throughout the rest of the cell protoplasm. These cells have not, in my preparations, the appearance of being ciliated. Their surface is, however, covered with a faintly staining substance, which might possibly represent broken-down cilia, but is more probably a layer of the food-contents of the intestine, which is being absorbed by the cells. In the same sections the cilia are often sufficiently well-marked on the cells of the intestinal groove. The nucleus is situated near the base of the cell. In the condition now being described (fig. 45) it is large in size and stains deeply (diffuse blue with red granules in methyl-blue-eosin preparations). It consists of an outer membrane filled with granules, and possesses a single nucleolus. This nucleolus is surrounded by a clear space, the space being bordered by a membrane which carries on its outer side a deeply staining, hemispherical cap. The nucleus thus resembles very closely the nuclei of the parapodial gland-cells already described (cf. fig. 26 and p. 98). Nuclei showing clearly all the points mentioned are not, however, met with very frequently in the preparations. The bases of these cells lie close to the blood-sinus which completely surrounds the intestine (fig. 45, *i.bl.s.*).

If one may be permitted to hazard a guess at the physiological processes which are going on in these cells, merely from a study of their appearance and the arrangement of their parts, it may be suggested that the cells at their free ends are absorbing from the cavity of the intestine food material already partly digested by the action of the secretion from the gland-cells. A portion, at least, of this material appears in the cells in the form of the yellowish-brown granules, which are thickly congregated at the surface of absorption. The nucleus is obviously in a very active state, and its position at the base of the cell, at the point of contact of the cell with the intestinal blood-sinus, seems, if we accept the view advocated by Korschelt that the nucleus is generally to be found where the chief function of the cell is in active progress, to suggest that the food substance there undergoes transformation and is passed through the cell-wall into the blood.

The second condition in which the epithelial cells of the intestine are found (when the intestine does not contain food) is illustrated in fig. 46. The gland-cells (*gl.*), which in the former state were shrivelled and inert, are now large and active. They are pear-shaped, filled with granules (which in methyl-blue-eosin preparations stain bright red), and their necks extend quite to the surface of the epithelial layer. The nuclei are clear and transparent, with deeply staining chromatin, the greater part of which is concentrated in a single large nucleolus.

The columnar cells (*ep.*), on the other hand, contain no granules; their protoplasm stains faintly and diffusely (blue in methyl-blue-eosin preparations), and shows only an indefinite reticulation probably due to the action of the reagents. The nuclei are much smaller than in the active epithelial cells previously described (cf. figs. 45 and 46), the chromatin granules stain less deeply (red), and the whole nucleus is diffusely tinted (blue). It would seem, therefore, that whilst the gland-cells are now active the columnar cells are inert.

The epithelium in only two other parts of the alimentary canal calls for mention, namely, that in the ventral ciliated groove and that in the terminal segments of the body.

The cells of the ciliated groove are elongated and distinctly ciliated, though they do not show the layer of deeply staining short rods, which was found in the ciliated cells of the œsophagus.

The epithelium of the intestine in the posterior region of the body (rectum) differs only from that already described for the intestine in the fact that all the cells are ciliated, the cilia being very long. The action of these cilia can be clearly seen in the living worm.

Body-cavity.

The well-marked segmentation of the body seen externally is equally distinct internally, each segment being separated from that which follows it by a transverse septum. The septa, the first of which lies between the first and second segments, appear to divide the body-cavity into a number of separate compartments, between which no communication can be shown to exist. These compartments are not, however, of equal size, for in the region occupied by the muscular pharynx the septa, instead of lying in a vertical plane corresponding to that of the external segmentation of the body, are pushed backwards for a considerable distance. This pushing backwards of the septa, which is shown in the sagittal section represented in fig. 47 (Pl. 11) and in the horizontal section fig. 43, commences with the septum at the posterior end of segment 5, reaches a maximum in segment 8, and is still obvious in segment 12. The posterior septa of segments 8, 9, 10, and 11 all extend back to the region, which external segmentation indicates as segment 12, and that of segment 12 is pushed back into 13. The septa of segment 8 to 11 join the alimentary canal immediately behind the point where the pharynx passes into the intestine (fig. 43, *v.*). These septa are also noteworthy from the fact that the muscle-fibres, which are present to a considerable extent in the septa of most of the segments of the body, are here developed to a very remarkable extent, so that septa 8 to 11 have become highly muscular organs. This muscular character of the septa, combined with the manner in which they are pushed backwards, seems to suggest that they are concerned with the protrusion of the anterior portion of the alimentary canal in the form of a proboscis, and probably also with the extension of the palps. I have only once seen a protrusion of the proboscis, and it did not then extend much beyond the front of the head. The structures just described, however, appear to suggest the possibility of a much greater protrusion.

In living specimens of Pœcilochætus an indication of the backward extension of the septa of segments 5 to 12 can be seen in the backward course of the lateral blood-vessels, which run in the septa (fig. 1 and p. 126).

In the segments from the thirteenth backwards, the internal and external segmentation correspond.

Each of the septa dividing the body-cavity consists of a double layer of cœlomic epithelial cells with a layer, more or less strongly developed, of muscle-fibres between. The epithelium is extended over the main body muscles, and over the other organs of the body. On most organs, however, the cells are seldom much developed, their presence being often only indicated by occasional nuclei.

Extensions of the body-cavity into the interior of the nuchal organ and of the palps are mentioned in the paragraphs dealing with those structures.

Musculature.

The muscles of the body-wall, as is usual in the Polychætes, are arranged in two layers, a layer of annular muscles and a layer of longitudinal. Of these two layers, however, the annular is very feebly developed in Pœcilochætus, whilst the longitudinal is well developed. The principal muscles in each segment are massed into four bundles, two dorsal lying on either side of the dorsal blood-vessel and two ventral on either side of the nerve-cord. The slight development of the annular muscles would appear to be connected with the more or less sedentary habits of the worm. The annular muscles attain their greatest development in worms which burrow constantly and rapidly in the soil (e. g. Nephthys, Aricia).

Bands of oblique muscles run from the outer dorsal edge of the ventral nerve-cord on each side, pass over the longitudinal ventral muscle-bands, and are inserted in the lateral walls of the body between the parapodia.

External Muscles of the Lateral Organs and Muscles of the Chætal Sacs.—Four large bands of muscle are inserted at the apex of each lateral organ (Pl. 10, figs. 34 and 37, *musc.*), viz. (1) a band which runs downwards and inwards to the inner end of the neuropodial chætal sac, which is clearly one of the two bands used to protrude the chætæ; (2) a similar band running upwards and inwards to the base of the notopodial chætal sac; (3) a broad band of muscle which runs from the lateral organ downwards, passes behind the chætal sac and is inserted in the ventral body-wall below the base of the neuropodial cirrus, and (4) a similar band running upwards and inserted in the dorsal body-wall above the base of the notopodial cirrus. Lying in contact with the muscle-fibres of bands 3 and 4 are a number of fibres, which run direct from the dorsal to the ventral body-wall. These pass close to the apex of the lateral organ, to which they are joined by connective tissue, but they have no free ends inserted in that apex.

In addition to the muscle-bands described above, (1) and (2), running from the apex of the lateral organs to the inner ends of the two chætal sacs, a second band runs from the inner end of each sac, passes in the one case downwards and outwards and in the other upwards and outwards and is inserted in the body-wall. Thus each sac has two strong muscles from its apex to the body-wall, one above and one below, by the contraction of which it and its chætæ are protruded.

Blood System.

The anatomy of the vascular system constitutes one of the most striking and interesting features of Pœcilochætus. The bright scarlet of the blood gives to the anterior portion of the body its characteristic colour, and the alternate filling and emptying of the larger vessels produces an appearance of rapid colour-change. A further change of colour is seen also, which is due to changes in the chemical character of the blood. If a worm be allowed to remain for some time in a vessel containing only a small quantity of sea-water, the bright scarlet of the blood changes to a dull purple-red, but the original colour immediately reappears on the addition of a new supply of water, as it does under similar circumstances in Magelona (cf. Benham, 1896). The red colour therefore would seem to be due to the presence in the blood of one of the respiratory pigments.

The general arrangements of the principal vessels is illustrated in fig. 1, which has been constructed from observations on the living worm, corrected and extended by the examination of sections. For the purposes of description the body of the worm must be divided into three regions, an anterior region consisting of segments 1 to 11, an intermediate region, comprising the four segments 12, 13, 14, and 15, and a posterior region from segment 16 to the end of the body.

Anterior Region.—Between the alimentary canal and the dorsal body-wall there is in the anterior region a large, muscular, dorsal vessel of cylindrical shape capable of very considerable expansion, waves of expansion and contraction passing along it from behind forwards.

Corresponding with each of the body segments from the third to the eleventh, a lateral vessel is given off on each side from the dorsal vessel, and runs outwards and downwards in the posterior septum of the segment. Owing to the fact already described that the posterior septa of segments 5 to 11 are pushed backwards, the origins of the lateral vessels in these segments, running, as the vessels do during the first part of their course, actually in the septum, are also carried backwards, the vessels being in consequence much elongated and running forwards (Pl. 7, fig. 1). In this way the lateral vessels belonging to segment 7 arise from the dorsal vessel at about the plane of the junction of the ninth and tenth parapodia, whilst the lateral vessels of segments 8, 9, 10 and 11 arise close together about the level of the twelfth parapodia.

On reaching the base of the parapodium of the segment to which it belongs, the lateral blood-vessel in each case leaves the septum and sends a loop forwards into the parapodium, the loop returning upon itself and joining the septum again in the neighbourhood of the internal opening of the nephridium. The vessel here divides into two branches. One of these branches passes downwards and inwards and opens directly into the large longitudinal ventral blood-vessel, the other passes through the septum close to the tube of the nephridium, and in the segment behind divides up into a number of blind, finger-shaped processes, which spread out in the body-cavity of that segment. Under favourable circumstances these finger-shaped processes can be seen in the living worm, alternately expanding and contracting as they fill with the bright red blood and empty themselves again. On one occasion, in a worm the body-wall of which had burst on compression, I was fortunate enough to see one of these clusters of finger-shaped vessels lying outside the body and to satisfy myself that each process visible ended blindly. The vessels when filled with blood are very conspicuous, and easily followed in sections (Pl. 11, figs. 48 and 49), and in spite of repeated attempts I have never been able to find that this cluster of vessels has any communication with the rest of the blood system, excepting through the branch of the lateral vessel of the segment in front, which accompanies the nephridial tube through the septum dividing the two segments. Fig. 51 (Pl. 12), drawn from a longitudinal vertical section, shows clearly the branch of the lateral vessel (*b. lat. v.*) passing back through the septum into the segment behind and there breaking up into finger-shaped processes (*f. p.*). Fig. 49 (Pl. 11) represents a transverse section through the finger-shaped processes (*f. p.*), and shows the great enlargement of the blood-vessel which can take place at the point where the processes are given off. Fig. 48 (Pl. 11) shows well the latter part of the course of the lateral vessels (*lat. v.*) to the ventral vessel.

Shortly after leaving the dorsal vessel, each lateral vessel gives off a branch, which breaks up upon the wall of the œsophagus and pharynx, uniting with and helping to form a rich network of blood-vessels, which extends over the surface of these organs (Pl. 7, fig. 1). This network also gives rise to vessels which start from the under surface of the œsophagus and pharynx and pass directly downwards to the ventral vessel (fig. 48, *int. v.*) Blood can thus pass either directly from the dorsal to the ventral vessel through the laterals, or indirectly after passing through the network on the walls of the alimentary canal.

At its anterior end, immediately behind the brain, the dorsal vessel bifurcates (Pl. 7, fig. 1), sending a large vessel to each of the palps. These large vessels pass along the axes of the palps (Pl. 10, fig. 30), and in the living worm are subject to rhythmical pulsations, which keep the blood within them constantly in motion. The palps appear to be one of the principal organs of respiration of the worm (see p. 86).

Immediately after entering the palp the large blood-vessel gives off a branch, which passes downwards and backwards through the first and second segments. It sends one secondary branch to the œsophageal network and another through the posterior septum of the second segment to form a cluster of blind, finger-shaped vessels in the third segment, and then, passing below the œsophagus, joins with its fellow of the opposite side to form the anterior end of the ventral vessel. These structures can best be understood from an examination of fig. 1.

As only one blood-vessel passes along the axis of each palp, it would seem that the pulsations of the vessel itself must take place in such a manner as alternately to drive blood in and then out of the vessel, but owing to the readiness with which the palps are thrown off on the slightest irritation, direct observations on the point are not easy to make.

The Middle Region.—The modification of the vascular system in segments 12, 13, 14 and 15, the middle region of the body, is of special and peculiar interest.

In each of these segments the dorsal vessel is itself much enlarged, forming on either side large lateral pouches, which are alternately inflated with blood and emptied (Pl. 7, fig. 1; Pl. 11, figs. 43 and 47, *p. dv.*). When fully inflated the pouches occupy almost the whole of the body-cavity, and the wave of expansion and contraction, passing from segment to segment from behind forward, is a striking phenomenon.

The forward movement of the blood from one segment to the next in front is regulated by a series of valves situated in the dorsal vessel between each successive pair of pouches, as well as immediately anterior to the first pair and posterior to the last. There are thus five valves altogether. These valves, two of which are shown in sagittal section in fig. 50 (Pl. 11), consist of somewhat stout membranes composed of spindle-shaped cells, attached ventrally to the wall of the blood-vessel, but with a free dorsal edge, which pressed from in front comes into contact with the wall of the vessel and prevents the blood from passing backwards. In fig. 50 the anterior valve (*vl. seg.* 14) is open, whilst the posterior valve (*vl. seg.* 15) is closed. It is clear that contraction of the walls of the blood-vessel and its lateral pouches will force the blood forwards, whilst the valves will prevent any blood from going in the opposite direction.

It must be pointed out that the lateral pouches of the dorsal vessel in segments 12, 13, 14 and 15 are not swollen lateral vessels, such as are described by Benham (1896) in Magelona, for in sections the true lateral vessels, similar in their general relations to those of the anterior segments, and like them giving rise to a cluster of finger-shaped processes in the segment behind, are easily seen and followed. These lateral vessels arise from the dorsal vessel in each case behind the lateral pouches, at the point where the dorsal vessel passes through the posterior septum of the segment, and they run throughout the greater part of their course in this septum.

The Posterior Region.—In the posterior region of the body, from segment 16 backwards, the arrangement of the vascular system undergoes a great change. The dorsal vessel can no longer be distinguished as a separate organ, but the dorsal vessel and the network of blood-vessels which surrounded the œsophagus and pharynx, have as it were run together to form one large sinus, which completely surrounds the intestine (figs. 45 and 59, *i. bl. s.*). The circulation of the blood is now brought about, not by the contraction of a blood-vessel with highly muscular walls, but by the contraction and expansion of the segmental pouches of the intestine.

The intestinal sinus communicates with the ventral vessel by short, vertical branches, and it also gives off in each segment, from the region of the narrowed portion of the intestine behind the intestinal pouches, the lateral blood-vessels. Each lateral blood-vessel runs in the posterior septum of the segment, at first upwards and outwards, then outwards and downwards, to the base of the gills on the notopodium. It enters the first gill filament, to the tip of which it runs; it there turns sharply on itself and comes back again to the base of the gill, thus forming a single, simple loop, which occupies the whole of the interior of the gill filaments (Pl. 10, fig. 31). After having formed a similar loop in all the other gill filaments the blood-vessel again runs in the posterior septum of the segment, its course being inwards and downwards to the ventral vessel, which it joins. During this latter part of its course the vessel sends back a branch along the tube of the nephridium into the segment behind, which appears to supply not only the nephridium, but also the genital organs, which lie along the tube of the nephridium (Pl. 12, figs. 52 and 60, *b. lat. v.*). There is, however, no obvious formation of a cluster of blind, finger-shaped processes such as was met with in the anterior segments of the worm.

One point of interest in connection with the lateral vessels remains to be noticed. In describing the course of the lateral vessels of the anterior segments, it was stated that each vessel, before sending back its branch to the finger-shaped processes in the segment behind, ran forwards and formed a simple loop at the base of the parapodium. It will be remembered that the parapodia of these anterior segments have no gills, but the loop just mentioned would seem to represent in a rudimentary way the loops of the lateral vessels which supply the gill filaments in the posterior gill-bearing segments.

The Structure of the Walls of the Blood-vessels.—The different layers of the walls of the blood-vessels attain their greatest development in the dorsal vessel. This vessel is lined internally by an epithelial layer consisting of flattened cells, the general height of which is less than the diameter of their nuclei, so that the portion of the cell in the immediate neighbourhood of a nucleus often appears to protrude into the blood-space. The bodies of the cells generally remain clear and unstained.

Proceeding outwards from this epithelial layer, one finds a layer of longitudinal muscle-fibres, which is followed by several layers of annular muscles, this part of the wall being especially developed in the dorsal vessel. The whole vessel is covered externally by a layer of cœlomic epithelial cells, which form the lining of the body-cavity. Like that of the cells lining the vessel internally, the protoplasm of these external cells remains clear and unstained (Pl. 11, fig. 50).

The differences met with in the structure of the walls of the other blood-vessels of the body are due to the reduction of the various layers, more especially of the muscular layers. In the ventral vessel, as well as in the lateral pouches of the dorsal vessel, the epithelial layers are well developed, but the muscular layers, though still obvious, are greatly reduced. In the lateral vessels and their various branches, especially when extended with blood, only a thin membrane in which an occasional nucleus is seen can generally be recognised. It is probable, however, that both epithelial layers are present, whilst the muscular layer has almost, if not entirely, disappeared.

In the external wall of the intestinal blood-sinus the two epithelial layers can be made out, with a layer of muscle-fibres between them. Internally the bases of the intestinal epithelial cells appear to be separated from the blood-space by a thin layer of very flat cells, but the existence of this layer is not easy to demonstrate satisfactorily. Strands of tissue cross the blood-space at intervals, having the appearance of prolongations of the epithelial-lining-cells.

It should be noted that in the walls of the intestinal pouches no muscle-fibres can be demonstrated excepting those in the outer wall of the blood-sinus, and the contractions of the pouches would seem to be brought about by these muscles (figs. 45 and 46).

The Blood.—The blood of Pœcilochætus is a bright scarlet coloured, homogeneous fluid without corpuscles of any kind. Very occasionally in sections an isolated cell, having a similar appearance to the cells of the epithelial lining of the blood-vessels, is seen in the blood-space. Such cells are probably only cells of this epithelium which have become detached.

The change of colour of the blood caused by want of oxygen has already been described (see p. 126).

Nephridia and Nephromixia.

In small living examples of Pœcilochætus viewed from the ventral surface the nephridial organs can be seen as short greenish-brown tubes, one pair in each segment, commencing at the level of the anterior septum, running first backwards and then turning outwards and forwards, and ending on the antero-ventral face of the parapodium. By examining the more transparent segments near the tail end of the worm with a moderately high power it can be further seen that anteriorly the nephridium opens in a large ciliated funnel, and that the whole length of the tube from the anterior internal opening to the external opening at the base of the parapodium is strongly ciliated.

The details of the structure of these organs can be made out with some clearness in series of sections of specimens preserved in Hermann's fluid, more especially in longitudinal vertical (sagittal) and in horizontal sections of the worm.

Adopting the nomenclature of Goodrich (1900, p. 742), it may be stated that both nephridia and nephromixia are found in Pœcilochætus. Nephridia, opening by nephridiostomes into the next segment in front, are found in the anterior segments (4 to 16), whilst compound organs (nephromixia), consisting of nephridia with large genital funnels (gonostomes) attached to the nephridiostomes, are found in the genital segments from segment 17 backwards.

In the two anterior body segments (1 and 2) no trace of a nephridium has been detected. In segment 3 the nephridiostomes of the organs of the following segment are well developed, and they, as well as the organs to which they belong, have the structure about to be described, which is typical of that in all the segments from 4 to 16. The nephridial tubes in each of these segments are simple and J-shaped (cf. fig. 58), running from the anterior septum of the segment straight backwards, then turning outwards and forwards to the external opening on the parapodium, as already described. The cells lining the tubes are low, elongated, ciliated cells, which contain large numbers of excretory granules. The lips of the nephridiostomes, which lie close to the posterior septum of the segment next in front, form a structure of considerable size, with a small ciliated aperture which puts the lumen of the nephridial canal into communication with the body-cavity of the latter segment. Fig. 55 (Pl. 12) represents a transverse section through a nephridiostome of one of these segments, and fig. 54 a sagittal section. The lips (*lp.nst.*) form masses of swollen cells filled with vacuoles and granules. These masses of cells are attached to the posterior septum of the segment along a somewhat narrow border, and protrude for some little distance into the cavity of the segment (cf. fig. 47). The nephridiostome itself (*nst.*) lies near the lateral wall of the body, but the swollen masses of cells forming its lips run inwards almost to the median line of the body. This inward extension of the lips is seen in the transverse section (fig. 55), and is also well shown in horizontal sections. Externally the lips are covered by a layer of cœlomic epithelium (fig. 54).

Fig. 57 (Pl. 12) shows the appearance presented by cells of the nephridial lip under a high power, the figure being drawn from a section of material preserved in Hermann's fluid and stained with methyl-blue-eosin solution. The cells are much swollen and vacuolated, and contain, in addition to the nuclei (*n.*), large numbers of granules of various sizes, which stain bright red in the preparations. The protoplasmic ground substance of the cells stains blue, but the cells, being highly vacuolated, this blue-staining substance is not uniformly distributed through them. The red granules are often surrounded by a spherical mass of blue-staining protoplasm, in the case of the smaller granules two or three being found within each sphere. The appearances suggest that the red granules are first formed within the blue spherical masses, that they gradually increase in size within these masses, whilst the latter subsequently become swollen and break down, giving rise to the vacuolated appearance of the general cell protoplasm with free red granules floating in it.

In the segments from 17 backwards the structure and general shape of the nephridia themselves (fig. 58) remain practically the same as in the anterior segments, excepting for the fact that a large ciliated genital funnel is added to the nephridiostome. The arrangement of this genital funnel will be gathered from the sagittal section shown in fig. 52 (Pl. 12). The upper portion of the funnel is formed by a great development of the cells of the cœlomic epithelium covering the face of the septum, which are much increased in size and richly ciliated (*lp. gst. d.*). These ciliated cells cover a large part of the anterior face of the posterior septum. The lower portion of the genital funnel (*lp. gst. v.*) is composed of ciliated cells attached to the lower lip of the nephridiostome, which form a membrane hanging freely in the cavity of the segment, and with the upper lip constituting a funnel-shaped structure surrounding the nephridiostome. This genital funnel (gonostome) is composed of cells of quite different structure to those of the nephridium, and the line of demarcation between the nephridiostome and gonostome is well marked. Fig. 56 shows the appearance of these cells. Their protoplasm is clear, staining only feebly, and contains no granules such as are found in the nephridial epithelium. The cilia are long and their bases extend into the cell-body as deeply staining rods.

The funnels as well as the nephridiostomes and upper portions of the nephridial tubes are often filled with the genital products.

From the description above given it will be seen that in these genital segments we have to do with a compound organ, consisting of a nephridium and a genital funnel combined, which Goodrich, to whose very valuable papers we are indebted for much of our recent knowledge of similar structures amongst polychætes, has termed nephromixia.

Genital Products.

The genital products in Pœcilochætus are first found in the seventeenth segment, and occur in every segment behind that, with the exception of the segments at the extreme end of the body.

Ova.—The gonads lie along the inner and upper sides of the nephridial tubes (Pl. 12, figs. 58 (horizontal), 59 (transverse) and 60). As the ova increase in size they separate off from the gonads and pass upwards into the general body-cavity, where the process of maturation continues (fig. 59).

In their earliest recognisable stages (fig. 60) the developing ova appear simply as a number of enlarged nuclei, lying in a mass of cell substance in which no definite cell outlines are shown in the preparations. As the nucleus and cell-body enlarge, the individual ova become clearly marked out by a definite cell membrane, although for a time they continue to adhere together. The nucleus develops one large, deeply staining nucleolus and a number of smaller granules of chromatin (fig. 61). A well-developed yolk nucleus, horse-shoe shaped in section, forms a cap over about one half of the nucleus. This yolk nucleus consists of deeply staining granules (fig. 60 and 61, *yk. n.*) which in methyl-blue-eosin preparations stain blue, in contrast to the nucleolus and chromatin granules, which stain red. It disappears as the egg continues to mature, when the whole of the protoplasmic contents of the egg becomes crowded with yolk granules, which stain blue in the preparations (figs. 62, 63 and 64).

The ripe eggs are lenticular in shape, the long diameter being about double the short. Around the line of greatest circumference there is a single row of vesicles, seen clearly in the optical section of a fresh egg represented in fig. 64. These vesicles are pear-shaped and open on the exterior surface of the egg by means of fine tubes passing through the thick egg membrane. In fresh eggs the vesicles look more clear and transparent than the general egg substance; in sections a small, shrunken mass of slightly staining substance appears in the centre of each (figs. 62 and 63). The function of these vesicles is unknown, though their appearance suggests that they may contain a fluid which is at some stage secreted on to the surface of the egg. That the vesicles are intimately connected with the egg membrane is shown by the fact that when the protoplasmic contents of the egg shrink, as they do when the egg is allowed to remain soaking for some time in sea water, the vesicles completely retain their position around the circumference of the egg membrane, their bases being connected by threads of protoplasm with the shrunken mass of the cell contents. This is shown in fig. 65, drawn from a fresh egg which had remained for some hours in sea-water.

Vesicles similar to those just referred to were described and figured by Claparède (1868) in Nerine cirratulus, in which form one circle of them is found round the equator, just as in the eggs of Pœcilochætus. In Nerine auriseta, on the other hand, Claparède found three irregular rows of similar vesicles arranged round the greatest circumference of the elliptical eggs. In neither case, however, does Claparède describe the fine tubes which place the vesicles in communication with the exterior. The following observation, which he records concerning the eggs of Nerine auriseta, is of interest:—" L'action d'une faibles solution de carminate d'ammoniaque les modifie d'une manière remarquable. Elles se colorent assez rapidement en rouge intense, tandis que le vitellus ne se teint qu'en rouge pâle, et que le chorion reste parfaitement incolore." This observation appears to me to agree better with the suggestion made above that the vesicles may contain a secretory product than with the view set forth by Claparède:—"Je ne puis m'empêcher de supposer que ces vésicules (ou peut-être mieux ces sphères protoplasmiques) jouent un rôle important dans la formation du blastoderme" (Claparède, 1868, p. 333).

The egg membrane of the ripe egg of Pœcilochætus is very thick and stains deeply (blue in methyl-blue-eosin preparations). Its surface is ornamented by raised lines, which form an irregular pattern upon it (fig. 66, from a fresh egg). These lines or ridges are clearly visible in sections (figs. 62 and 63).

The germinal vesicle is large, its diameter being little less than the smaller diameter of the egg. It contains one large nucleolus, which is composed of a larger and a smaller spherical portion (cf. fig. 64, from a fresh egg, and fig. 63, from a section). Fig. 62 shows a condition of the nucleolus which is very often seen in preserved material. It here consists of a very deeply staining portion, which takes the form of a cap resting upon a more or less spherical, transparent vacuole. Such a form of the nucleolus is not uncommon in the eggs of other animals (for literature see Korschelt and Heider, 1902). When the nucleolus is in the state just described, a number of other deeply staining granules are present in the germinal vesicle.

Nothing has been ascertained as to the history of the eggs after they leave the body of the worm.

The Spermatozoa.—The place of origin of the male germinal cells is less restricted than that of the female. They sometimes arise, like the ova, from the cœlomic epithelium which surrounds the nephridial tube, but may also be derived from cœlomic epithelium in other parts of the segment, more especially from that of the anterior septum. In ripe males the body-cavity in the genital segments is filled with a mass of sperm-cells in various stages of development and of spermatozoa.

The spermatozoa (fig. 53) have pear-shaped heads, rounded in front, and with straight posterior ends, to which the flagella are attached. A deeply staining portion at the posterior end of the head (*mp.*) probably represents the "middle-piece."

The Divisions of the Body.

Now that a description has been given both of the external characters and of the internal anatomy of Pœcilochætus, we are in a position to discuss more fully the question of the regions into which the body of the worm can properly be divided. These are (1) the prostomium, or head; (2) an anterior region, from the first segment to the eleventh; (3) an intermediate region, comprising segments 12, 13, 14, 15 and 16; (4) a genital region commencing at segment 17 and continuing backwards until it passes gradually into (5) the terminal region, or tail segments, and (6) the pygidium.

1. The prostomium, or head, has already been described. To it must be reckoned the median tentacle, the palps, the nuchal organ and two pairs of eyes.

2. The anterior region (segments 1 to 11) is characterised by the straight, muscular, cylindrical dorsal vessel; by the straight and muscular œsophagus and pharynx; by the presence, excepting in segments 1 and 2, of nephridia with nephridiostomes, but without genital funnels; by the absence of gonads; by the backward extension of the septa separating the body segments (segments 7 to 11), and consequent great elongation of the lateral blood-vessels which run in these septa; by the great development of the blind, finger-shaped vessels given off from each lateral vessel into the segment behind; by the peculiar modification of the parapodial cirri (segments 7 to 11); by the absence of hairy bristles; and by the pear-shaped lateral sense-organs protruding from the surface of the body.

It will be noted that the hindermost segments of this region (7 to 11) have several characters which distinguish them from those in front. These are the backward extension of the septa, the presence of spiny bristles, which are absent in segments 1 to 6 (excepting for one bristle in each parapodium of segment 2), and the peculiar modification of the parapodial cirri, which character in P. fulgoris and in the larvæ from Norway and Normandy is, according to Claparède, confined exclusively to these segments, as it is also in the pelagic larvæ of Pœcilochætus found at Plymouth.

3. The intermediate region (segments 12 to 16) is chiefly noteworthy from the presence of the large, contractile, lateral pouches of the dorsal vessel, which are found in its first four segments. The nephridia are still without genital funnels, and no gonads are developed. In the adult P. serpens the modified parapodial cirri of segments 7 to 11 extend back to segments 12 and 13; but this is not the case in P. fulgoris nor in any known larvæ of Pœcilochætus. In the latter the cirri of all the segments in this region have the conical form found in the genital region, and this is true also for the cirri of segments 14, 15 and 16 of P. serpens.

In segments 12, 13, 14 and 15 the segmental enlargements of the alimentary canal commence to appear, becoming more pronounced in each succeeding segment, whilst in segment 16 these enlargements are fully developed and the intestine is completely surrounded by a blood-sinus, the dorsal vessel ceasing to exist.

The hairy bristles of the genital segments are absent in this region (12—16), and the lateral organs still protrude from the body surface as in the anterior region.

4. The genital region, from segment 17 to within about thirty segments of the end of the body of a full-grown worm, is characterised by the presence of gonads and well-developed genital funnels; by the large intestinal pouches and intestinal blood-sinus; by the presence of large numbers of well-developed hairy bristles (figs. 14 and 16) and of flattened, membranous, spined bristles (fig. 17), which commence sud-

denly in segment 17; by the comparatively small size and conical shape of the parapodial cirri; by the change in the character of the lateral sense-organs, which no longer protrude beyond the body-wall; and by the presence (commencing on the twenty-first segment) of gill filaments on the posterior faces of the parapodia.

5. The terminal region, or tail segments, may be said to commence about the thirtieth from the end of the body, though the line of demarcation is not very definite. The segments are at first characterised by the presence of stout bristles with brush-like ends (fig. 18), instead of large hairy bristles; by the change in the character of the lateral organs; and in the last sixteen or seventeen segments, by the modifition of the notopodial bristles into large curved hooks lying on the dorsal surface of the body (fig. 6).

6. The pygidium is characterised by the lobes surrounding the anus and by the two pairs of anal cirri.

Parasites.

In the body-cavity of almost every adult specimen of Pœcilochætus examined there occurred one or more examples of a parasitic Trematode. These were always encysted, and were readily recognised by the two large suckers.

Systematic Position.

The Family **Disomidæ**, Mesnil.

Mesnil (1897) formed the family Disomidæ for the reception of the two genera Disoma and Pœcilochætus.

The genus Disoma was founded by Oersted (1844), who described and figured one species, Disoma multisetosum. This species was again found by Möbius (1873), who gives further details of its anatomy and some figures.

Michaelsen (1897) was the first to obtain complete specimens of the worm, and he shows that the tail end of a specimen described and figured by Levinsen (1883) under the name Trochochæta Sarsi almost certainly belongs to Oersted's species, Disoma multisetosum.

Mesnil (1897), from an examination of the type specimens, confirms the specific identity of Michaelsen's specimens with those of Oersted. He gives some further details, with figures, of the structure of the worm, and expresses the opinion that Thaumastoma singulare, described by Webster and Benedict (1884, p. 737), from the American coast, is the same species.

Claparède (1868, p. 337) discussed the relations of Disoma with Polydora and with Chætopterus, being inclined to place it near to the latter.

Levinsen (1883, p. 106) pointed out that the two genera, Disoma and Pœcilochætus, were closely related to each other, and emphasised their resemblance to the Spionidæ.

Adopting Levinsen's view of the relation of the two forms, "sans avoir pourtant une conviction bien ferme," Mesnil (1897) placed both in his family Disomidæ, which he characterises as follows :

Prostomium very simple, with two long tentacular palps analogous to those of the Spionids. Parapodia biramous, at any rate in the anterior region, always with simple bristles. Bristles of various kinds, especially large spiny bristles, hairy bristles, and large lancet-shaped bristles. Stout hooks (soies aciculaire) in the neuropodia of segments 2, 3, and even 4. Never two regions of the body clearly marked off. Ventral and dorsal cirri elongate or fimbriate.

Mesnil considers this family as intermediate between the Spionidæ and Chætopteridæ, being somewhat nearer to the latter. He also points out that in certain characters the two genera show some affinities with the Aphroditidæ and Amphinomidæ, and that this is particularly true of Pœcilochætus on account of the median tentacle and the large spiny bristles. The two long palps and the tendency of the first segment to enclose the prostomium also point in the same direction.

My own observations on Pœcilochætus and a study of the different descriptions of Disoma lead me to agree with

Levinsen and Mesnil in regarding the two genera as nearly related, and Mesnil's foundation of the family Disomidæ appears justified.

I am inclined, however, to consider this family as more closely allied to the Spionidæ than to any other Polychæte family, as was maintained by Claparède and Levinsen. In addition to the presence of the large palps this view is supported by the line of vesicles surrounding the eggs, a striking character which appears to be found only amongst the Spionidæ. The median tentacle of Pœcilochætus in all probability represents the fusion of two lateral tentacles, and may be homologous to the two lateral processes at the front end of the head in such forms as Nerine (Scolelepis) vulgaris. The great development of the nuchal organ might be held to mark Pœcilochætus off from the Spionidæ and to bring it nearer to the Amphinomidæ, where, according to Racovitza, the caruncle is a very large nuchal organ. This argument, however, can have little weight, as the nuchal organ varies greatly in its development in closely allied forms within other families (e. g. Syllidæ, Phyllodocidæ), and the organ is present in the form of ciliated grooves at the posterior end of the head of Polydora, as I have been able to demonstrate on sections.

The Species of Pœcilochætus.

The chief points in which Claparède's description of P. fulgoris (Claparède in Ehlers, 1874) differs from the description given in the present paper of the Pœcilochætus found at Plymouth are as follows:

1. The large palps of the Plymouth species are not described in P. fulgoris. This, however, is not surprising, and is certainly due to the imperfection of the specimens, it being exceedingly difficult to prevent the worm from throwing these palps off.

2. The nuchal organ, though indicated by Claparède both in his figure and text, appears much less developed in

P. fulgoris. Here, again, imperfect preservation may account for the difference.

3. The tubercles (openings of epithelial glands), which cover both the dorsal and ventral surfaces of Pœcilochætus fulgoris, are scarcely represented on the dorsal surface of Plymouth specimens, though moderately common on the ventral.

4. Only one pair (dorsal or posterior) of eyes is described by Claparède, the ventral (anterior) pair not having been observed.

5. Claparède describes the buccal segment as having a single cirrus on each side. The rudimentary dorsal cirrus was either not present or was overlooked.

6. The long dorsal cirrus of segment 5 is not described or figured by Claparède. The cirri of the seventh to the eleventh segments differ in shape from the others, being flask shaped with long, stiff necks in Claparède's specimen, whilst in the Plymouth specimens this character is constant for segments from the seventh to the thirteenth. As, however, all larvæ seen at Plymouth agree with P. fulgoris in this respect, the difference may be due to the fact that Claparède's specimens were not adult.

7. The second, the third, and the fourth segments of the "Lightning" specimens have short, stout spines in the neuropodium; in the Plymouth specimens such spines are confined to the second and third segments.

The differences expressed under the headings (3), (6) and (7) appear to render it necessary to regard the Plymouth specimens, at least provisionally, as belonging to a new species for which I propose the name Pœcilochætus serpens.

Definitions.

Family **Disomidæ**, Mesnil.

Polychæta having a simple prostomium without tentacles or with one median tentacle, and with four simple eyes. A pair of large palps capable of great elongation. Mouth ventral with a short proboscis. Parapodia of the first segment greatly developed and directed forwards, provided with long chætæ which meet in front of the head. Parapodia with well-developed dorsal and ventral cirri. Chætæ simple, and either smooth or bearing hairs or spines. Neuropodia of the second and third (and even fourth) segments, with three or four short, stout bristles or hooks. Notopodial chætæ of the terminal segments modified into stout, strong hooks or spikes situated on the dorsal surface of the body. Distinct posterior (genital) region of the body commencing at the seventeenth segment. Segments from about the twentieth backwards having three or four filamentous gills.

Genus **Disoma**, Oersted.

Polychæta having the general characters of the family Disomidæ. Prostomium without tentacles. Both neuropodial and notopodial cirri well developed in the first segment. Notopodial cirri from the third to the sixteenth segments having the form of elongated, crenated plates, running transversely on the dorsal surface. Notopodial and neuropodial cirri from segment 17 backwards conical. Gills on either side of the mid-ventral line commencing at the twentieth segment. Notopodial bristles of the most posterior segments stout spines arranged in star-like clusters on the dorsal surface of the body.

One species only known—

Disoma multisetosum, Oersted.

Synonyms: Trochochæta Sarsi, Levensen.

Thaumastoma singulare, Webster and Benedict.

Genus **Pœcilochætus**, Claparède.

Polychæta having the general characters of the family Disomidæ. Prostomium with one anterior median tentacle. Nuchal organ in the form of three lobes or tentacle-like processes arising from the posterior end of the prostomium. Neuropodial cirrus of the first segment well-developed, notopodial cirrus rudimentary. Neuropodial and notopodial cirri from the seventh to the eleventh (or to the thirteenth) segments flask-shaped, with long, stiff necks. Gills on the parapodia from segment 21 backwards. Chætæ from the seventeenth segment backwards mostly with long hairs; those of the notopodium in the most posterior segments stout hooks, forming transverse rows on the dorsal surface of the body. Anus dorsal, with two long and two short cirri. Dorsal blood-vessel with large, lateral pouches in segments 12, 13, 14, and 15.

Two species (provisionally)—

Pœcilochætus fulgoris, Claparède. Anterior dorsal surface of the body richly provided with tubercles. Parapodial cirri of segments 7 to 11 different from those on the rest of the body, being flask-shaped, with long, stiff necks. Second, third and fourth segments with short, stout spines in the neuropodium. Nuchal organ moderately developed (?).

Pœcilochætus serpens, n. sp. Anterior dorsal surface smooth, with few tubercles. Parapodial cirri of segments 7 to 13 (in the adult) different from those on the rest of the body, being flask-shaped, with long, stiff necks. Second and third segments only with short, stout spines in the neuropodium. Nuchal organ greatly developed, forming three long tentacle-like processes.

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EXPLANATION OF PLATES 7—12,

Illustrating Dr. E. J. Allen's paper on "The Anatomy of Pœcilochætus, Claparède."

List of Reference Letters.

b. lat. v. Branch of lateral blood-vessel passing into the next following segment. *br.* Brain. *c.* Cilia. *cal.* Callosities on cuticle. *com.* Œsophageal commissure. *cu.* Cuticle. *cu.g.* Thickened cuticular layer of nuchal groove. *dors. v.* Dorsal blood-vessel. *ep.* Epithelium. *ep. r.* Epithelial rim of lateral organ. *f.p.* Finger-shaped processes into which the backwardly directed branch of the lateral vessel breaks up. *g.* Masses of protoplasm in which granules are formed in the lip of the nephridiostome. *gang. plp.* Palp-ganglion. *g. l. o.* Ganglion-cells of lateral sense-organ. *g.f.* Giant-fibres. *gl.* Gland-cell. *gl. 1, gl. 2, gl. 3.* Three types of goblet-shaped gland-cells of the œsophagus. *gst.* Gonostome. *i. bl. s.* Intestinal blood-sinus. *intest.* Intestine. *int. v.* Blood-vessel from walls of alimentary canal to ventral vessel. *lat. v.* Lateral blood-vessel. *l. o.* Lateral sense-organ. *lp. gst. d.* Dorsal lip of gonostome. *lp. gst. v.* Ventral lip of gonostome. *lp. nst.* Lip of nephridiostome. *l. r.* Long rods of lateral sense-organ, nuchal organ, and epithelium of œsophagus. *m. b.* Mid-brain. *m. f.* Muscle-fibres. *m. p.* Middle-piece of spermatozoon. *m. tent.* Median tentacle. *mth.* Mouth. *musc.* Muscle. *n.* Nucleus; *n.'* see page 97. *nh.* Supposed nuclei of hair-bearing cells. *n. p. 1, n. p. 2.* First and second roots of nerve of palp-ganglion. *nph.* Nephridial tube. *nr. c.* Neuropodial cirrus. *nst.* Nephridiostome. *nt. c.* Notopodial cirrus. *nuch.* Nuchal organ. *nuc. gan.* Nuchal ganglion. *œs.* Œsophagus. *p.* Process from callosity, see page 97. *p. bv.* Palp blood-vessel. *p. dv.* Lateral pouch of dorsal blood-vessel. *ph.* Pharynx. *plp.* Palp. *plp. div.* Diverticle of palp. *plp. v.* Palp-valve. *sep.* Septum dividing body segments. *sh.* Sensory hairs of lateral sense-organs. *sr.* Short rods of lateral organs, nuchal organ, and epithelium of œsophagus. *sr. 2.* Secondary layer of short rods in lateral organs. *v.* Point where pharynx joins intestine. *vent. v.* Ventral blood-vessel. *vl. seg. 14.* Valve in dorsal blood-vessel between segments 14 and 15 (open). *vl. seg. 15.* Valve in dorsal blood-vessel between segments 15 and 16 (closed). *yk. n.* Yolk nucleus.

All sections and the majority of the other figures were drawn with the camera lucida.

PLATE 7.

FIG. 1.—Anterior segments of Pœcilochætus serpens. The vascular system is somewhat diagrammatic, having been reconstructed from sections. × *ca* 25.

FIG. 2.—Parapodium 3, left side. × 66.

FIG. 3.—Parapodium 5, left side. × 66.

FIG. 4.—Parapodium 7, left side. × 66.

FIG. 5.—Parapodium 13, left side. × 66.

PLATE 8.

FIG. 6.—Terminal segments, dorsal view. × *ca* 50.

FIG. 7.—Head end, dorsal view. × *ca* 50.

FIG. 8.—Head end, ventral view. × *ca* 50.

PLATE 9.

FIG. 9.—Parapodium 14, left side. × 66.

FIG. 10.—Parapodium 18, left side. × 66.

Fig. 11.—Parapodium 30, left side. × 66.

Fig. 12.—Pœcilochætus serpens in burrow constructed in sand between two glass plates. Natural size.

Fig. 13.—Smooth bristle from parapodium 7. × 380.

Fig. 14.—Large, stiff, hairy bristle from parapodium 30. × 380.

Fig. 15.—Spined bristle from parapodium 10. × 380.

Fig. 16.—Small, flexible, hairy bristle from parapodium 30. × 380.

Fig. 17.—Membranous spined bristle from parapodium 20. × 380.

Fig. 18.—Bristle with hairy terminal brush from twentieth parapodium from end. × 380.

Fig. 19.—Stout hooks of the notopodium from the dorsal surface of the seventh segment from the end. × 100.

Fig. 20.—Transverse section of epithelium from the anterior dorsal surface. × 1180.

Fig. 21.—Transverse section of epithelium from the ventral surface, just behind the mouth. × 1180.

PLATE 10.

Fig. 22.—Unicellular epithelial gland from anterior portion of body. × 1180.

Fig. 23.—Section of gland-cells and tubercle from posterior end of body. × 1180.

Fig. 24.—Section of parapodial cirrus (about segment 20). × 220.

Fig. 25.—Cirrus from near tail of living worm.

Figs. 26—29.—Gland-cells from parapodial cirri. × 1180.

Fig. 30.—Transverse section through the base of the palps and palp-ganglia. × 135.

Fig. 31.—Transverse section of a gill filament. × 400.

Fig. 32.—Transverse section of the ventral nerve-cord. × 220.

Fig. 33.—Sagittal section through a ventral eye. × 640.

Fig. 34.—Horizontal section through a lateral sense-organ of the genital region. × 600.

Fig. 35.—Transverse section through a lateral sense-organ of the genital region passing through the anterior row of muscle-bands. × 690.

Fig. 36.—Transverse section through a lateral sense-organ of the genital region passing through the hair-bearing cells. × 690.

Fig. 37.—Transverse section through a lateral sense-organ of the genital region passing through the posterior row of muscle-bands. × 690.

Fig. 38.—Section through the extremity of a lateral sense-organ of the genital region in the longitudinal vertical (sagittal) plane of the body. × 375.

Fig. 39.—Section through a lateral sense-organ of the anterior region. × 690.

PLATE 11.

Fig. 40.—Section through a ciliated groove of the nuchal organ. × 640.

Fig. 41.—Enlarged view of ciliated cells of the nuchal organ. × 1180.

Fig. 42.—Sagittal section through the mouth and median tentacle. × 66.

Fig. 43.—Horizontal section through segments 8 to 14. × 42.

Fig. 44.—Transverse section through ciliated epithelium of the œsophagus. × 690.

Fig. 45.—Transverse section through epithelium of the intestine, when the latter is filled with food and digestion is actively going on. × 690.

Fig. 46.—Transverse section through epithelium of the intestine, when digestion is not active. × 690.

Fig. 47.—Sagittal section through the first sixteen segments. × 42.

Fig. 48.—Transverse section through anterior region, showing junction of the lateral vessels with the ventral vessel. × 42.

Fig. 49.—Transverse section through anterior region, showing cluster of finger-shaped processes uniting to the branch of the lateral blood-vessel. × 42.

Fig. 50.—Sagittal section through the dorsal blood-vessel in segments 14 and 15, showing the valves. × 132.

PLATE 12.

Fig. 51.—Sagittal section through two segments of the anterior region, showing the branch of the lateral vessel going into the segment behind and breaking up into finger-shaped processes. × 88.

Fig. 52.—Sagittal section of a nephridium and genital funnel of a male genital segment. × 212.

Fig. 53.—Spermatozoa. × 1770.

Fig. 54.—Sagittal section through the nephridiostome of an anterior segment. × 424.

Fig. 55.—Transverse section through the lip of the nephridiostome of an anterior segment. × 424.

Fig. 56.—Ciliated epithelium of the dorsal lip of a genital funnel × 1180.

FIG. 57.—Enlarged portion of the lip of a nephridiostome. The dark black dots stain red, the grey shading blue in methyl-blue-eosin preparations. × 1180.

FIG. 58.—Horizontal section through three genital segments, showing the relation of the ovary to the nephridium. × 66.

FIG. 59.—Transverse section through a genital segment. × 66.

FIG. 60.—Section through a nephridial tube, showing the development of the ova. × 380.

FIGS. 61—63.—Sections of ova in different stages of maturation. × 380.

FIG. 64.—Optical section of living mature ovum. × 212.

FIG. 65.—Optical section of living mature ovum after remaining some hours in sea-water. × 212.

FIG. 66.—Surface view of living mature ovum. × 212.